To the Graduate Council:

I am submitting herewith a dissertation written by Michael Allen Gibson entitled "Paleogeography, Depositional Environments, Paleoecology, and Biotic Interactions in the Rockhouse Limestone and Birdsong Shale Members of the Ross Formation (Lower Devonian), Western Tennessee." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Geology.

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and recommend its acceptance:

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and Dean of The Graduate School

PALEOGEOGRAPHY, DEPOSITIONAL ENVIRONMENTS, PALEOECOLOGY, AND BIOTIC INTERACTIONS OF THE ROCKHOUSE LIMESTONE AND BIRDSONG SHALE MEMBERS OF THE ROSS FORMATION (LOWER DEVONIAN), WESTERN TENNESSEE

A Dissertation

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Michael Allen Gibson

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To my wife, Edie.

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ABSTRACT

The Rockhouse Limestone and Birdsong Shale members of the Ross Formation (Lower Devonian, Lockhov) of western Tennessee are a mixed limestone - shale sequence, approximately 30 m thick, that accumulated on a shallow, predominantly carbonate, platform, termed the Ross Shelf. The Ross Shelf was situated 25° to 30° south latitude during the Devonian and was structurally bounded by the Illinois Basin to the north, Reelfoot Rift and Ozark Uplift to the west, Nashville Dome to the east, and the continental margin to the south. Terrigenous mud was supplied by storm systems crossing the shelf from offshore.

The Rockhouse Limestone Member consists of well-washed bioclastic limestone and shale with locally developed bryozoan-dominated mudmounds. Four vertical phases of development are recognized in the mudmounds: (1) introduction of terrigenous mud containing allochthonous skeletal debris, (2) colonization and stabilization of patches of the muddy substrate, (3) a Buskopora-dominated phase characterized by an irregular surface with open cavities, and (4) interruption of the bryozoan dominated phase coinciding with a marked increase in terrigenous influx.

The overlying Birdsong Shale Member was dominated by

muddy bottoms which were frequently scoured by storms to produce graded limestone - shale couplets. Although the seafloor consisted of soft substrata much of the time, the substrate sometimes underwent compaction and dewatering to form firmgrounds of fine-grained bioclastic debris. Early marine cementation is noticably absent in these rocks.

Biotic assemblages of the Birdsong Shale developed along different pathways depending upon the consistency of the substrate. When the substrate was soft mud, the fauna was characterized by adaptations that retarded sinking (e.g., Favosites foerstei) or by adaptations for avoiding the sediment altogether (e.g., epibiosis). Some of the fauna (e.g., Favosites conicus) were adapted for living between major influxes of mud.

Although epizoans are abundant in the Birdsong, they do not show abundant obvious interactions with each other or with their hosts. Most associations with hosts were epitaphic in response to substrate conditions. Facultative associations occured between Macropleura macropleura and Spirorbis laxus in which S. laxus preferentially lived in the troughs between the plications of the host brachiopod and avoided the fold and sulcus region, probably due to the poorer quality of the excurrent water flow of the host. Colonial epibionts show little preference for location or orientation; however, preferred directions of growth toward

the commissure are exhibited in some species. Two recurrent associations are present. The first is a symbiotic mutualism between Aulopora schohariae and a fistuliporid bryozoan to form either a massive intergrowth or a ramose growth form. Both members benefited from the structural support the mutualism offers. The second association is an epitaphic relationship between A. schohariae and brachiopod host for avoiding the substrate or a commensal relationship in which the coral benefited from feeding currents generated by the host.

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CHAPTER 1

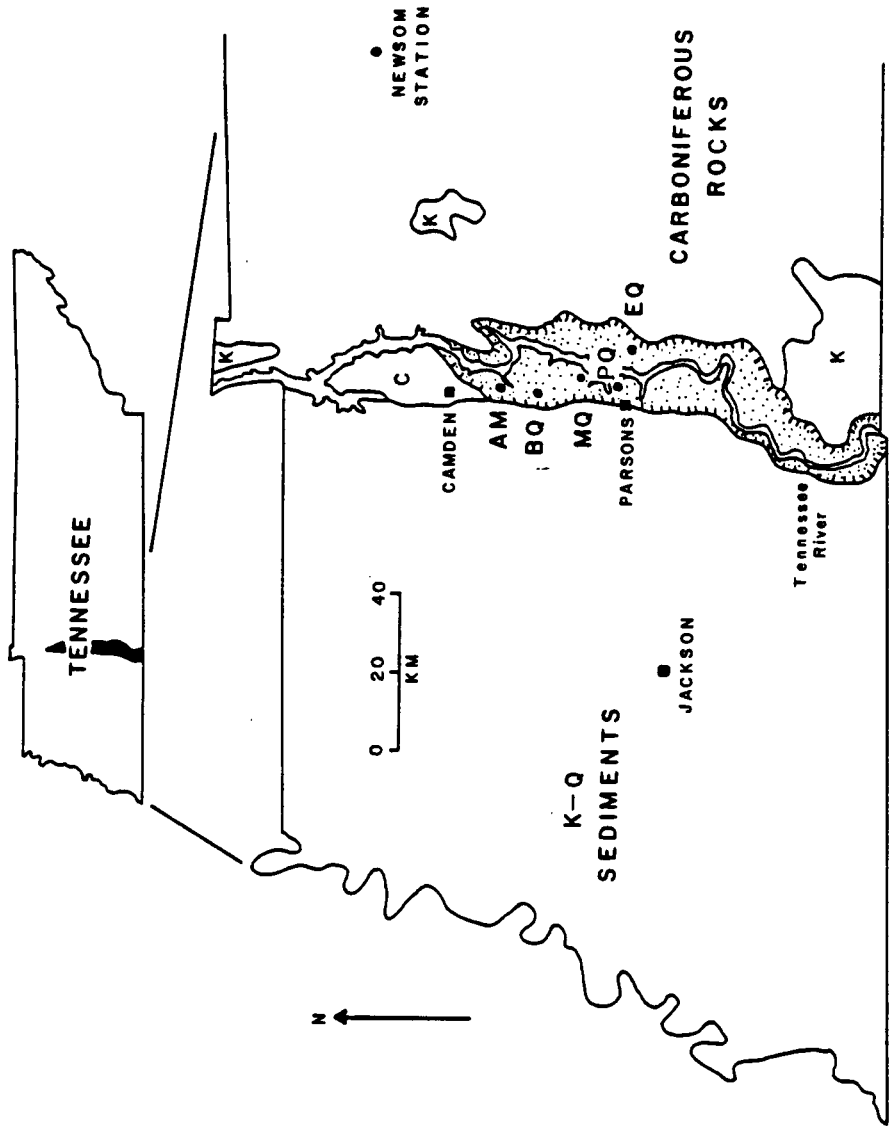
INTRODUCTION

General Introduction

The Ross Formation (Lower Devonian, Lochkov) is a continuous succession of Upper Silurian to Lower Devonian rocks that is exposed in a north-south trending belt along the Tennessee River in west-central Tennessee (Fig. 1). The Ross consists predominantly of interbedded skeletal carbonate and fossiliferous marine non-deltaic gray shale. The Birdsong Shale Member and, to a lesser degree, the underlying Rockhouse Limestone Member of the Ross have long been known as a "happy hunting ground" among paleontologists since the late 1800's (Dunbar, 1919, p. 55). Many leading North American paleontologists, including August Foerste, James Safford, Charles Schuchert, Frank Springer, Carl Dunbar, Harrell Strimple, and Thomas Amsden, have worked in the Silurian and Devonian outcrop belt of western Tennessee over the past 150 years.

The Ross Formation has only recently, however, become the focus of intense paleontological, paleoecological, and paleoenvironmental study. Most of the early investigations of the Ross were primarily concerned with defining

FIG. 1. Location of study area in a north-south trending belt of Silurian to Devonian age rocks along the Tennessee River. Exposures used in this study include Parsons Quarry (PQ), Benton Quarry (BQ), McClanahan's Quarry (MQ), and Elkins Quarry (EQ). K = Cretaceous, Q = Quaternary, and C = Carboniferous.


TENNESSEE
NEWSOM STATION
K
K
C
CAMDEN
AM
BQ
MQ
PQ
EQ
PARSONS
CARBONIFEROUS ROCKS
K
Tennessee River
0
20
40
KM
JACKSON
K–Q SEDIMENTS
N

stratigraphic units and identifying fossil occurrences within these units. The majority of these earlier works predate the development and understanding of plate tectonics or paleoecologic, paleogeographic, and facies concepts. As a result, these concepts as well as those learned from studies of modern marine sedimentation and the use of thin-sections to study rock composition, cementation, texture, and fabric have not been widely applied to the Ross Formation.

Exposures of the Ross in western Tennessee are important for several reasons. First, continuous exposures of Upper Silurian to Lower Devonian rocks are rare in North America, especially in the southeastern United States. This outcrop area offers an opportunity to study environmental and faunal characteristics across this system boundary. Second, this area occupies a geographically intermediate position between two regions of North America in which rocks of Early Devonian age have been more intensely investigated, namely in New York State and Oklahoma. Third, paleogeographic, paleoenvironmental, and petrographic study of the area is useful in understanding the processes involved in the formation of mixed carbonate-siliciclastic sequences. Finally, the present study represents one of the first investigations to address

the biological consequences of these settings.

Portions of the Ross Formation, in particular the Birdsong Shale Member, are abundantly fossiliferous and are also rich in epibionts. The paleoecology of non-deltaic gray shale environments has not been well studied especially with respect to organism-substrate relationships. Epibionts, which seem to be very common in gray shale settings during the Middle Paleozoic (Broadhead and Gibson, 1986), are currently the focus of intense study by paleoecologists. Epibionts represent one of the best tools with which to study biotic interactions, such as parasitism, commensalism, as well as non-interaction associations such epitaphism in the fossil record. Most previous studies concerning epibionts and their interactions have been conducted in rocks of Silurian to Devonian age, hence, the Birdsong Shale is idealy suited for more extensive epibiont analysis.

Previous Studies on the Ross Formation

19th Century Stratigraphic Study

In his fifth geological report of the geology of Tennessee in 1839, Gerard Troost became the first person to describe rocks belonging to what is now considered to be the Devonian system in west-central Tennessee and to

publish a geologic map of the state of Tennessee (fide Dunbar, 1917a, 1919). Dunbar (1917a) reported that Troost applied the Wernerian classification scheme in his report and recognized four formations in Tennessee: Primordial, Graywacke (=Transitional), Mountain Limestone, and the Coal Measures. Within this scheme, Troost considered the strata, later to be identified as Silurian and Devonian, to be equivalent to strata exposed near Nashville, which he considered to be part of the "Mountain Limestone Formation" (= Lower Carboniferous in Britain) based on lithology and not fossil content.

In his sixth geologic report, Troost (1841) placed the entire Mountain Limestone Group, including all exposures along the Tennessee River, in the Upper Silurian, based on Murchison's newly established "Silurian System" (fide Dunbar, 1917a). By the time of his seventh report in 1843, Troost recognized four subunits within the "Mountain Limestone Group" of the Silurian System, in ascending order: a lower limestone unit, an upper limestone unit (which included what are now the Decatur and Ross formations), an aluminous slate (Chattanooga Shale), and a silicious group (Fort Payne Chert).

James Safford contributed greatly to improving the understanding of the stratigraphy of western Tennessee. He named the Harpeth Group (also called the Tennessee River

Group) to include all limestone strata below the Black Shale (Chattanooga Shale) along the Tennessee River (Safford, 1851). It was at this point that the age assignment of the western Tennessee rocks became part of a great Silurian-Devonian controversy. The Devonian System was first recognized in Europe in 1835, but the term was not applied in North America until 1842 (Fischer, 1981). The French stratigrapher de Verneuil visited North America and assigned rocks in New York State, identified as belonging to the Helderberg Group, to the Silurian System (de Verneuil, 1848). Hall (1859) adopted de Verneuil's assignment, as did nearly all other North American workers (Dunbar, 1917a, 1919). Safford (1856, fide Dunbar, 1919) suggested that the strata exposed in western Tennessee were Helderberg in age. He also suggested, however, that the Helderberg age rocks should be placed within the Devonian System, in spite of Hall's assignment (Dunbar, 1917a, 1919). Safford became the first person to correctly identify the Ross lithologies as being Devonian in age (Dunbar, 1917a, 1919).

Safford (1861) reviewed Ferdinand Roemer's (1861) Die Silurische Fauna Des Westlichen Tennessee in which Roemer compared the western Tennessee fauna with that of Europe and suggested a Silurian age for western Tennessee strata. Safford (1861) suggested that, in addition to Roemer's

Silurian fauna, he had identified Helderberg fossils stratigraphically above the Silurian fauna. Safford suggested that the Helderberg sea had transgressed over a Silurian unconformity. The positive identification of Helderberg fossils and the separation of the Helderberg from the Silurian System had not been done prior to 1859, when Hall began the "Palaeontology of New York State" series, in which the first systematic descriptions and figures of Devonian fossils in North America were published.

In the first edition of Geology of Tennessee Safford (1869) listed exposures of Helderberg rocks along the Tennessee River. He also listed 42 fossil taxa which occurred in the Helderberg, figured nine of these, and named one new taxon.

The controversy concerning the age of the Helderberg strata in western Tennessee continued when Worthen (1870, fide Dunbar, 1917a, 1919) suggested that the lower Helderberg series was Niagaran in age. This conclusion was based upon the occurrence of a single unspecified formation in Illinois which contained Niagaran fossils. Worthen additionally believed that this formation was equivalent to the rocks that Safford had identified as Helderberg at the same stratigraphic position in western Tennessee and which Worthen argued contained a mixture of Helderberg and

Niagaran fossils. Worthen concluded that the lower Helderberg was not distinct and therefore represented a useless designation that should be dropped from usage. Dunbar (1917a, 1919) noted that the debate heated until 1873, when Hall presented a chart in which he correlated the known distribution of all Helderberg and Niagaran strata in North America. Hall's correlation showed that the Niagaran series thinned eastward into New York, thickened westward into Iowa, and could be traced southward into Tennessee; however, it always contained characteristic fossils. On the other hand, the Helderberg was shown to thin westward, but it too always contained characteristic fossils, and no mixtures were present. The controversy over the age of the Helderberg strata was resolved (Dunbar, 1919) when the New York State Geological Survey officially adopted a Devonian age for the Helderberg of New York State (Clarke and Schuchert, 1899).

Safford and Killebrew (1876) proposed the name Linden for rocks exposed in western Tennessee that were equivalent to the New Scotland, Coeymans, and Keyser formations of New York State and Maryland. Safford and Schuchert (1899) discussed the Camden Chert, which Safford had assumed to be part of the Mississippian cherts, until finding fossils in it. Safford and Schuchert (1899) determined that the 32 species of fossils from the Camden were equivalent to the

fauna contained in the Clear Creek Chert of Illinois. In that paper, Schuchert proposed an Oriskany age (Early Devonian) for the Camden.

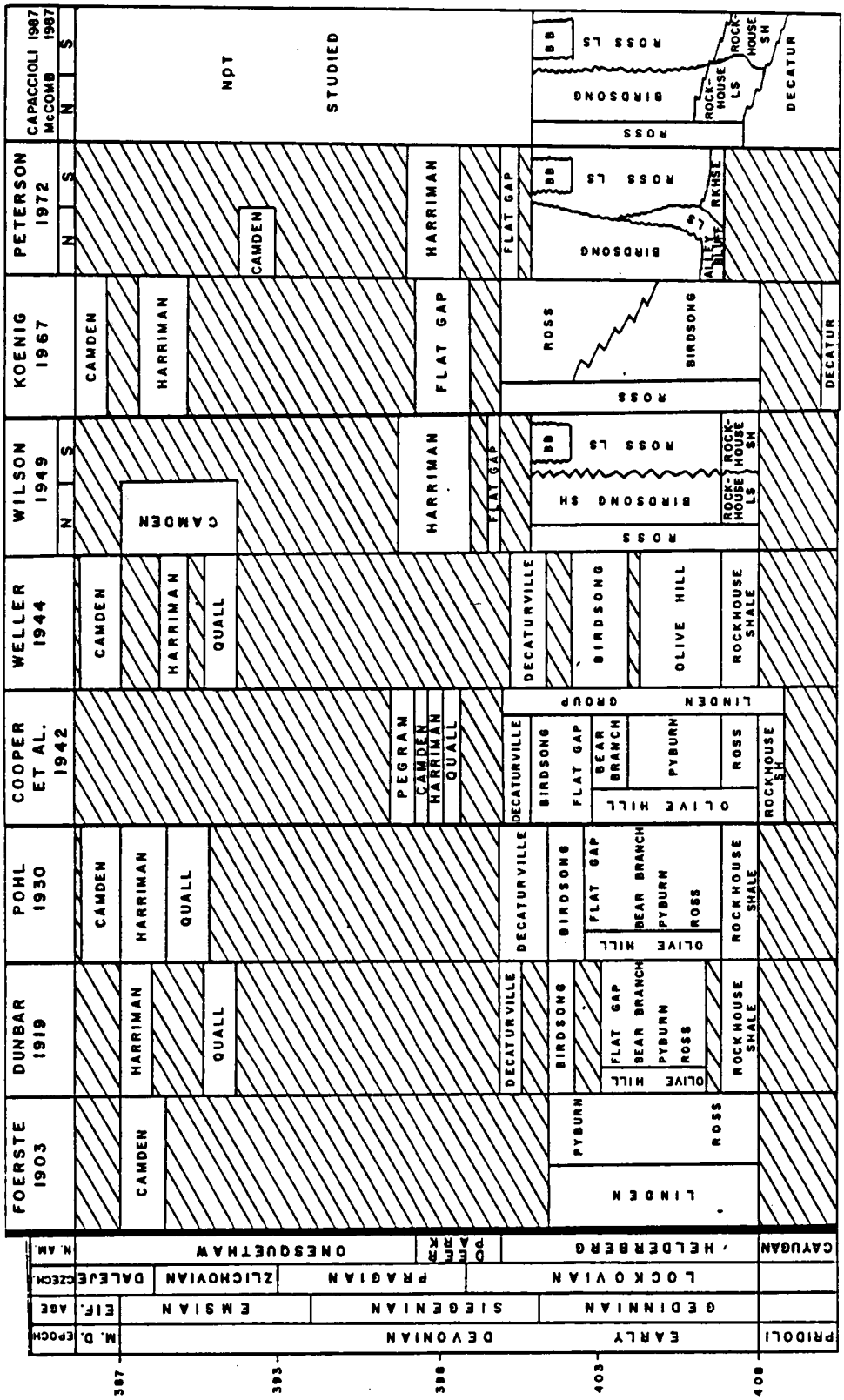
Since that time the Camden has been assigned to various stages within the Devonian based mostly on stratigraphic or lithologic criteria. The Camden has not been extensively studied, so that precise age assignment of the Camden and associated chert-rich facies, such as the Harriman and Decaturville cherts remains in question.

20th Century Stratigraphic Study -

In a detailed discussion of the Silurian and Devonian strata in western Tennessee, Foerste (1903) described and presented correlations of numerous measured sections that included Linden strata (Fig. 2). Based upon both lithologic and faunal criteria, he subdivided the Linden into two formations, the Ross and Pyburn limestones. The lowermost Ross Limestone was distinguished by the presence of abundant Camarocrinus (= Scyphocrinites) bulbs.

Detailed investigations of the geology of various counties in western Tennessee began in the early 1900's. Wade (1914) described the geology of Perry County and published the first detailed map of any portion of the Western Valley of Tennessee (Dunbar, 1917a, 1919). His discussion included identifying the easternmost extent of

FIG. 2. Historical development of Early Devonian stratigraphic nomenclature in western Tennessee since 1903. Cross hatched areas imply missing time interval.


FOERSTE 1903
DUNBAR 1919
POHL 1930
COOPER ET AL. 1942
WELLER 1944
WILSON 1949
KOENIG 1967
PETERSON 1972
CAPACCIOLI 1987
McCOMB 1987
NOT STUDIED
CAMDEN
HARRIMAN
QUALL
PEGRAM
DECATURVILLE
BIRDSONG
FLAT GAP
BEAR BRANCH
PYBURN
ROSS
OLIVE HILL
ROCKHOUSE SHALE
ROCKHOUSE SH
ROCK-HOUSE LS
LINDEN GROUP
OLIVE HILL
BIRDSONG SH
BIRDSONG SS
ROSS LS
ROSS
ALLEY BLUFF
RKHSE
DECATUR
PRIDOLI
EARLY
GEDINNIAN
SIEGENIAN
EMSIAN
LOCKOVIAN
PRAGIAN
ZLICHOVIAN
DALEJE
HELDERBERG
ONESQUETHAW
CAYUGAN
EPOCH
M. D.
AGE
ELF.
CZECH.
N. AM.
387
393
398
403
408

the Linden, which occurs in Perry county (Wade, 1914, Born, 1944).

As an outgrowth of his field studies on the Camden and Linden faunas, Schuchert urged C.O. Dunbar, in 1916, to study the stratigraphy and paleontology of the western valley of Tennessee as his dissertation topic (Dunbar, 1918). Dunbar spent two months in the field collecting fossils from stream exposures (now mostly flooded due to damming of portions of the Tennesee River) and glades (now mostly heavily vegetated) and measuring sections exposed along the Tennessee River. He also introduced a relatively new invention to fieldwork by using a motorcycle as his primary means of transportation.

Dunbar (1917b) briefly discussed his preliminary findings and suggested that the Linden was a New Scotland equivalent and that the Camden was of very late Oriskany age. Dunbar was subsequently funded by the Tennessee State Geological Survey for an additional field season to continue his research (Dunbar, 1918). An abstracted portion of his combined findings (Dunbar, 1918) was followed by a more complete treatment, which included the palegeographic reconstructions of Schuchert (Dunbar, 1919). It is this 1919 bulletin that has served as the major basis for all subsequent investigations, and Dunbar's faunal lists are still cited.

Dunbar conducted his work prior to the widespread use of facies concepts in North America. Although facies concepts were widely used in Europe (Johnson, 1987), E.O. Ulrich was the dominant influence in the North American geologic community and did not subscribe to them, in spite of Grabau's repeated atttempts to champion facies (Johnson, 1987). Consequently, Dunbar (1918, 1919) subdivided the Linden into seven units, in ascending order, the Rockhouse Shale, Olive Hill Formation (which was further subdivided into the Ross Limestone, Pyburn, Bear Branch, and Flat Gap members). Dunbar suggested unconformities between the Rockhouse Shale, Olive Hill and Birdsong and also described 43 new species of fossil invertebrates (Dunbar, 1917a, c, 1920). A more complete discussion of the taxonomic works for this area is presented in Systematic Paleontology (Appendix D).

Regional Correlations

Pohl (1930) accepted Dunbar's "layer-cake assessment" of the stratigraphy of western Tennessee. His correlation chart, however, suggested conformable relationships between all of Dunbar's subunits of the Linden including the overlying Decaturville chert, rather than each unit being separated by a hiatus.

Jewell (1931) mapped the geology of Hardin County and adopted Dunbar's interpretation of Devonian stratigraphy, noting that Devonian age rocks were not well represented in Hardin County. Jewell recognized only 8 feet (2.7 m) of Birdsong Shale at a single locality near Saltillo, in the northern part of Hardin County.

One of the few faunal studies conducted in the Birdsong was done by Wilson (1935). He described ostracode species from the Birdsong, concurring with Dunbar's conclusion that the Birdsong was a New Scotland equivalent.

Cooper et al. (1942), presented the first comprehensive correlation chart for the Devonian and made three major changes in the interpretation of the west Tennessee stratigraphic section. First, the Rockhouse Shale was re-assigned to the Silurian, but was still considered conformable with the overlying Olive Hill Formation. He gave no reason for the change; however, in a personal communication to Mellon (fide, Lundin and Petersen, 1974) Cooper said he based this placement on the occurrence of Dictyonella and a species of brachiopod that resembled Uncinulus stricklandi. Second, the Flat Gap Limestone was removed from the Olive Hill Formation and included as part of the lower Birdsong Shale (although the Flat Gap is now known to be entirely younger than the Birdsong). These two units combined were correlated with

the Bailey Limestone in southeastern Missouri. Third, the Rockhouse Shale, Olive Hill (Ross, Pyburn, and Bear Branch limestones), Flat Gap Limestone, Birdsong Shale, and Decaturville Chert were all assigned to the Linden Group, which thus spanned the Silurian-Devonian boundary. Cooper et al. (1942) suggested an earlier age (Late Deerparkian-Early Onesquethaw) than previously suggested for the Camden by Foerste (1903), Dunbar (1919), or Pohl (1930).

Born (1944) summarized the Devonian of west-central Tennessee as part of a symposium on Devonian stratigraphy of Illinois and adjacent states. His summary drew heavily from Dunbar's (1918, 1919) interpretations; however, the resulting correlation chart only recognized Birdsong Shale and Decaturville Chert equivalents for Helderberg age rocks (Cooper, 1944a). Born (1944) concluded that the equivalents of the Rockhouse Shale and lower Olive Hill Formation were missing in Illinois. Weller (1944) suggested that the Bailey Limestone of Illinois was probably a Rockhouse Shale equivalent and that the Bailey probably also contained Birdsong and Olive Hill equivalents, although they could not be positively identified at that time. Weller (1944) presented a correlation chart in which the Rockhouse was assigned to the Devonian (Helderberg) and there was no gap between the

Rockhouse and the overlying Olive Hill. Gaps were suggested between the Olive Hill, Birdsong, and Decaturville. No clear age or correlation with surrounding states could be agreed upon as of 1944.

Wilson (1949) was the first person to recognize facies changes in these strata. It should be noted, however, that Dunbar (1917a) had recognized the possibility of lateral equivalents, but argued against lateral equivalency based upon faunal evidence (Dunbar, 1918, 1919). For example, Dunbar (1919) argued that Eospirifer (=Macropleura) macropleura, a New Scotland guide-fossil, was abundant in the Birdsong, but absent in the Ross Limestone. Wilson (1949), however, argued that M. macropleura was not confined to the Birdsong, but also occured in the adjacent Ross Limestone Member making these two units time equivalent lithofacies.

Wilson (1949) extensively modified Dunbar's nomenclature scheme. He dropped the name Olive Hill and erected the name Ross Formation to include the Ross Limestone and its lateral equivalents the Birdsong Shale and Bear Branch Limestone, all of which overly the Rockhouse Limestone and its lateral equivalent the Rockhouse Shale. All beds overlying the Decatur Limestone but underlying the Flat Gap Limestone were considered Helderberg in age. Wilson also dropped the name Linden

without any replacement. He listed several critria by which the Decatur-Ross contact could be identified including: a marked increase in grainsize and silt content in the Rockhouse, the presence of Atrypa and Gypidula in the Rockhouse, and a color discontinuity between the two units. Wilson's classification has since become the most widely accepted scheme although some modifications concerning age have been made.

Modern Paleoenvironmental, Biostratigraphic, and Paleoecologic Studies

Petersen (1972), studied the stratigraphy and ostracodes of the Birdsong and attempted to clarify some of the stratigraphic problems in western Tennessee by: (1) removing the term Ross Formation and elevating all units within that interval to formation status, (2) proposing the name Alley Bluff Formation for what Wilson (1949) called the Rockhouse Limestone Member, and (3) replacing the name Rockhouse Shale with Rockhouse Formation. In addition, Petersen's correlations suggested that a more complex facies relationship existed among the Birdsong, Alley Bluff, and Ross Limestone than has been recognized prior to or since his work. Lundin and Petersen (1974) published descriptions of the ostracode fauna from the Rockhouse Formation (= Rockhouse Shale of Dunbar and Wilson), but

failed to discuss their stratigraphic revisions, namely, the ones outlined by Petersen (1972). This scheme has not been used by any subsequent workers.

Walker and Pruitt (1975) described the stratigraphic succession at the Vulcan Material's Parsons Quarry (PQ of this study), again basing their description heavily upon Dunbar's and Wilson's earlier conclusions. They recognized the Decatur Limestone, Rockhouse Limestone, Birdsong Shale, and Camden Chert exposed in the quarry.

The age problem of the Rockhouse Limestone was settled by McComb and Broadhead (1980) and McComb (1987) based on studies of conodonts from the Decatur Limestone and Rockhouse Limestone. They found that the conodont Icriodus woschmidti, which closely approximates the Silurian and Devonian boundary by its first appearance, occured in the upper 2 m of the Decatur at Parson's Quarry. They suggested that the Rockhouse was therefore Early Devonian (Lockov) in age, at least in the northern part of the Ross outcrop area in Decatur County.

Capaccioli (1987) studied the conodont fauna of the Ross Formation to the south and noted that Ozarkodina remscheidensis eosteinhornensis is present in the lower 2 m of the Ross and Icriodus woschmidti occurs approximately 2 m above the base of the Ross. She suggested that the Silurian-Devonian boundary cuts upsection through the

Rockhouse Limestone and Rockhouse Shale respectively from north to south. These studies also confirmed that there is no recognizable depositional break across the system boundary in the Silurian-Devonian section in western Tennessee.

Reid (1983) was the first to petrographically study any portion of the Ross Formation. She made 50 thin-sections of the limestone beds from the Rockhouse and Birdsong members at four localities including the type section of the Birdsong at Birdsong Creek. She recognized eleven petrographic facies which she correlated throughout her sections and concluded that the Rockhouse to Birdsong sequence represented a transgressive or deepening event beginning with the subtidal crinoidal sandbanks of the Decatur and continuing through the quiet water, terrigenous-dominated, offshore shelf environment of the Birdsong.

Capaccioli (1987) equated the depositional setting of the Ross in the southern part of the outcrop belt to that of the Helderberg of New York State. She proposed a depositional model in which a northward transgressing subtidal shelf (Decatur) underwent deepening during the Early Devonian along with an increase in clastic influx. This formed a muddy shelf (Birdsong) to the north that graded laterally into a subtidal lagoonal setting (Ross

Limestone) to the south. Localized shoaling of skeletal sands formed the Bear Branch oolitic ironstone facies.

McComb (1987) concentrated on the Decatur and Rockhouse Limestone exposures in the central and northern part of the Ross outcrop belt. His findings for the Rockhouse were in agreement with Capaccioli (1987) suggesting that the Rockhouse represented a generally subtidal, near wavebase environment of deposition. These more recent studies have since been summarized by Broadhead et al. (1988) and the Decatur-Ross sequence placed within a more regional context for the entire southeastern United States by Broadhead et al. (1983).

Reid (1983) and Reid and Broadhead (1983) were the first to specifically address paleoecological questions of the Ross fauna. They looked at epibiont relationships on two species of brachiopod host (Leptaena and Atrypa) and used the epibionts to indicate life orientations for the hosts and hydrodynamic stability of Leptaena.

Paleogeographic and Tectonic Studies

Speculations concerning the paleogeography and paleoceanography of the region occupied by western Tennessee date back to the earliest attempts to develop paleogeographic models for North America (see reviews by Bambach, 1979 and Johnson, 1987). The first

paleogeographic map for the early Paleozoic of North America (Chamberlain, 1882) depicted the western Tennessee region as a seaway between what was called the Appalachian Highlands and the Missouri Archipelago. Williams (1897), who formally named the Appalachian Highlands "Appalachia", published a paleogeographic map for the Devonian in which western Tennessee was depicted as part of an intercontinental seaway bounded to the west by the "Missouri Islands" and to the east by the "Cincinnati Plateau". Willis (1909) published the first series of paleogeographic maps for North America that covered the entire Phanerozoic. He similarly depicted western Tennessee as part of an epicontinental sea flanked by landmasses in the area of the Cincinnati and Ozark uplifts.

Schuchert visited the western Tennessee region during summer field seasons from 1876 to 1907 (Dunbar, unpublished field notes, 1916-1917). Schuchert (1910) published his work on the paleogeography of North America and used the crinoid faunas of the western Tennessee region and the presence of the Linden as evidence of a seaway in west Tennessee during the Devonian. Schuchert (1910), a modern catastrophist, invoked continental-scale cyclic patterns of tectonism to form repeated transgressions and regressions to explain the numerous breaks he saw in the stratigraphic record (fide, Johnson, 1987). Dunbar (1918, 1919) applied

Schuchert's paleogeographic reconstructions to western Tennessee and suggested that, at the beginning of the Devonian, western Tennessee was above sealevel as a relatively flat area with low relief. Subsequently, repeated transgressions flooded the area, during which, the Nashville Dome remained a positive, although broad and low, arch. Dunbar concluded that the sediments for the Linden were derived from the surrounding low uplands and he attributed the irregular thickness and distribution of the Linden to the repeated transgressive-regressive events he believed separated each of the units.

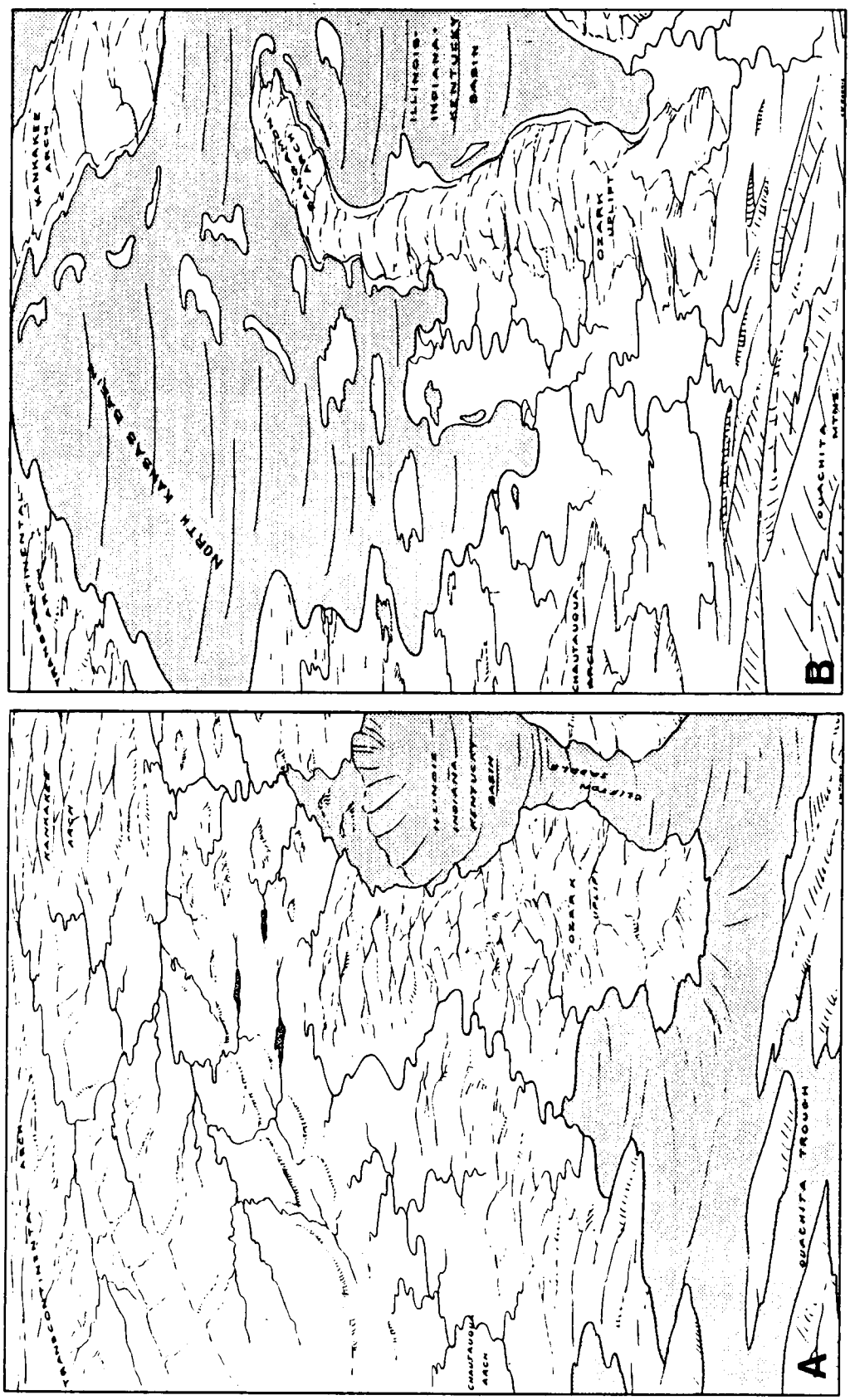
Koenig (1967) discussed the stratigraphy of west-central Tennessee within the context of the structural features that were developed in the mid-continent region. He addressed the development of the Ozark Uplift, Nashville Dome, and Pascola Arch, and the probable tectonic and paleogeographic influence of these features. He also presented the first paleogeographic configuration for this region since Schuchert (1910). Koenig was the first to fully recognize the influence of structural and tectonic features on the pattern of sedimentation in the region and he interpreted the Ross as representing deposition on the flanks of the Illinois Basin, which he interpeted as a deep water basin. Koenig erroneously concluded that the Pascola Arch and Clifton Saddle were active features during the

Late Silurian and Early Devonian thereby partly isolating the Illinois Basin (Fig. 3). He also suggested that the southern midcontinent region was uplifted in the Middle Devonian as part of the Ouachita Uplift to the south. Koenig's stratigraphic section only depicted the Birdsong as laterally and vertically grading into the Ross Limestone, both of which were considered to be lateral equivalents to the Bailey Formation in Missouri.

General Approach Of This Study

The regional biostratigraphic (Petersen, 1972; McComb and Broadhead, 1980; Capaccioli, 1987; McComb, 1987) and limited-scope paleoenvironmental studies (Reid, 1983; Capaccioli, 1987; McComb, 1987), recently summarized by Broadhead et al. (1983, 1988), have provided the basis from which a detailed paleogeographic, sedimentologic, and paleoecologic reconstruction of individual units within the Ross Formation, and their relationships to the overall tectonic setting, have now been attempted. This study focuses on the Rockhouse Limestone and Birdsong Shale members exposed within the central part of the Ross outcrop belt. The ultimate goal here has been to develop a model for the Rockhouse-Birdsong depositional sequence that spans all scales of observation from paleogeography and

FIG. 3. Paleogeographic reconstruction for the midcontinental U.S. during: A. Middle Silurian and B. late Early Devonian (from Koenig, 1976).


A
B
OUACHITA TROUGH
OUACHITA MTNS.
ILLINOIS-INDIANA-KENTUCKY BASIN
OZARK UPLIFT
CHAUTAUQUA ARCH
NORTH KANSAS SWELL

paleoceanography through bed-by-bed depositional setting, to biotic interactions among the fauna.

The study is subdivided into three parts, each part focusing on a different scale of observation and the manner in which the processes active at that scale affect the processes and patterns that develop on succeedingly finer scales. First, regional stratigraphic relationships and three-dimensional facies distributions derived from outcrop and core data are used to refine the regional paleogeographic setting for the Ross. Structural and tectonic data, available because of previous extensive study of the New Madrid seismic area, are incorporated with global paleogeographic reconstructions to suggest the configuration of the Ross depositional setting during the Early Devonian and to propose large scale constraints on sedimentation patterns, including oceanic circulation patterns, and the formation of a mixed carbonate-siliciclastic sequence.

The second part of the study focuses on the depositional setting and history of the Rockhouse and Birdsong members by analyzing both the carbonate and shale beds of each unit on a bed-by-bed scale using outcrop data and thin-section analyses. Local sedimentary processes active during the deposition of each bed are emphasized, including the development of bryozoan mudmounds in the

lower Rockhouse Limestone. These processes will be viewed within the regional setting established in part one of this study.

Part three emphasizes the paleoecology and biotic interactions of the Birdsong Shale. Documenting the range of interactions present within the fauna and determining the ecological and environmental factors responsible for these interactions is the ultimate goal of this part of the study. It also addresses more general questions concerning epibiont paleoecology, such as recognizing specific biotic interactions, the influence of environmental conditions on epibiont development, and biotic associations that developed during deposition of the Ross sequence.

Because this study approaches different problems at differing scales, each chapter is approached as a separate study with introduction, methods, results, and interpretations. Thus, each chapter has a different focus that contributes to the overall reconstruction of the depositional environment, processes, and biotic interactions that produced the Rockhouse-Birdsong sequence.

CHAPTER 2

PALEOGEOGRAPHIC SETTING

Introduction

Depositional models of sedimentary environments are constrained not only by their immediate suitability to explain local situations, but also by whether or not they are valid in the context of regional, and ultimately, global paleogeography (Dineley, 1984). All depositional regimes consist of processes that are active at different hierarchical scales of observation ranging from a narrowly focused scale (e.g., constituent particles in a rock) to a widely focused scale (e.g., global climatic conditions). The range of sedimentary processes acting at successively finer scales of observation, and consequently the range of environmental and biotic responses to these processes, are partly constrained by broader regimes such as regional climate, current patterns, and tectonics.

The goal of this chapter is to suggest the regional paleogeographic setting of the Ross Formation within the context of recently developed global paleogeographic reconstructions and to provide a regional depositional

framework for the environments of the Rockhouse Limestone and Birdsong Shale members of the Ross Formation.

Global Devonian Paleogeography

Although there have been several global reconstructions for the Silurian and Devonian (see reviews by Dineley, 1984 and Barrett, 1985), only four seem to have become widely accepted. In the reconstruction by Scotese et al. (1979), Bambach and Scotese (1979), and Ziegler et al. (1979), which was based primarily on paleomagnetic data, western Tennessee was approximately 5° to 10° south latitude and is rotated clockwise by 40° to 45° during the Early Devonian (Fig. 4). This reconstruction places the western Tennessee area within either the trade wind belt (10° south) or within the doldrums (0-5° south) (Walker Smith, pers. comm., 1986). Recent revision of this reconstruction now places the western Tennessee region closer to 30° south latitude (Scotese et al., 1985, 1987). This revision places their model more in agreement with that of Heckel and Witzke (1979) discussed below.

Smith et al. (1981) published Late Silurian and Late Devonian reconstructions which show very little difference. Interpolations for the Early Devonian place the western Tennessee region approximately 20° south latitude and North

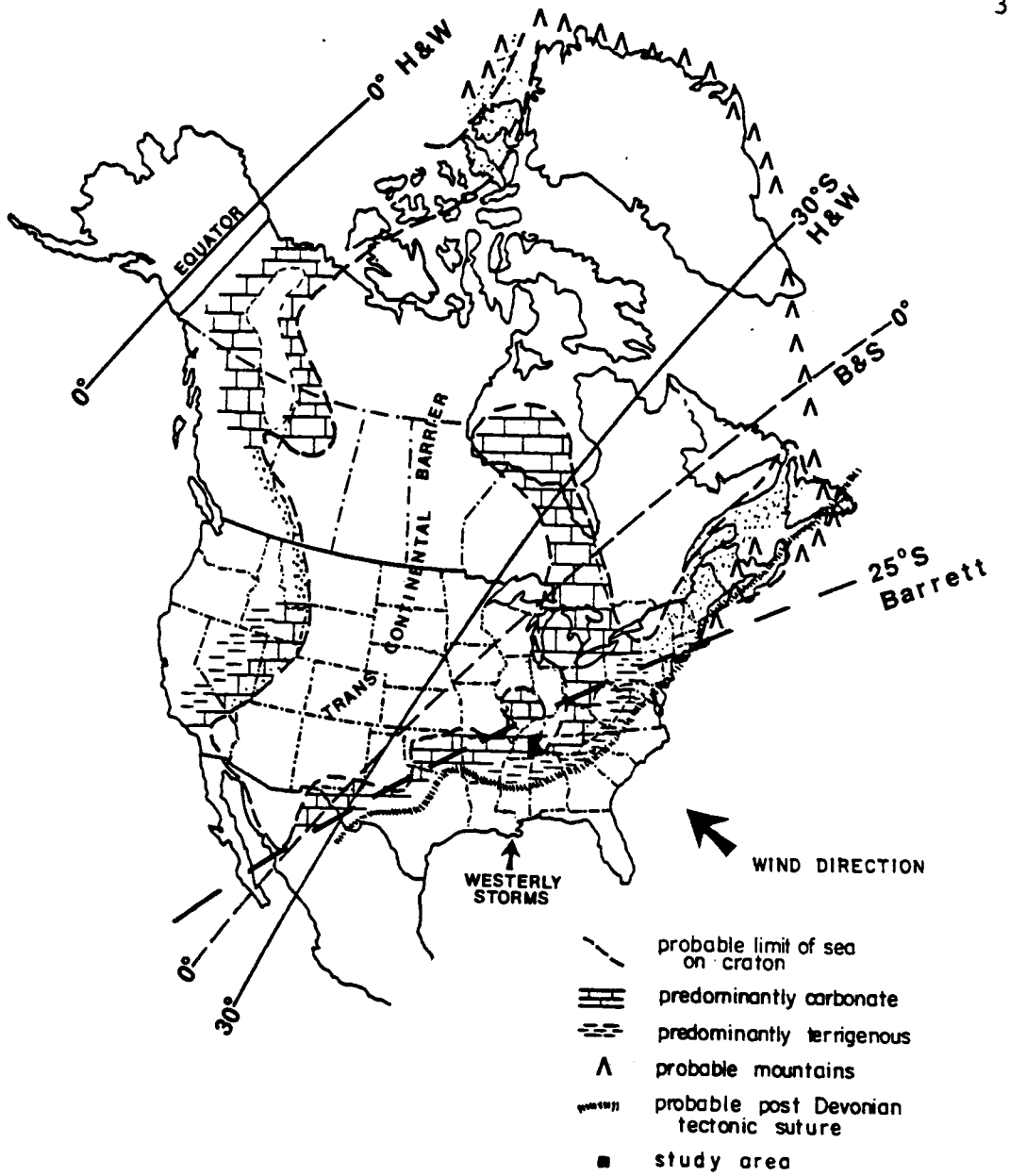


FIG. 4. Generalized distribution of lithofacies for North America during the Early Devonian. Paleolatitudes are plotted for the Bambach and Scotese (1979), Heckel and Witzke (1979), and Barrett (1985) reconstructions. Heckel and Witzke interpret this region to have been under the influence of westerly derived storms (small arrow). Barrett interpreted a southeasterly wind direction (large arrow).

America is again rotated clockwise about 40 to 45°. Boucot (1985a) used paleobiogeographic evidence, however, to suggest that this reconstruction is untenable for the Late Silurian.

The third reconstruction (Heckel and Witzke, 1979) was based primarily on lithofacies distributions and the distribution of paleoclimatically sensitive sediment types such as evaporites and limestone. Their reconstruction places western Tennessee approximately 30° to 35° south latitude under the influence of northward moving warm water currents flowing into the Illinois Basin and within a westerly storm track (Fig. 4). Witzke and Heckel (1987) have revised their original reconstruction based upon paleomagnetic, paleoclimatologic, paleobiogeographic, and tectonic data; however, their revised reconstruction does not differ significantly from their earlier version with respect to the position of North America during the Early Devonian.

Barrett (1985) modified the Scotese et al. (1985) reconstruction using data derived from paleomagnetics, climatically sensitive sediment distributions, and paleobiogeography. He used this new reconstruction to model atmospheric and ocean current patterns for the Early Devonian (Emsian). In Barrett's reconstruction, western Tennessee was situated 15° to 30° south latitude and near

the northern limit of the storm track suggested by Heckel and Witzke (1979) (Fig. 4). Additionally, Barrett proposed that the Acadian volcanic arc terrain was located farther south along the North American margin than did Scotese et al. (1979) and was located to the southeast of the western Tennessee region (Fig. 5a).

Recently, Van der Voo (1988) used the newest paleomagnetic data, which have become available in the past five years, to refine paleolatitude positions from the Ordovician to the Devonian. He found that the Late Silurian to Early Devonian equator ran through Greenland, Hudson Bay, and British Columbia (Fig. 5b). This reconstruction places the western Tennessee region approximately 30° south latitude during the Early Devonian. This continental configuration is nearly the same as that of Barrett (1985), although Van der Voo rejected the placement of the Acadian volcanic arc terrain to the south of the western Tennessee area.

Van der Voo (1988) noted that his reconstruction solves many of the problems put forth by biogeographers concerning endemism of Lower Devonian faunas, especially brachiopods (Boucot and Gray, 1983; Boucot, 1985b). The Eastern America Realm was "reproductively connected" (i.e. within the range of effective larval dispersal) to northern South America and the western United States, but isolated

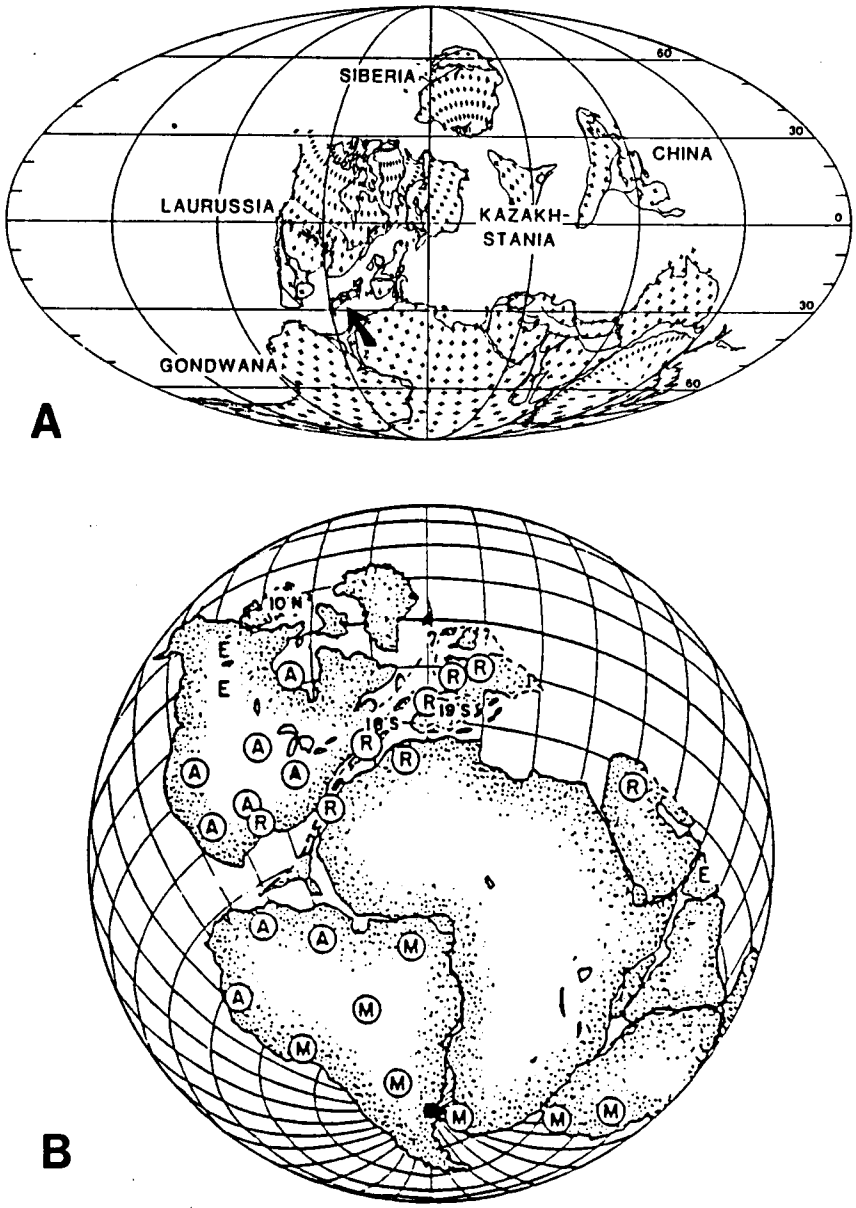


FIG. 5. Paleogeographic reconstruction for the Early Devonian. A. Early Devonian reconstruction of Barrett (1985). Note the position of Acadia (arrow) to the southeast of the North American craton. B. Reconstruction of Van der Voo (1988). A=Eastern Americas Realm, R=Rhenish-Bohemian Subprovince of Old World Realm, M=Malvinokaffric Realm.

from Europe, northeastern Appalachians, and the rest of Gondwana (Van der Voo, 1988). Brachiopods of the Old World Realm are found in Oklahoma, Europe, the Canadian Maritime Province, and northern Africa. Fahraeus (1976) and Oliver (1976) noted that conodont and coral distributions show this same provinciality. Van der Voo (1988) suggests that the Caledonian barrier landmass was responsible for this endemism; however, this does not adequately explain the occurrence of Old World Realm brachiopods in Oklahoma.

Methods

Bambach (1979) summarized the types of data and steps used to develop global and regional paleogeographic reconstructions which include: (1) establishing a spatial and temporal scale for sampling intervals, (2) defining primary (carbonate versus terrigenous) lithologies, (3) defining regional stratigraphy, (4) defining climatic indicators (evaporites, limestone), (5) defining special lithologic suites indicative of certain depositional settings and paleogeographic significance (reefs, coals, bedded chert, authigenic ores). Data derived from fossils and inferred paleoenvironments provide information on local conditions, and structural and tectonic evidence provides a regional paleogeographic framework. Three of these types

of data, structural and tectonic setting, regional stratigraphy, and special lithologic suites, are available to interpret the regional paleogeography for the western Tennessee region during the Late Silurian to Early Devonian.

The U.S. Nuclear Regulatory Commission (NUREG) has funded detailed studies of the western Tennessee region, because of its proximity to the New Madrid Seismic Zone (Bushbach, 1986). Structural and tectonic data resulting from this project were used to reconstruct the paleogeographic configuration and tectonics of the western Tennessee region during the time interval from Decatur deposition (Late Silurian) to Camden deposition (Early Devonian).

The second type of data, stratigraphic relationships, was used to construct panel diagrams, one north-to-south and two east-to-west. The panels were used to interpret the regional stratigraphic relationships and facies distributions of the western Tennessee region within the context of the structural setting based on the NUREG data. Stratigraphic data come from three sources. Previously measured outcrop sections were taken from Dunbar (1919), Wilson (1949), Reid (1983), and Capaccioli (1987). Two previously unstudied sections at McClanahan's and Elkins quarries were measured as part of the present study.

Additional measured sections and subsurface sections from well logs were made available by the Tennessee Division of Geology. These include interpreted outcrop and well log descriptions that are part of an unpublished manuscript by H.B. Burwell (compiled subsurface data) and Charles Wilson, Jr. (compiled surface data). Although most of the data for the manuscript were collected between 1937 and 1941, disagreement over interpretations of the data prevented publication of the report (Edward Luther, pers. comm., 1987). Both authors are now deceased and the Tenneseee Division of Geology is currently completing the manuscript posthumously (Burwell et al., in prep).

The panels were constructed using the top of the Decatur Limestone as a datum. It was not possible to display all of the minor lithologies that make up each unit; therefore, each lithologic unit is displayed according to its dominant lithology. For example, the Birdsong Shale Member is predominantly a terrigenous shale with interbedded thin limestone, but is depicted on the panels as shale. In this way, major lithologic and facies trends can be more easily identified.

The presence of special lithologic suites, such as bedded chert, bryozoan mudmounds, and oolitic ironstone provide additional evidence concerning paleolatitude, paleogeographic configuration of the shelf area, facies

distribution on the shelf, paleobathymetry, and paleocurrent directions.

Results

Structural Setting

The present structural and tectonic features in the New Madrid seismic zone show that, to the east, the Devonian outcrop belt in Tennessee is bounded by the Nashville Dome, which is the southern continuation of the Cincinnati Arch (Fig. 6). Together, these two structures separate the Illinois Basin from the Appalachian Basin. The Nashville Dome was a positive structure throughout most of the Paleozoic (Buschbach, 1986; Hiedlauf et al., 1986; Stearns and Reesman, 1986; Braile et al., 1984; Schwalb, 1983; Hinze et al., 1977; Ervin and McGinnis, 1975). Marcher and Stearns (1962) and Stearns and Reesman (1986) studied the vertical movement and changes in orientation of the dome crest and noted that, during Late Silurian to Early Devonian, the dome had a N50E trend. Although the Nashville Dome was structurally high during the Late Silurian and Early Devonian, it probably did not contribute much detrital sediment to the western Tennessee area (Buschbach, 1986). It is not clear whether or not the Nashville Dome was actually exposed above sea level during

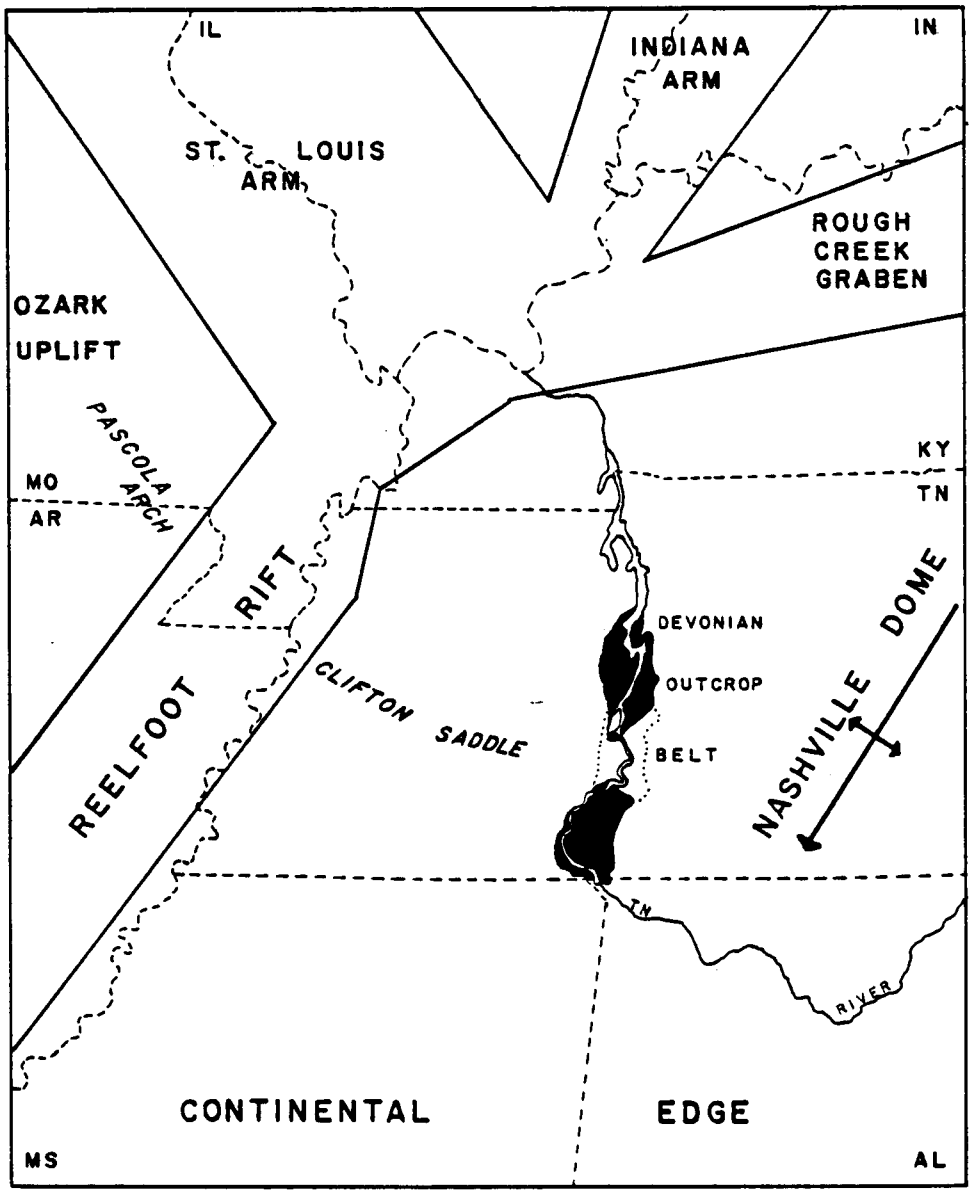


FIG. 6. Structural features of the New Madrid Seismic Zone and location of the western Tennessee Devonian outcrop belt (black). The St. Louis Arm, Indiana Arm, and Rough Creek Graben are part of the present day Illinois Basin. The Devonian continental edge to the south is the present Black Warrior Basin.

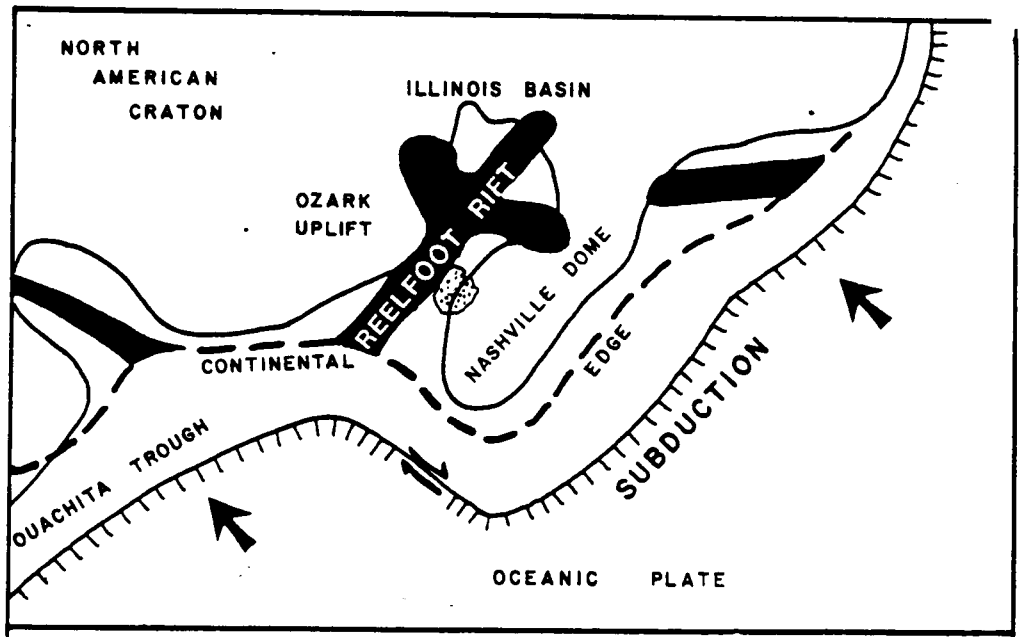
the Early Devonian; however, most workers suggest that it was exposed probably as a low broad area (Buschbach, 1986; Hiedlauf et al., 1986; Stearns and Reesman, 1986).

Two major structural features occur to the west of the Devonian outcrop belt (Fig. 6), the Ozark Uplift and the Reelfoot Rift. The Ozark Uplift was a positive feature during the Paleozoic, but only contributed minor amounts of sandstone and shale to the New Madrid area, mostly to the north in the Illinois Basin (Buschbach, 1986; Schwalb, 1983). The Reelfoot Rift system consists of the northeast trending Reelfoot Rift, and three radiating grabens to the north (St. Louis Arm, Indiana Arm, and Rough Creek Graben), which together form the New Madrid Complex. The northern boundary of the Devonian outcrop belt is the Rough Creek Graben.

Ervin and McGinnis (1975) proposed that the Mississippi Embayment represented reactivation of a precursor rift system. This model has since been elaborated by Heinze et al. (1977), Keller et al. (1983), and Braile et al., (1984). The rift system formed as a result of tensional forces associated with the Late Precambrian breakup of North America to form Laurentia and Gondwana (Fig. 7). The rift represents the failed third arm, or aulacogen, of one of the triple junctions which formed the Early Paleozoic Iapetus Ocean margin

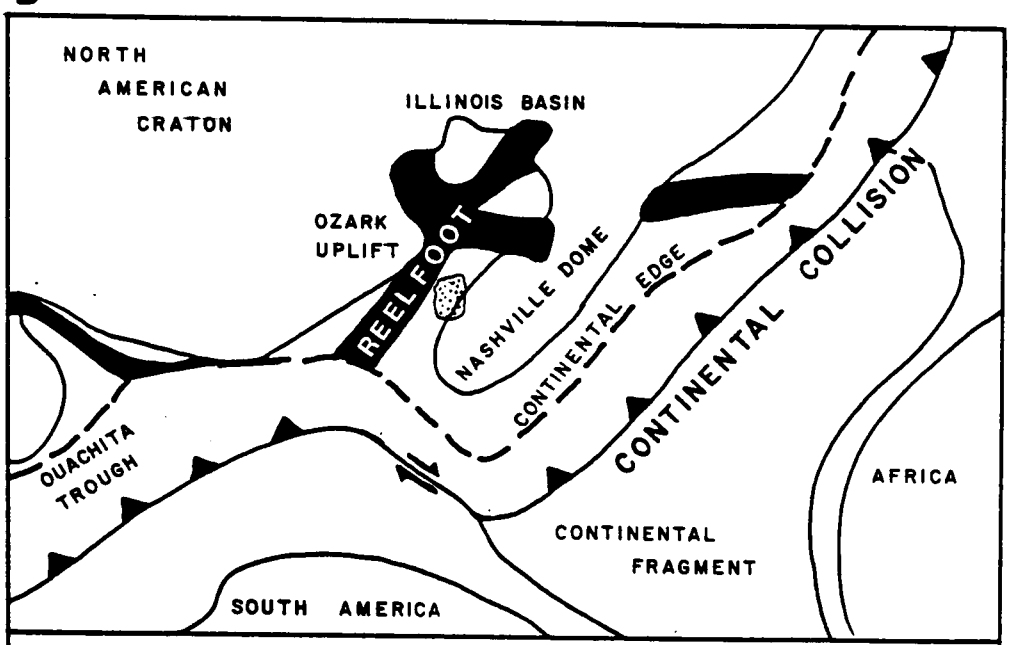
FIG. 7. Schematic showing eastern North America and adjacent plates after the initial rifting event during the Late Precambrian (after Braile et al., 1984). Study area outlined in stiple pattern. Solid black areas represent aulocogens. A. Early to Middle Paleozoic continental margin showing subduction of Iapetus oceanic plate. B. Late Paleozoic collision to form Pangea.

A



EARLY TO MIDDLE PALEOZOIC
TACONIC OROGENY & SEDIMENTATION IN RIFTS

B



LATE PALEOZOIC
CONTINENTAL COLLISION

(after Braile, et al., 1984)

(proto-Atlantic of Buschbach, 1986; Braile et al., 1984). Three other arms to the north also formed at this time as splays of the Reelfoot Rift (Fig. 6). As rifting continued, both the Reelfoot aulacogen and the southern edge of the North American craton, which had developed into the southern continential margin, received sediment eroded from the craton (Fig. 7a). The Late Paleozoic collision of North America with Africa and South America to form Pangea closed the Iapetus Ocean forming a sediment receiving basin, the Black Warrior Basin, at a location roughly coincident with the Early Devonian continental margin (Fig. 7b). Reactivation of the rift system during the Mesozoic was responsible for the development of the Mississippi Embayment (Ervin and McGinnis, 1975).

Subsequent to the initial subsidence caused by the Late Precambrian rifting event, this area began receiving sediment beginning in the Cambrian (Heidlauf et al., 1986; Schwalb, 1983), and the three northern grabens are now part of the Illinois Basin. Heidlauf et al. (1986) have summarized the tectonic development of the Illinois Basin since the initial rifting event (Fig. 8). Thermally induced subsidence during the Early Silurian to Middle Devonian caused the Illinois Basin to deepen. Because of the low surrounding uplands, low amounts of sedimentation (relative to the rate of tectonic subsidence) caused the

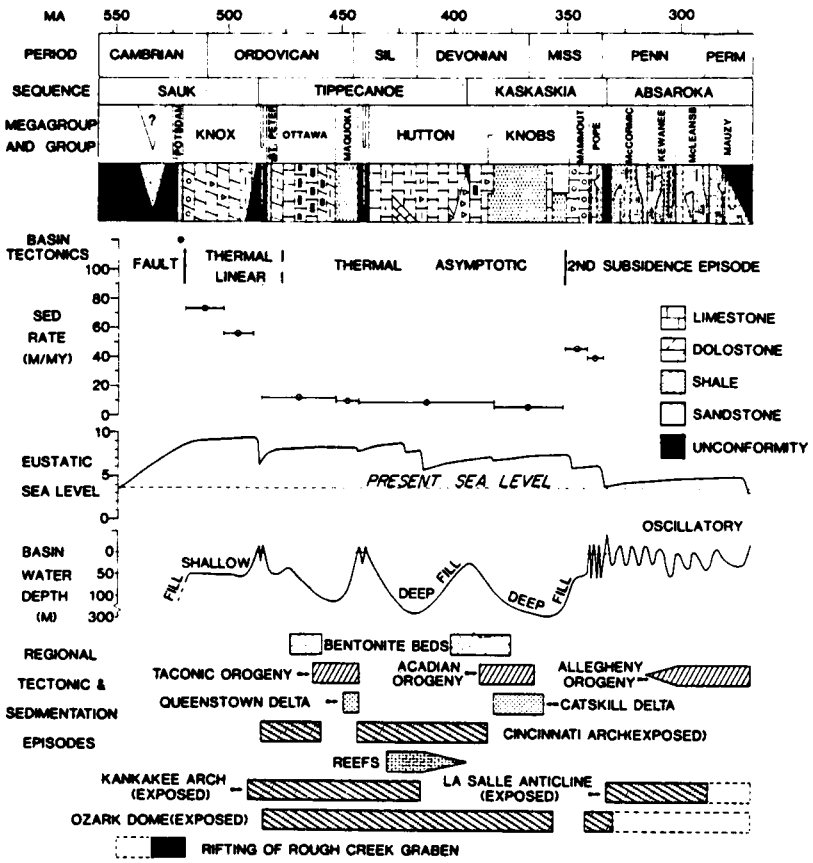


FIG. 8. Paleozoic history of the Illinois Basin showing stratigraphy, cratonic sequences, sediment accumulation rates, basin tectonics, eustatic sealevel, basin water depth, and tectonic and sedimentation episodes (from Klein, 1987, redrawn from Heidlauf, et al., 1986).

Illinois Basin to become a sediment-starved deep-water basin during this time. In spite of the supposed starved nature of the basin, more than 1800 feet (558 m) of rock represent sediment that accumulated in the basin during the Silurian and Devonian (Fig. 9).

Two other structural features in the New Madrid region that historically have affected the interpretation of Silurian to Devonian rocks in western Tennessee are the Pascola Arch and Clifton Saddle. The Pascola Arch is a southeastward extension of the Ozark Uplift (Fig. 6) and was first recognized by Wilson (1935, 1939) and named by Grohskoph (1955). The connection between the Pascola Arch and the Nashville Dome is topographically lower than the Ozark Uplift and the Nashville Dome, but higher than the Illinois or Black Warrior basins and is called the Clifton Saddle (Wilson, 1949). Although both the Pascola Arch and Clifton Saddle are connected to structural features that were active during the Silurian and Devonian, neither was active during this time, contrary to Koenig (1967), based upon stratigraphic evidence. Rather, these features were uplifted at least 12,000 feet (3720 m) sometime between the Late Pennsylvanian and Late Cretaceous (Buschbach, 1986; Ervin and McGinnis, 1975; Stearns and Marcher, 1962; Marcher and Stearns, 1962). Erosion of as much as 4.6 km of strata, including Silurian and Devonian rocks west of

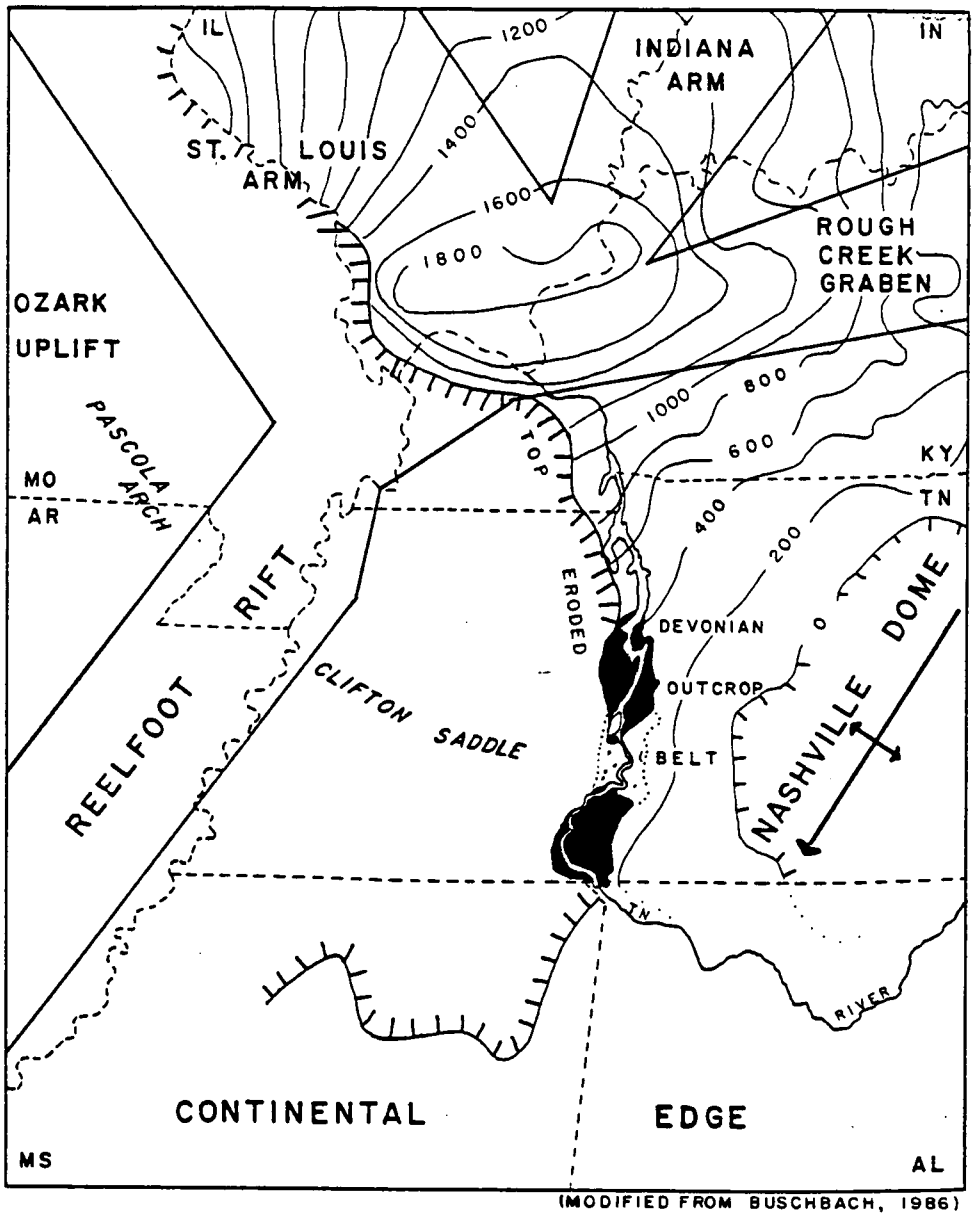


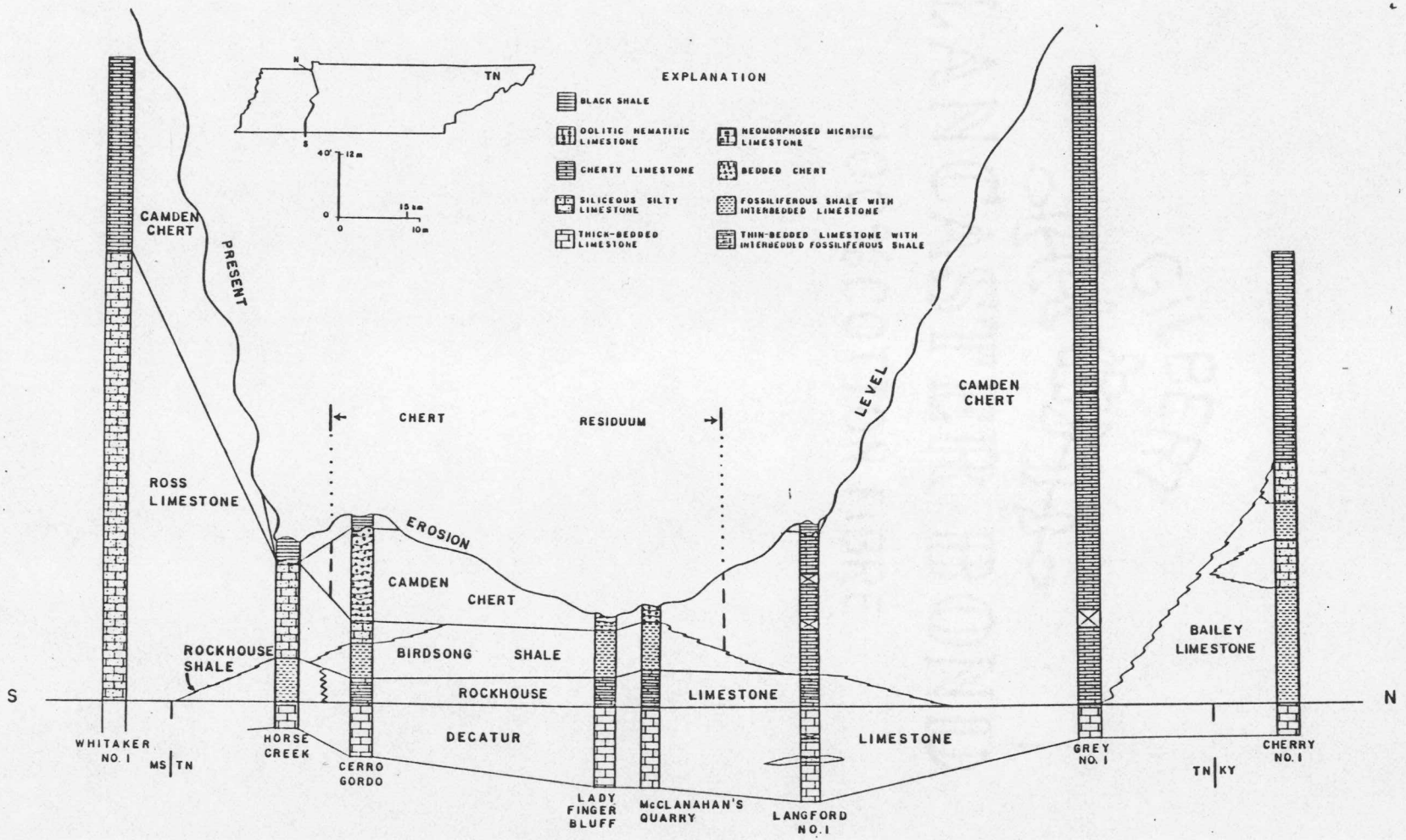
FIG. 9. Isopach contours showing thickness (in feet) of Silurian to Middle Devonian rocks in the Illinois Basin (modified from Buschbach, 1986).

the western Tennessee outcrop belt, has taken place exposing Cambrian rocks along the crest of the Pascola Arch (Stearns and Marcher, 1962; Marcher and Stearns, 1962). The Clifton Saddle cuts across the southern part of western Tennessee resulting in only scattered outliers of Silurian and Devonian rocks in that area (Fig. 9). Soon after the Late Cretaceous, the Pascola Arch and Clifton Saddle subsided and were subsequently covered by Cretaceous and younger sediments collecting in the Mississippi Embayment (Bushbach, 1986).

Stratigraphy

Surface and subsurface data from 14 outcrop and well sections were used to construct three panel diagrams across the Devonian outcrop belt. Several important trends occur from north to south (Fig. 10). First, the Decatur Limestone thins both to the north and south with the thickest accumulation in the central part of the outcrop belt. The Decatur consists of skeletal carbonate, with little terrigenous material, and extends into northern Alabama (Jewell, 1969, Lundin and Newton, 1970). McComb (1987) interpreted the Decatur as a transgressive shallow water carbonate shelf similar to the Coeymans Formation of New York. He recognized four successive environments in the Decatur: (1) deposition below wave base, (2) tidal

FIG. 10. North-to-south panel diagram of regional stratigraphic relationships of Lower Devonian rocks in Mississippi, Tennessee, and Kentucky based on core and outcrop data. Datum is the top of the Decatur Limestone.


TN
EXPLANATION
BLACK SHALE
OOLITIC HEMATITIC LIMESTONE
NEOMORPHOSED MICRITIC LIMESTONE
CHERTY LIMESTONE
BEDDED CHERT
SILICEOUS SILTY LIMESTONE
FOSSILIFEROUS SHALE WITH INTERBEDDED LIMESTONE
THICK-BEDDED LIMESTONE
THIN-BEDDED LIMESTONE WITH INTERBEDDED FOSSILIFEROUS SHALE
CAMDEN CHERT
PRESENT
CHERT
RESIDUUM
LEVEL
CAMDEN CHERT
ROSS LIMESTONE
EROSION
CAMDEN CHERT
ROCKHOUSE SHALE
BIRDSONG SHALE
ROCKHOUSE LIMESTONE
BAILEY LIMESTONE
DECATUR LIMESTONE
S
N
WHITAKER NO. 1
MS | TN
HORSE CREEK
CERRO GORDO
LADY FINGER BLUFF
McCLANAHAN'S QUARRY
LANGFORD NO. 1
GREY NO. 1
TN | KY
CHERRY NO. 1

channels draining an intertidal regime, (3) a variable energy regime slightly below wave base, and (4) a moderate energy regime at wave base.

The Ross Formation, which overlies the Decatur, shows a much more complex pattern and is interpreted to represent a series of intergrading facies. Rather than the northward and southward thinning exhibited by the underlying Decatur, the overlying Lower Devonian rocks thicken northward into the Illinois Basin and southward off the continental edge (incipient Black Warrior Basin) and are thinnest in the central portion of the outcrop belt, which was probably structurally higher during that time. The central portion of the outcrop belt contains the greatest accumulation of terrigenous sediment.

The Bailey Limestone (Fig. 10) is described as predominantly gray to greenish gray silty, cherty, and thin-bedded limestone (Collinson, 1967; Collinson and Atherton, 1975), but becomes increasingly shaly toward the south (Weller, 1944; Freeman, 1951). The present interpretation (Fig. 10) makes the Bailey in southern Kentucky equivalent to the lowermost Camden Limestone, which in turn, is partly equivalent to the Birdsong Shale and Rockhouse Limestone. This relationship supports the suggestion by Cooper et al. (1942), Weller (1944), and Koenig (1967) that the Birdsong and Rockhouse were probably

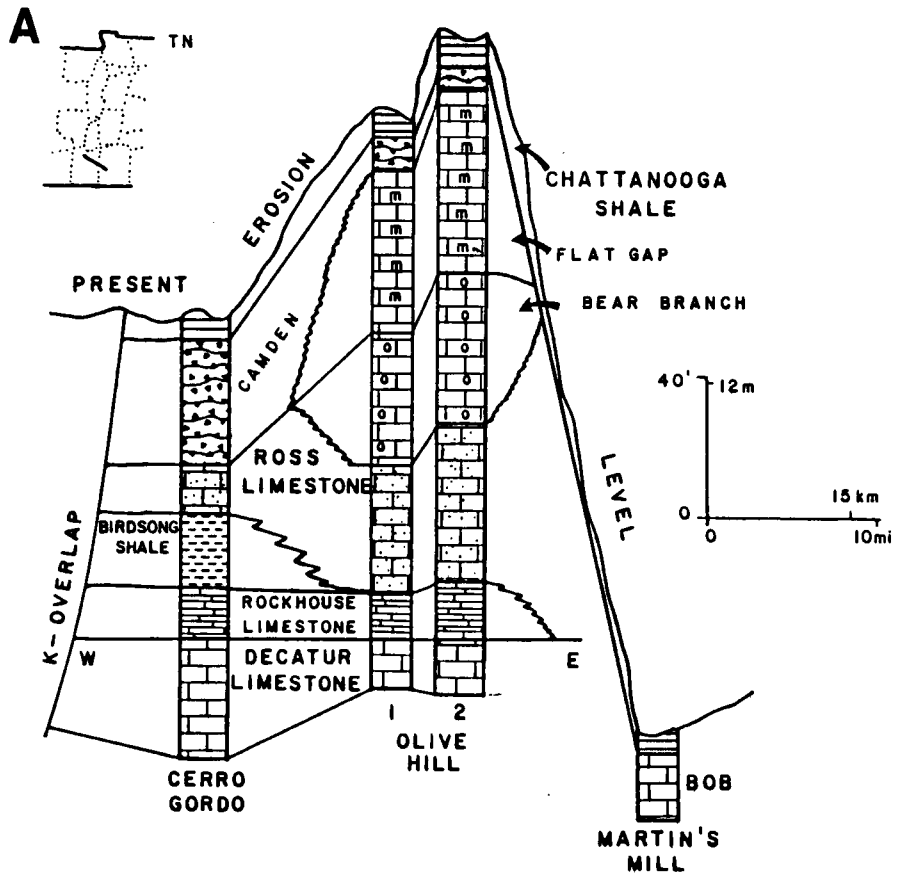
Bailey equivalents. In addition, Collinson (1967) identified Icriodus woshchmidti, a conodont that occurs in the Rockhouse, in core of the Upper Bailey.

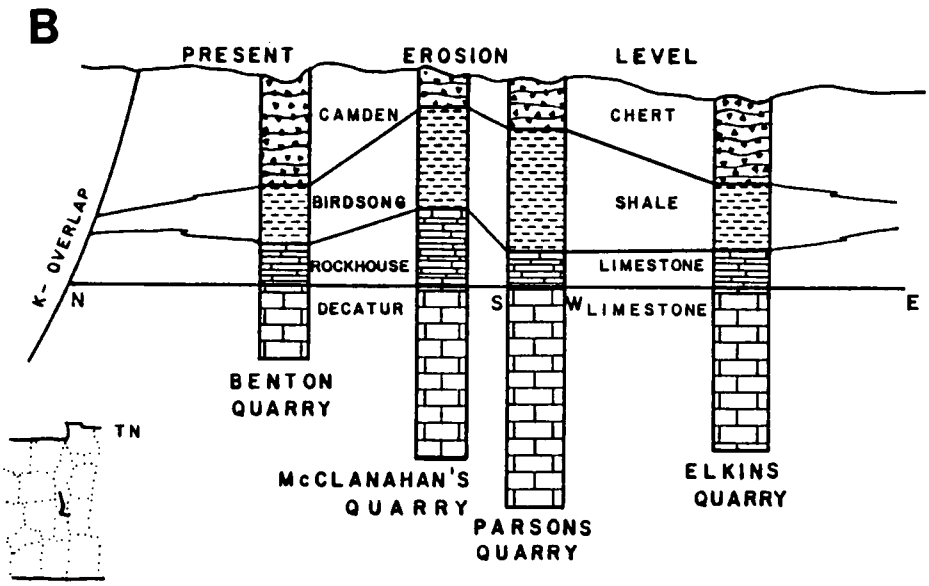
The Ross Limestone to the south consists of silty and cherty limestone that thickens to the south. The Ross Limestone extends into northern Mississippi (Bramlette, 1925) and northeastern Alabama (Dunbar 1919; Butts, 1926) and represents deposition on the Devonian continental margin (Thomas, 1972).

The Bear Branch Member of the Birdsong Shale (Fig. 11a) represents deposition of cross-stratified hematitic ooid and bioclastic debris in subtidal shoals (Capaccioli, 1987). The position of the Bear Branch near the Devonian continental edge suggests that the Bear Branch represented shoaling along the Ross shelf margin. The Flat Gap Limestone, which occurs above the Bear Branch and in areas of western Kentucky, is a massive-bedded crinoidal limestone interpreted to represent skeletal carbonate accumulations or buildups (Edward Luther, pers. comm., 1987; Burwell et al., in prep.) and probably developed subsequent to the Bear Branch shoals near the edge of the Ross Shelf as water depth increased. The Camden cherty limestone represents inter-buildup and back-buildup facies.

The Camden Chert exposed in the central part of the study area consists of bedded chert that is brecciated or

FIG. 11. Panel diagrams of east-west regional stratigraphic relationships of Devonian rocks in west-central Tennessee based on core and outcrop data. See figure 10 for legend. A. Northwest to southeast panel through central part of the Devonian outcrop belt showing bedded chert of the Camden overlain by Chattanooga Shale. B. Northwest to southeast panel across the southern part of the outcrop belt showing relationship between the Bear Branch and Flat Gap Limestone.


A
TN
EROSION
PRESENT
CAMDEN
ROSS
LIMESTONE
BIRDSONG
SHALE
ROCKHOUSE
LIMESTONE
DECATUR
LIMESTONE
K-OVERLAP
W
E
CERRO
GORDO
1
2
OLIVE
HILL
CHATTANOOGA
SHALE
FLAT GAP
BEAR BRANCH
LEVEL
BOB
MARTIN'S
MILL
40'
12m
0
15 km
0
10mi


B
PRESENT
EROSION
LEVEL
CAMDEN
BIRDSONG
ROCKHOUSE
DECATUR
CHERT
SHALE
LIMESTONE
LIMESTONE
K-OVERLAP
N
S
W
E
BENTON
QUARRY
McCLANAHAN'S
QUARRY
PARSONS
QUARRY
ELKINS
QUARRY
TN

exhibits contorted bedding in places (Fig. 11b). This part of the section represents Camden altered by extensive dissolution to form bedded chert that grades laterally into cherty limestone to the north and south (Fig. 10). The dissolution was concentrated on the structural high possibly coincident with the initial development of the Pascola Arch and Clifton Saddle. The timing of the dissolution can be narrowed to post-Camden deposition and pre-Chattanooga deposition because of the presence of undisturbed Chattanooga Shale above the Camden bedded chert (Fig. 10, 11a, b). The Camden represents a return to a predominantly carbonate shelf environment similar to that of the Decatur shelf, but with a much greater silica content.

Special Lithologies

The Rockhouse Limestone Member at Parson's Quarry contains a series of subparallel, elongate, bryozoan-dominated mudmounds (see Chapter 3). The crests of 48 mudmounds were mapped, and lengths of individual mounds range from 1 to 14 m with heights above the surrounding bench of 1 to 3 m. The mounds have an average present day orientation of N54W and exhibit other trends that are qualitatively discernable from examination of the geographic distribution of the mound crests. Some

researchers believe that bryozoan mudmounds developed only under a narrow range of conditions (R. Cuffey, pers. comm., 1988); however, this may be an over-generalization (K.R. Walker, pers. comm., 1988). Regardless, the shape and orientation of mudmounds can be of use in determining current directions and water energy.

Discussion

The close mutual proximity of the four structural features (Nashville Dome, Illinois Basin, Ozark Uplift, and continental edge) present during deposition of the Upper Silurian to Lower Devonian sequence and the stratigraphic relationships recognized in outcrop and core make it possible to reconstruct the regional paleogeographic configuration of the marine shelf present in western Tennesee during the Late Silurian to Early Devonian. This shelf is here called the Ross Shelf. The location of the Bear Branch Member and Flat Gap Limestone and the configuration of the Rockhouse Limestone mudmounds, along with published global paleolatitude and paleocurrent reconstructions, make it possible to determine the probable source direction for terrigenous influx during deposition of the Ross Formation and to suggest possible paleocurrent patterns on the shelf.

Paleogeography

Hypothetical oblique views (Fig. 12, 13) of the New Madrid region during the Late Silurian and Early Devonian show the relative positions of structural features active at that time. In this reconstruction, the Reelfoot Rift is depicted as being topographically lower than the Ross Shelf, based primarily on the conclusion that the rift was active during the Paleozoic (Bushbach, 1986; Braile et al., 1984). This interpretation is supported by the thickness of the Bailey limestone off the Ross Shelf edge into the Illinois Basin. This produced a steeply inclined margin, a configuration believed to have continued around the western margin of the shelf also.

During Decatur deposition (Fig. 12a), the shelf was shallow and dominated by the accumulation of well washed skeletal carbonate sediment (McComb, 1987). Some subsidence may have occurred in the central part of the shelf allowing a greater accumulation of carbonate sediment in that region. The Decatur shelf probably extended farther to the east, over or around the Nashville Dome, if the dome was a low feature, placing the shoreline farther to the east, if a shoreline existed at all. Subsequent erosion in the Dome area has removed any evidence of Late Silurian to Early Devonian sediment. It is likely that

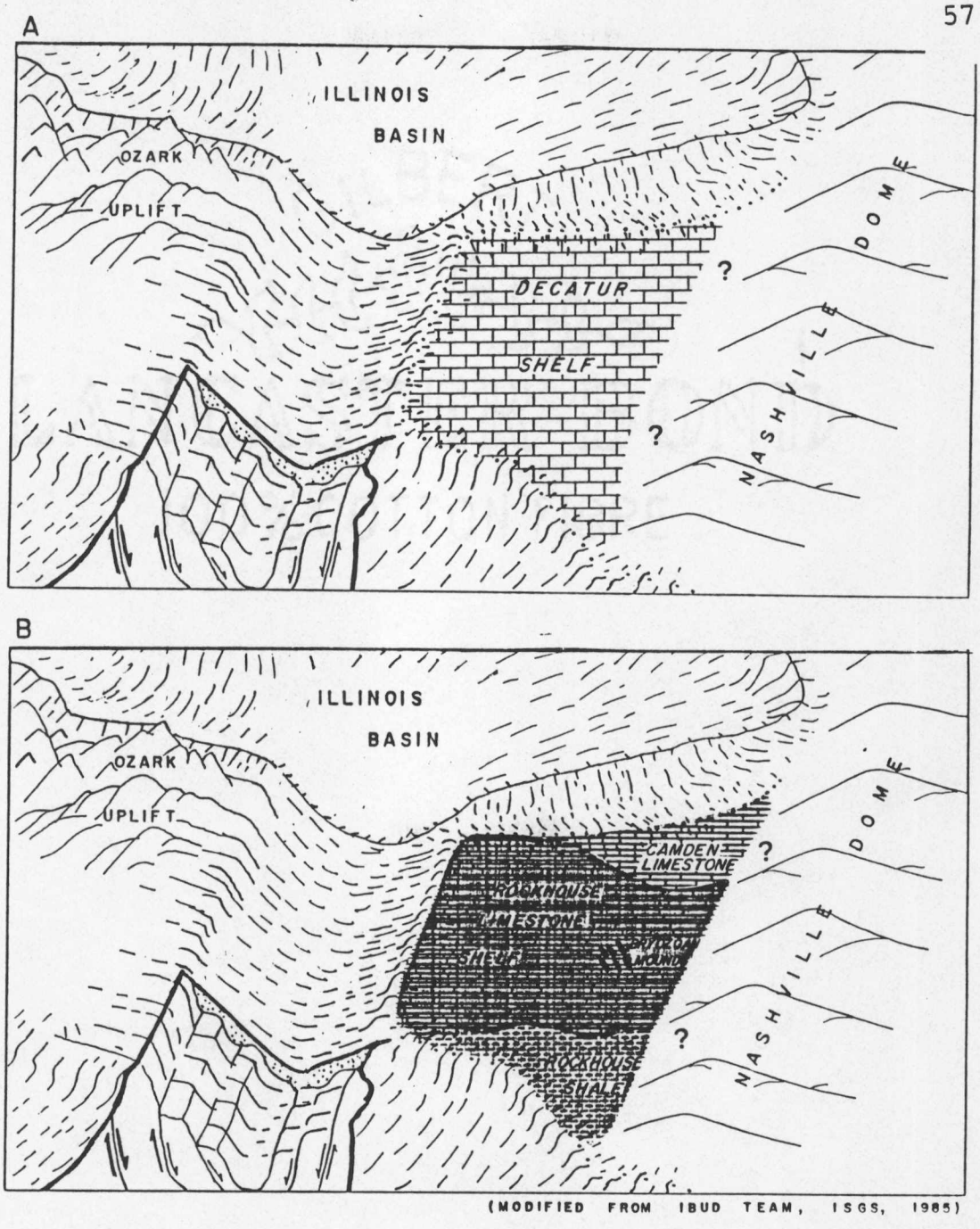


FIG. 12. Oblique view paleogeographic reconstruction of the Ross Shelf during Decatur and Rockhouse time (not to scale). Cutaway shows the structure of the Reelfoot Rift. A. Decatur carbonate shelf (Late Silurian). B. Rockhouse shelf (Early Devonian) with distribution of bryozoan mudmounds occurring in the Rockhouse Limestone in the central part of the study area.

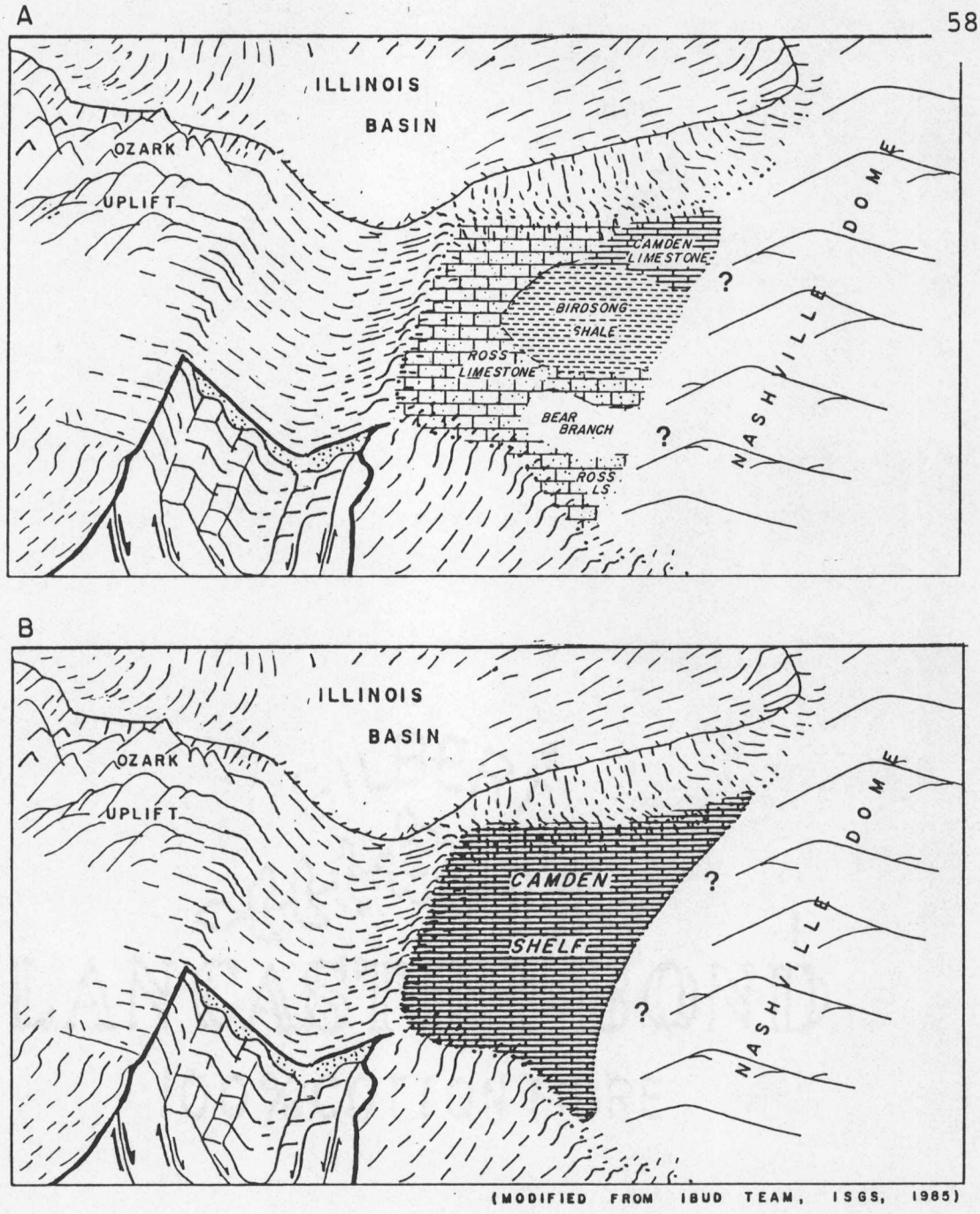


FIG. 13. Oblique view paleogeographic reconstruction of the Ross Shelf during Birdsong and Camden time (not to scale). Cutaway shows the structure of the Reelfoot Rift. A. Shelf during Ross Limestone and Birdsong deposition. B. Camden carbonate shelf.

the Decatur, Ross Formation, and Camden sediments did extend farther east than their present distribution suggests because no shoreline features have been recognized. The lithologic units show erosional boundaries to the east, and these units show an onlapping arrangement suggesting a transgressive event.

During the Early Devonian, an increase in clastic influx resulted in the deposition of the mixed siliciclastic-carbonate sequence of the Rockhouse Shale, Rockhouse Limestone (Fig. 12b), and overlying Birdsong Shale, Bear Branch, and Ross Limestones (Fig. 13a). During this time, the shelf was approximately 25-35° south latitude within a westerly storm track. Because the surrounding highlands did not supply great amounts of detrital sediment to this area (Buschbach, 1986; Schwalb, 1983), the source of the terrigenous mud was probably from offshore to the south and southwest (Gibson et al. 1986, 1988). Most of the mud was carried along the rift system into the Illinois Basin with some being deposited on the Ross shelf by periodic storms. Farther to the north, on the Illinois side of the shelf, less terrigenous material accumulated, allowing the clear water carbonate sediment of the Camden to accumulate as a northern facies of the Ross Formation. The Bailey Formation represents downslope shelf accumulations of predominantly mud brought through the

Reelfoot Rift system and around the Ross Shelf.

The increased thickness of the Ross Limestone and the Camden to the south, and the Camden and Bailey to the north (Fig. 10) suggests that the continental margin to the south and the Illinois Basin to the north were continuing to subside during this time. The Ross Shelf received less sediment than the surrounding deeper areas, but probably underwent some structural down-tilting to the north, allowing a greater accumulation of sediment on the deeper shelf in that direction (Fig. 10). The development of the Bear Branch shoaling facies (Capaccioli, 1987), behind which the Birdsong Shale accumulated, suggests that terrigenous influx was beginning to wane. The Bear Branch and subsequent Flat Gap may have developed on the structurally raised continental edge of the Ross shelf during this time. The Birdsong, therefore, represents a muddy shelf lagoon behind the Bear Branch shoals which rimmed the Ross Shelf to the south. Petrographic and paleoecologic evidence for the interpretation of the depositional setting of the Rockhouse Limestone and Birdsong Shale are given in Chapter 3.

Deposition of the Camden represents cutoff of the source of the terrigenous material to the Ross Shelf and a subsequent return to the dominantly carbonate-accumulating shelf similar to the Decatur (Fig. 13b). The Camden

differs from the underlying units, however, by being more siliceous. The source of the silica is not precisely known; however, the reconstruction of Barrett (1985) places the Acadian volcanic arc terrain to the south and southeast (Fig. 14a, b) with atmospheric circulation patterns blowing to the north and northwest in the summer. It is therefore conceivable that part of the source of the silica for the Camden is volcanism from Acadia. This interpretation is reinforced by the occurrence of K-bentonites in the basal Flat Gap Limestone in western Kentucky (IBUD, 1985). The Flat Gap represents skeletal accumulations or buildups that were probably continuations of the Bear Branch shoals suggesting that the Devonian margin of the Ross Shelf may have been rimmed during Camden time also.

Paleoceanography

Barrett's (1985) reconstruction of oceanic circulation patterns (Fig. 14c) is similar to that of Heckel and Witzke (1979) and shows the Ross Shelf under the influence of warm water currents moving toward the Illinois Basin from the west-southwest. The general circulation pattern on the Ross Shelf, at least during Rockhouse deposition, is suggested by the orientation and asymmetry of the Rockhouse mudmounds. During the Early Devonian, these mudmounds would have had an orientation of N5W - N15W. Individual

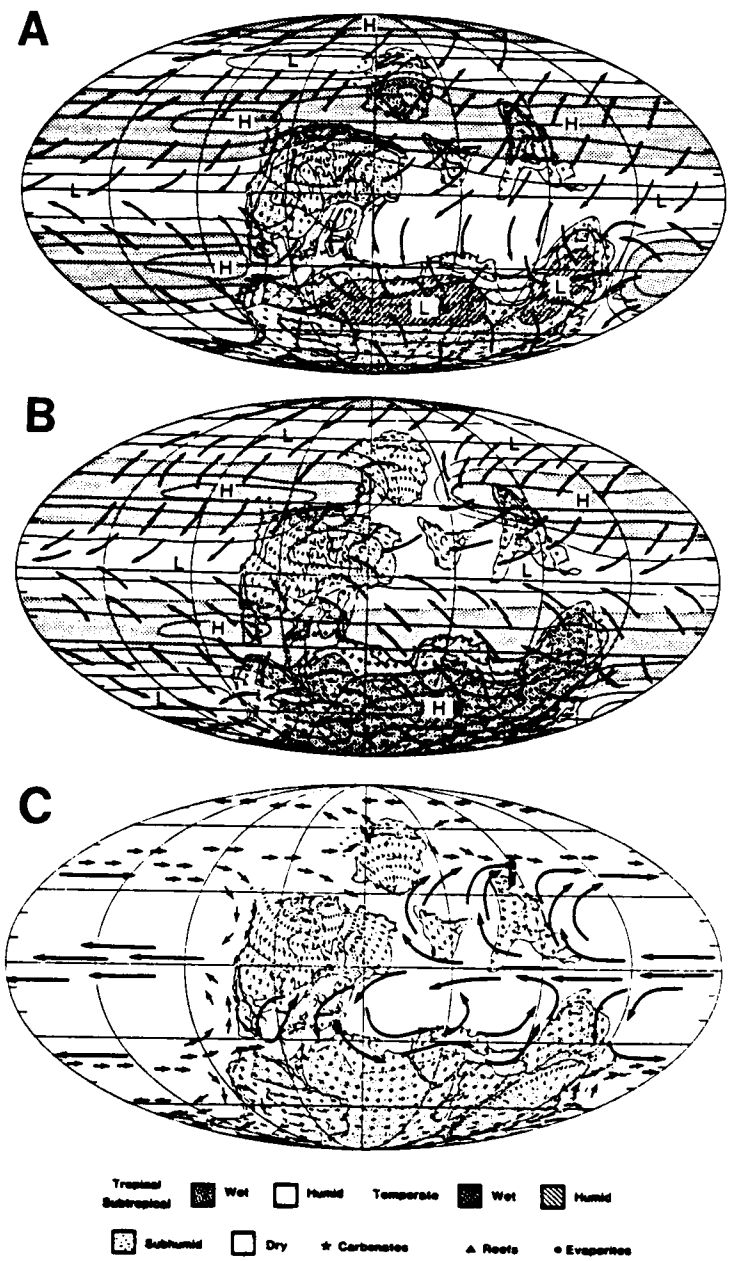


FIG. 14. Early Devonian oceanic and atmospheric circulation pattern and pressure systems of Barrett (1985). A. Summer atmospheric circulation pattern with wind direction from the south. B. Winter atmospheric circulation with wind from the southeast, near Acadia. C. Oceanic circulation pattern showing warm water currents entering the Illinois Basin from the southwest.

mound crests are oriented so that the highest portion of the mounds faced offshore in the direction of dominant current transport. During the Early Devonian, this direction was to the northwwest toward the Illinois Basin. Because of the shallow water depths on the Ross Shelf (probably less than 50 meters), and hence reduced influence of the coriollis effect, currents on the shelf would have been controlled primarily by winds blowing across the shelf from the southeast. Currents crossed the shelf moving northwestward toward the Illinois Basin (Fig. 15). Oceanic-derived currents probably entered the Illinois Basin via the Reelfoot Rift trough. This pattern could have created an upwelling condition on the southern margin of the Ross Shelf, providing nutrients that could support a rich fauna on the shelf.

Subsequent Events

Although the rocks in the western Tennessee region are essentially flat lying, the influence of structural features of the region has repeatedly exposed the area to numerous regional erosive episodes that confuse the sequence of stratigraphic events in the area (Fig. 16). Subsequent to the deposition of the Decatur, Ross, and Camden sequence, a period of erosion took place prior to Chattanooga deposition. The timing of this event can

FIG. 15. Suggested generalized paleocurrent directions on the Ross Shelf during Rockhouse Limestone deposition. Large black arrows indicate dominant oceanic current directions and sediment transport toward the Illinois Basin. Large white arrows indicate dominant wind direction. Small black arrows indicate northwestward wind generated currents toward the Illinois Basin.

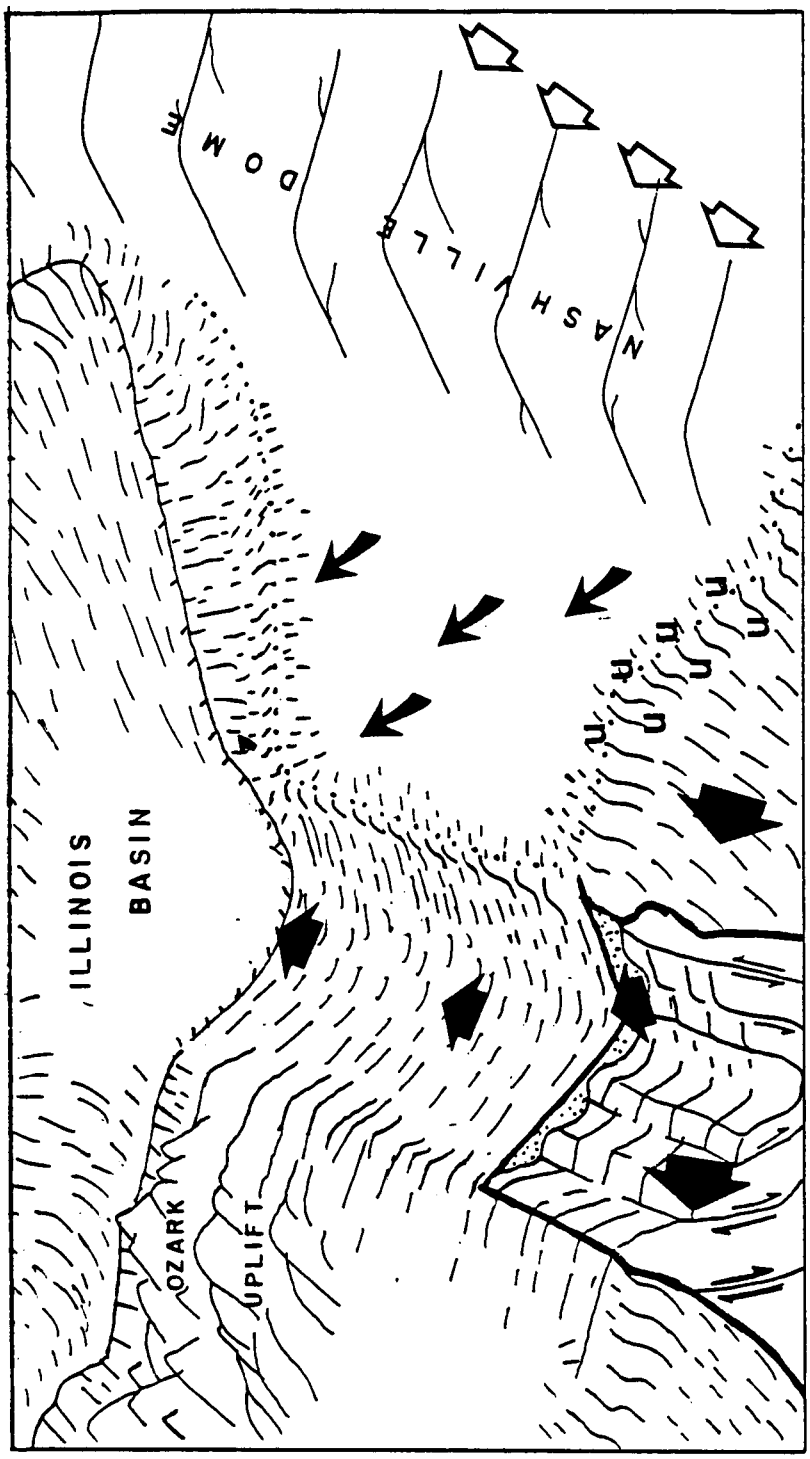
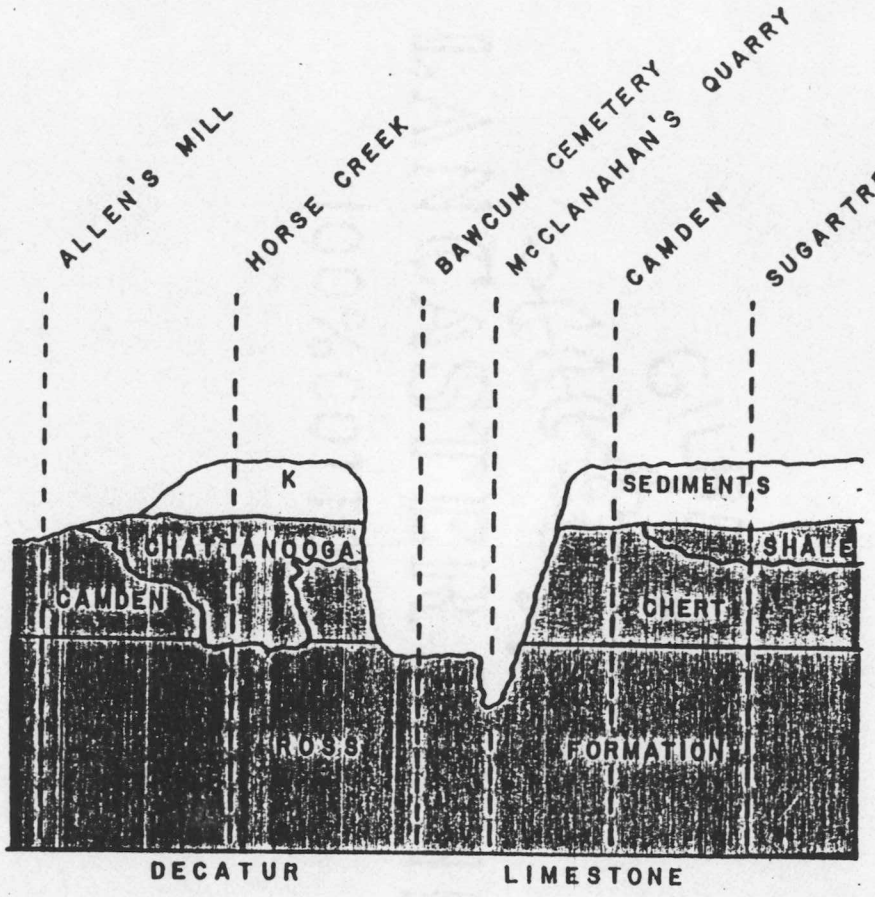

ILLINOIS
BASIN
OZARK
UPLIFT
WOOM
NASHVILLE
(MODIFIED FROM IBUD TEAM, ISGS, 1985)

FIG. 16. Schematic depicting relationships of erosive events that occurred in the study area after deposition of the Decatur-Ross-Camden sequence. A. Relationship of Camden and Ridgetop near Camden, Tennessee showing that the post-Chattanooga pre-Cretaceous event may have occurred as late as post-Ridgetop time. B. Relationship of Pegram to Camden showing that the post-Camden pre-Chattanooga event in the study area could have occurred post-Pegram deposition.



3 POST CRETACEOUS

2 POST CHATTANOOGA – PRE CRETACEOUS

1 POST CAMDEN – PRE CHATTANOOGA

A

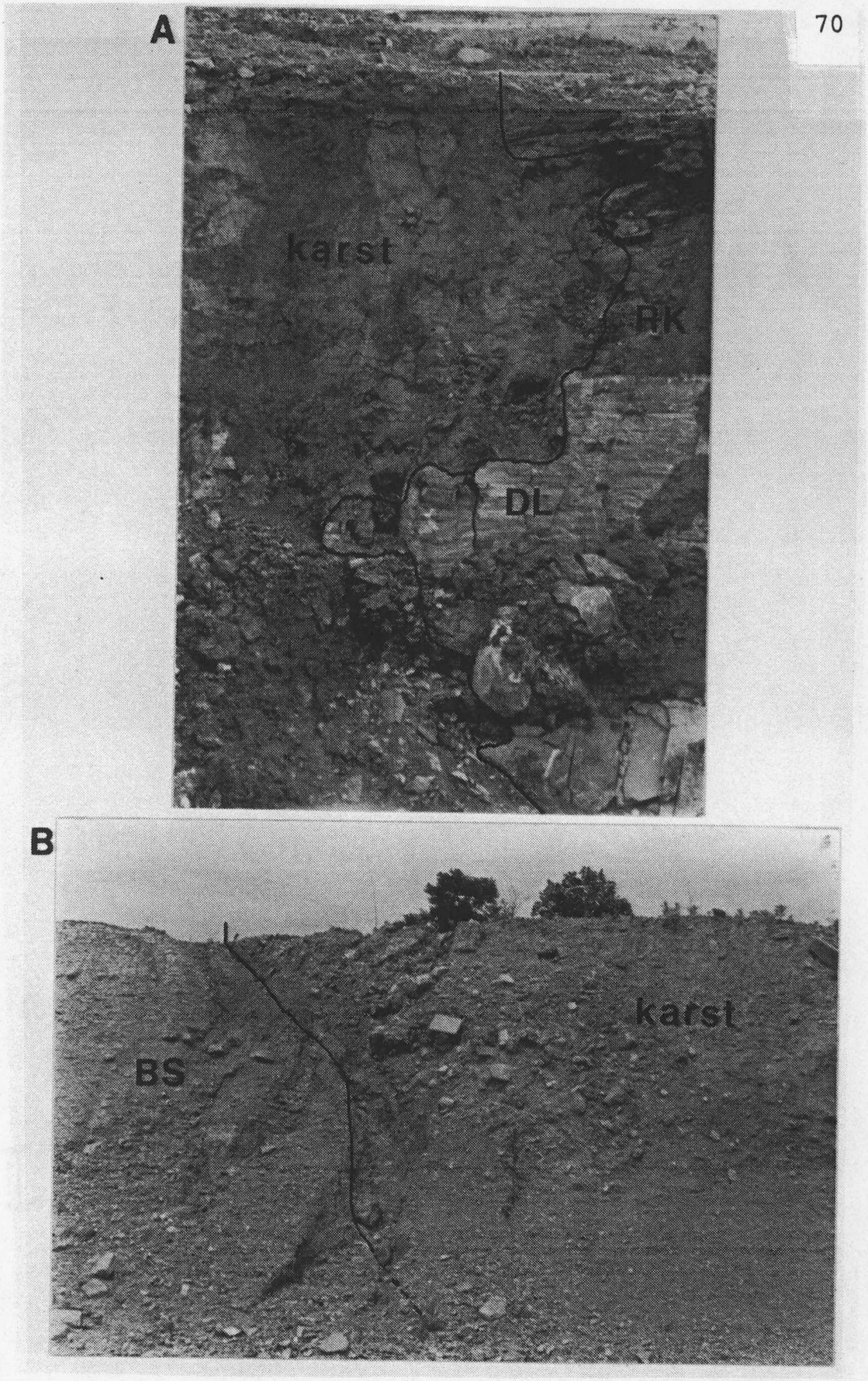
K
RIDGETOP
CHATTANOOGA
CAMDEN

B

CHATTANOOGA
PEGRAM
CAMDEN
ROSS

possibly be specified further by noting that, near Nashville, the Pegram Limestone (Middle Devonian) unconformably overlies the Camden (Fig. 16b), suggesting that the erosion of the Camden in western Tennessee could have occurred as early as pre-Pegram. A second erosive event (post-Chattanooga and pre-Cretaceous) is evident by the presence of Cretaceous sediment above the Chattanooga Shale. The presence of partially dissolved Ridgetop Limestone (Mississippian) above the Chattanooga in wells near Camden (Ross, 1942) suggests that this erosive event followed Ridgetop deposition (Fig. 16a). It also suggests a second period of subsurface limestone dissolution, after dissolution and chert alteration of the Camden (pre-Chattanooga), and prior to the deposition of Cretaceous sediments. Finally, one or more post-Cretaceous erosion events, including the present erosion level, is traceable over the entire outcrop area. In McClanahan's and Parsons quarries, karst development (possibly post-Cretaceous) is indicated by Camden and later age infill in collapse cavities that extend into the Birdsong and Rockhouse (Fig. 17).

FIG. 17. Outcrops of post-Ross karst development. A. Parsons Quarry. B. McClanahan's Quarry.


A
karst
RK
DL
B
BS
karst

CHAPTER 3

DEPOSITIONAL ENVIRONMENTS

General Introduction

The purpose of this chapter is to describe the depositional setting and processes of the Rockhouse Limestone and Birdsong Shale members at the localities studied. Emphasis is placed on the major biotic constituents and sedimentary processes active during the time of sediment accumulation. The diagenetic history of these units was studied only to the extent needed to assess the effects of post-depositional processes on the consistency and maturation history of the sediment.

The sedimentary processes active during deposition are viewed within the regional paleogeographic setting established in Chapter 2. The methods of analysis of each of the two members differ depending on the sampling procedure for the rocks and the specific purpose of study for each unit.

Rockhouse Limestone

Purpose

The Rockhouse Limestone, which overlies the Decatur Limestone, is an interbedded, thin- to medium-bedded, glauconitic limestone-shale sequence with a diverse brachiopod- and echinoderm-dominated fauna (Reid, 1983; McComb, 1987; Broadhead et al., 1988). Observed thicknesses range from 3.0 m in the study area to more than 5.0 m in the southern part of the Devonian outcrop belt. Reid (1983) recognized four vertical subdivisions of the Rockhouse Limestone. The basal Rockhouse consists of a thin terrigenous mudstone interbedded with thin skeletal packstone to grainstone. This subunit is overlain by a succession of interbedded skeletal packstone to grainstone and fossiliferous, thin-bedded, gray shale, which is in turn, overlain by the third subunit, an upper skeletal packstone. The fourth subunit is an echinoderm wackestone with minor amounts of bryozoans, especially Eridotrypa, and trilobites.

Gibson, et al. (1986) reported the occurrence of elongate, subparallel, bryozoan-dominated mudmounds within the lower Rockhouse at Parsons Quarry. These mudmounds are unusual in that stromatoporoids and corals were the common buildup producing organisms during the Devonian, a trend

carried over from the Silurian (Heckel, 1974; Longman, 1981; James, 1983). Other less important contributors to carbonate buildups were the calcareous algae, sponges, and bryozoans. Lower Devonian mudmounds are rare, especially from the eastern United States. The primary purpose for study of the lower Rockhouse was to describe and evaluate these mudmounds.

Methods

Quarrying of the Decatur Limestone at Parsons Quarry results in a bench approximately 2.5 m above the top of the Decatur at the stratigraphic level above which the shale-to-limestone ratio becomes too great for commercial quarrying to be profitable. The lower Rockhouse Limestone is exposed in highwall surfaces only, and the remainder of the Rockhouse and the entire overlying Birdsong Shale are removed as overburden. Direct sampling of those exposures was unsafe because of the highly fractured, unstable face produced by blasting. In order to sample the features of an individual mound, three cores were taken on the existing bench surface. The drilling apparatus used was a Joy 22 truck-mounted corer, which produced 11.8 m (total length) of 5 cm diameter core from three sites: intermound lithology (PQC-1), mound core (PQC-2), and the transition from mound to intermound (PQC-3). The core was logged in

the field. Twenty-five 5 x 7.5 cm thin section were prepared at lithologic changes in the core. Of these, six were point counted using 300 counts-per-thin section.

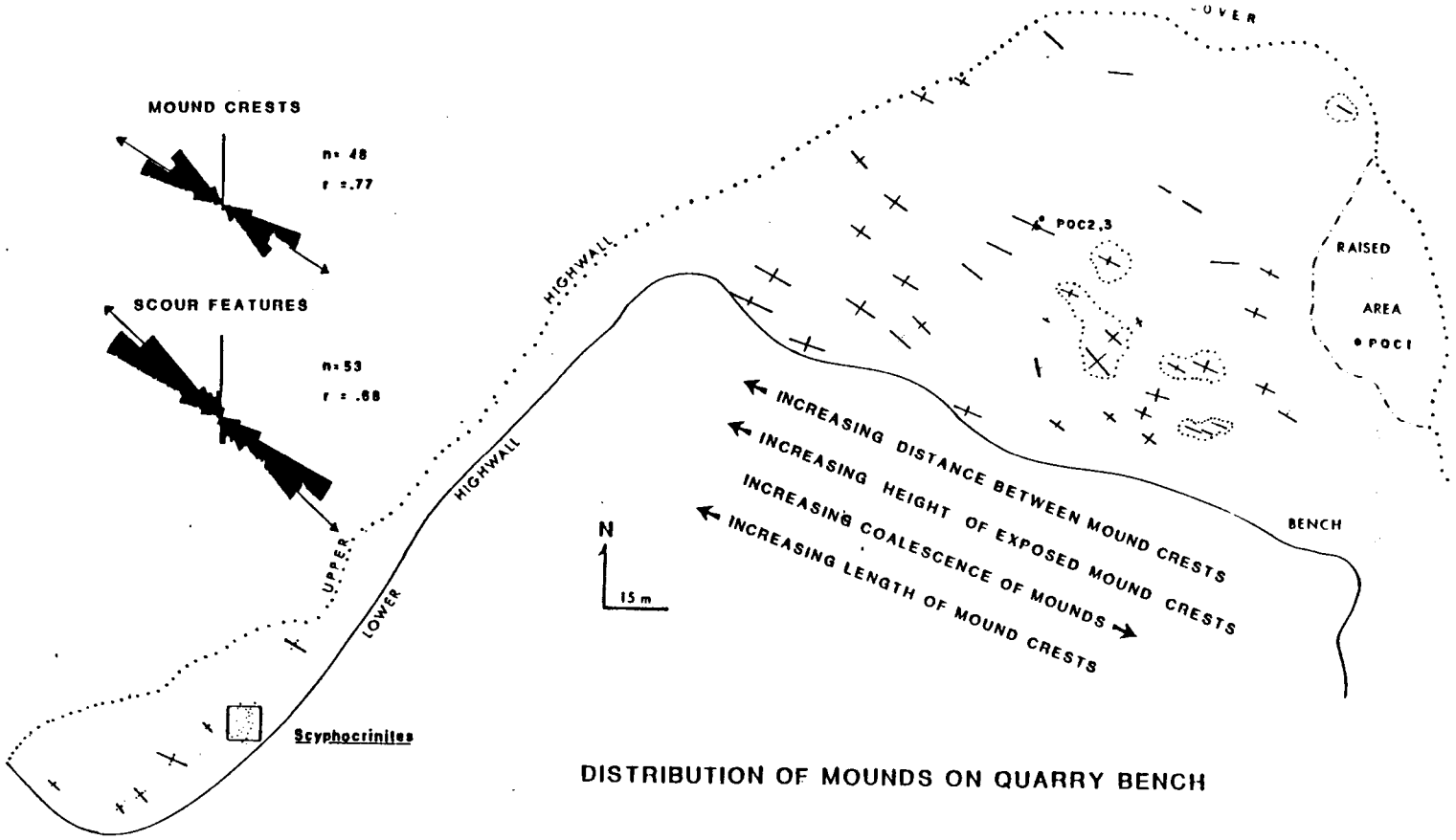
The remainder of the Rockhouse was not studied in detail. Hand samples and outcrop descriptions were taken, but no thin sections made. Rather, data on the upper Rockhouse are summarized from Reid (1983) and McComb (1987).

Mound Geometry

Distributional Features and Trends. Mudmounds within the Rockhouse Limestone at Parsons Quarry were originally observed by their crests, as a series of subparallel, elongate, low ridges on a bench surface of the quarry. This study, extending over a period of a year, has allowed for the mapping of 48 discreet mound crests (Fig. 18). Continuing active quarrying at the site has removed mounds initially observed, while exposing others.

Mapping of mound crests showed that most are elongate in plan view with lengths ranging from 1 to 14 m and widths ranging from 1 to 3 m. The maximum syndepositional relief of these mounds above the surrounding intermound areas probably did not exceed 0.5 m. Maximum relief was

FIG. 18. Map of bench surface in Parsons Quarry showing the distribution of the mudmound crests and scour features with observed trends. Long dimensions indicated by long bars. Width indicated by shorter cross bars, unless not measured. The mound crests have a present day mean orientation of N54W. The inset shows a 100 m^2 grid showing the distribution of Scyphocrinites flotation bulbs. Drill core locations are shown as PQC-1, -2, -3.



DISTRIBUTION OF MOUNDS ON QUARRY BENCH

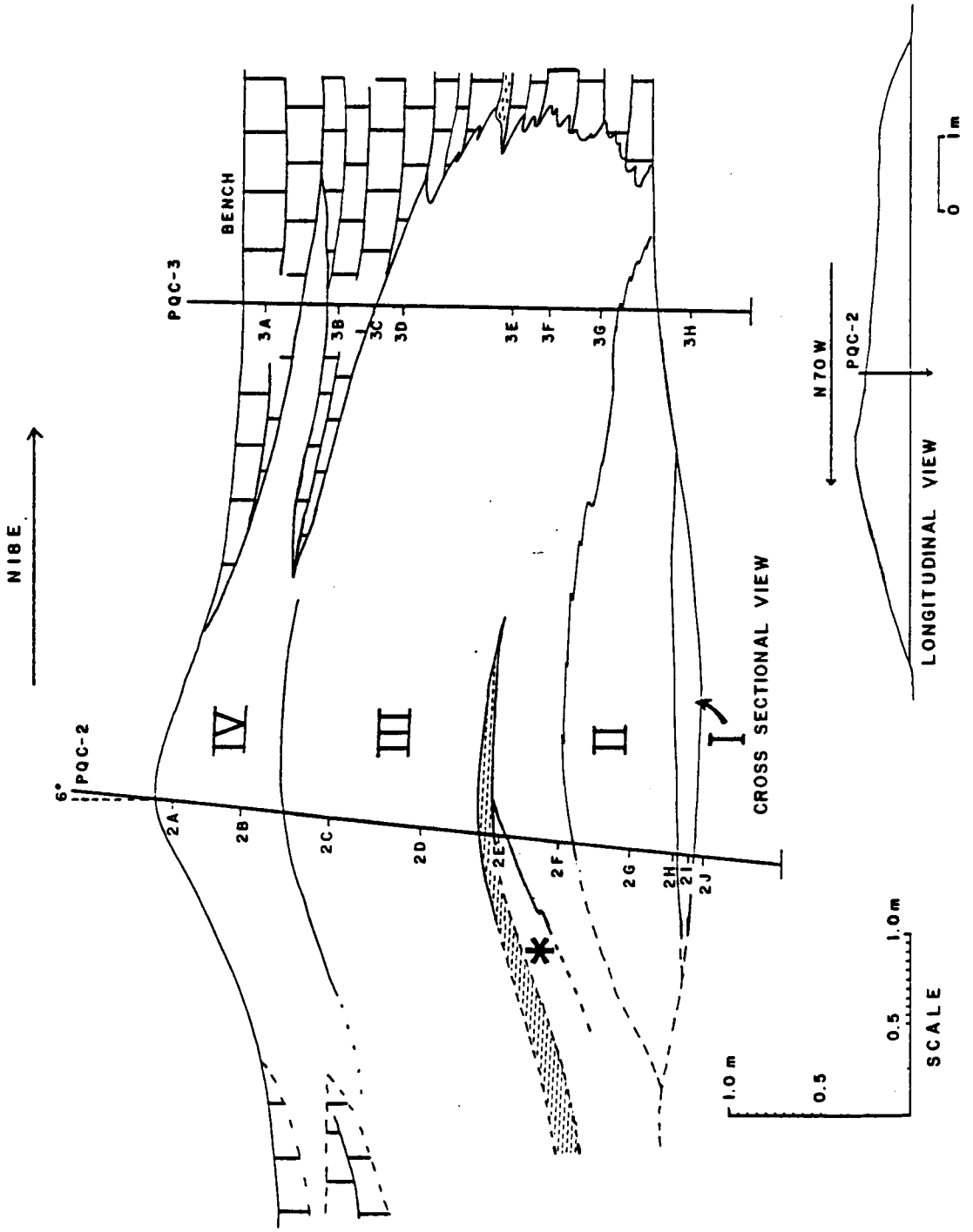
determined by tracing shale drapes from the intermound area onto the mound and measuring the vertical distance between the two areas. Mapping of crest elongation and calculation of mean orientation indicates a present day orientation of N54W (Fig. 18).

Certain trends are qualitatively discernible from the examination of the geographic distribution of the mound crests (Fig. 18). (1) Lengths of individual mound crests increase toward the northwest. (2) Heights of exposed mound crests increase toward the northwest. (3) Distances between mound crests increase toward the northwest. (4) Mound crests become less discreet or coalesce to the southeast. (5) Highest points on mound crests tend to be located near the northwest end of each mound (Fig. 19).

Vertical and Lateral Extent

A cross-section of the cored mound (Fig. 19), as well as cross-sections of three other mounds exposed by blasting of the highwall, shows that the mounds underwent little lateral migration during development, rather, they are characterized by relatively steep-sided edges. Cross sectional and bedding plane views of two different mounds are shown in figure 20. Bedding within the mounds is indistinct, whereas, bedding in the intermound areas is well developed. The lateral limits of each mound are

FIG. 19. Cross section and longitudinal profile of a mudmound from the Rockhouse Limestone based upon drill core data. The longitudinal profile illustrates that the development of the highest portions of the mudmounds occurs on the northern ends of the mounds. PQC-2 was taken through the center of the mound, whereas PQC-3 was taken through the mound-intermound transition. Numerals and letters along the vertical trace of the core refer to thin sections. Roman numerals refer to the four phases discussed in the text. I - allochthonous terrigenous mudstone (Phase I); II - echinoderm-bryozoan packstone (Phase II); III - Buskopora-dominated boundstone (Phase III); IV - interbedded echinoderm-bryozoan mudstone and grainstone (Phase IV). The asterisk marks the position of encroachment of intermound material onto the mound with associated slumping and overturned mound lithologies.


N18E
PQC-3
BENCH
3A
3B
3C
3D
3E
3F
3G
3H
PQC-2
6°
2A
2B
2C
2D
2E
2F
2G
2H
2I
2J
IV
III
II
I
CROSS SECTIONAL VIEW
N70W
PQC-2
LONGITUDINAL VIEW
0
1m
1.0m
0.5
0.5
1.0m
SCALE

characterized by a narrow zone of interbedded mound and intermound lithologies (Fig. 20a, 21b). This lateral transition from mound to intermound facies is offset by encroachment of intermound lithofacies onto the mound at various stages during mound development. Overturned and slumped parts of the mound can be seen along the edge of the mound at the transition into the intermound facies and are sometimes covered by shale drapes.

All of the mounds are believed to have begun at the same stratigraphic level, the uppermost bedding surface of the Decatur Limestone. Most mounds also terminate at the same stratigraphic level, approximately 2.0 m above the Decatur-Rockhouse contact, where they are overlain by a 5-10 cm thick bed of shale. The bases of all of the mounds seen in the highwall exposures show a depression of bedding below the mound.

Mound Setting

Submound Lithofacies. The submound Decatur consists of pink, medium-bedded, sparsely glauconitic, echinodermal packstone and grainstone (Fig. 21a) that is traceable throughout the quarry exposure. Graded bedding and cross bedding are commonly observed in thin sections and outcrops.

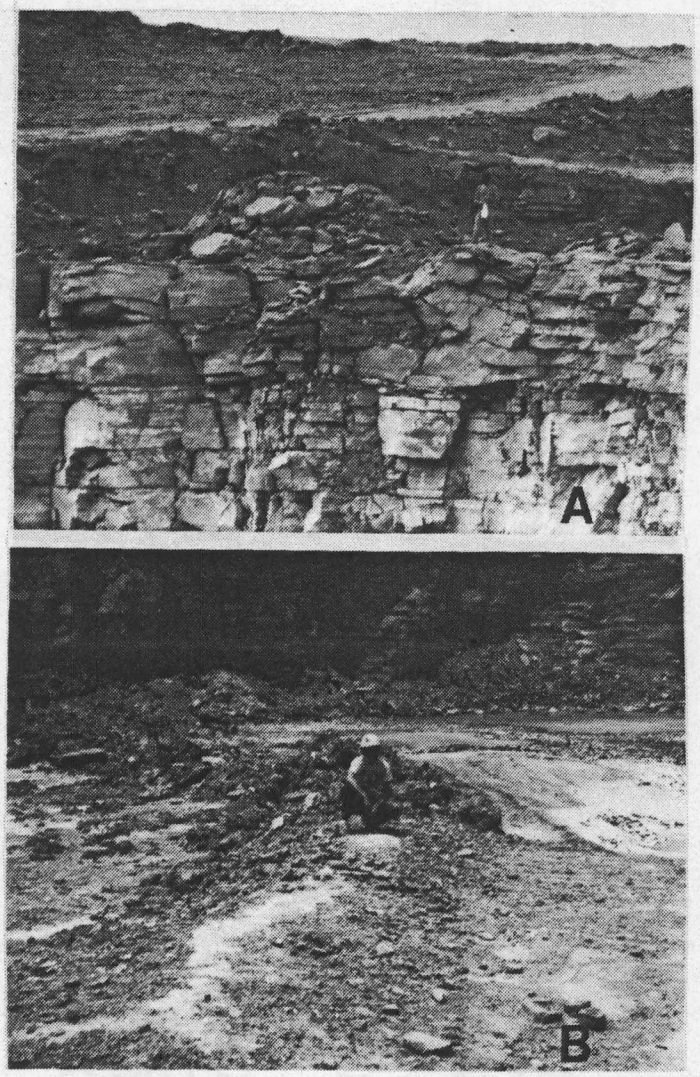


FIG. 20. Outcrop photographs of mudmounds. A. Distal end of a mudmound along highwall edge in the Rockhouse Limestone at Parsons Quarry. Note the depressed base, indistinct bedding within the mound relative to the intermound area, and the encroachment of intermound beds onto the mound causing a restriction in the width of the mound. B. Bedding plane view of the mound cored. Note the elongate nature of the mound crest.

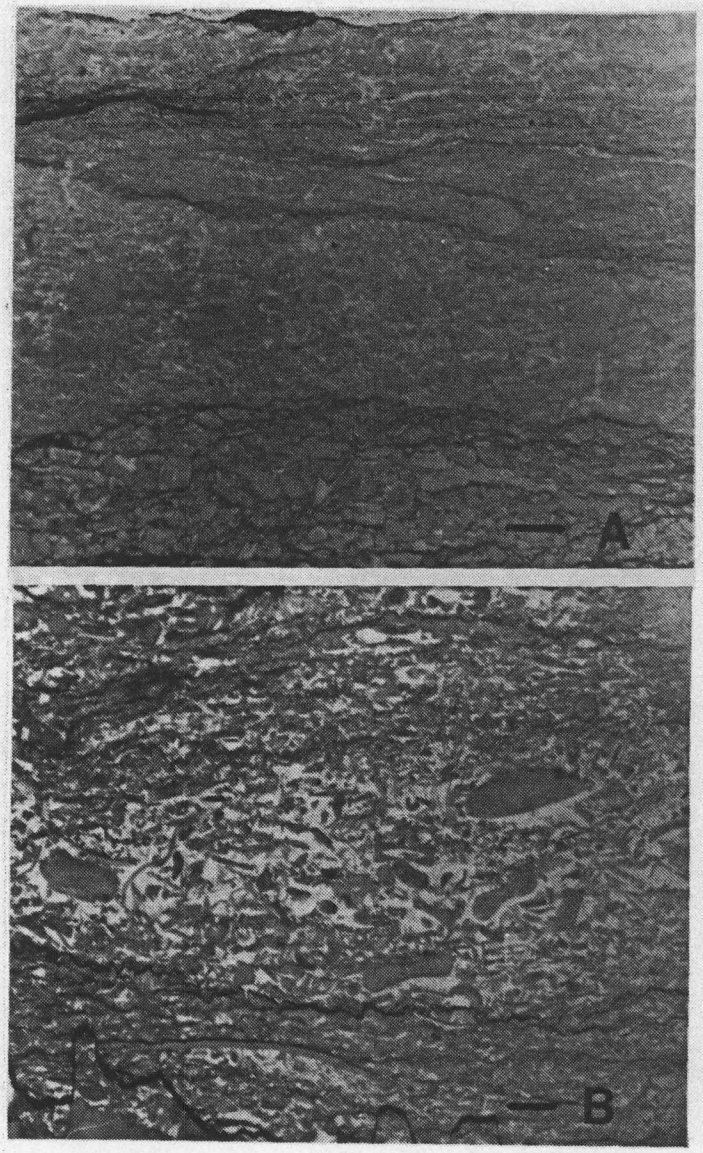


FIG. 21. Thin sections of submound and intermound lithologies. Bar scale = 3 mm. A. Contact between the echinoderm grainstone of the submound Decatur Limestone (lower portion of photo) and Phase I mudstone (upper portion) (PQC2-J). B. Intermound echinoderm grainstone of the Rockhouse Limestone (PQC1-B).

Intermound Lithofacies. The intermound material is gray skeletal packstone and grainstone containing small amounts of glauconite (Fig. 21b). The most common skeletal allochems are echinoderm debris (36-55%), cystoporate bryozoans (0-10%), cryptostome bryozoans (1-8%), and brachiopods (2-5%). Clear, equant spar cement ranges from 5% to 31%, carbonate mud ranges from 4% to 27%, and shale interbeds occur throughout. Both graded bedding and cross-bedding are common. Orientations of the scour features range from N45W to N55W (Fig. 18). Ripple marks with anastomosing crests are oriented approximately N5W. Scyphocrinites flotation bulbs are common on this surface (Fig. 18).

Mound Succession

Four distinct phases are recognizable from thin section data of the core (Fig. 19).

Phase I. The lowermost unit recognized within the mound (Phase I; Fig. 19, 22a) consists of an 8cm thick, greenish gray, echinoderm-rich terrigenous mudstone. Echinoderm fragments (35%) are broken (rather than simply disarticulated), angular, and bored (Fig. 22b) unlike those

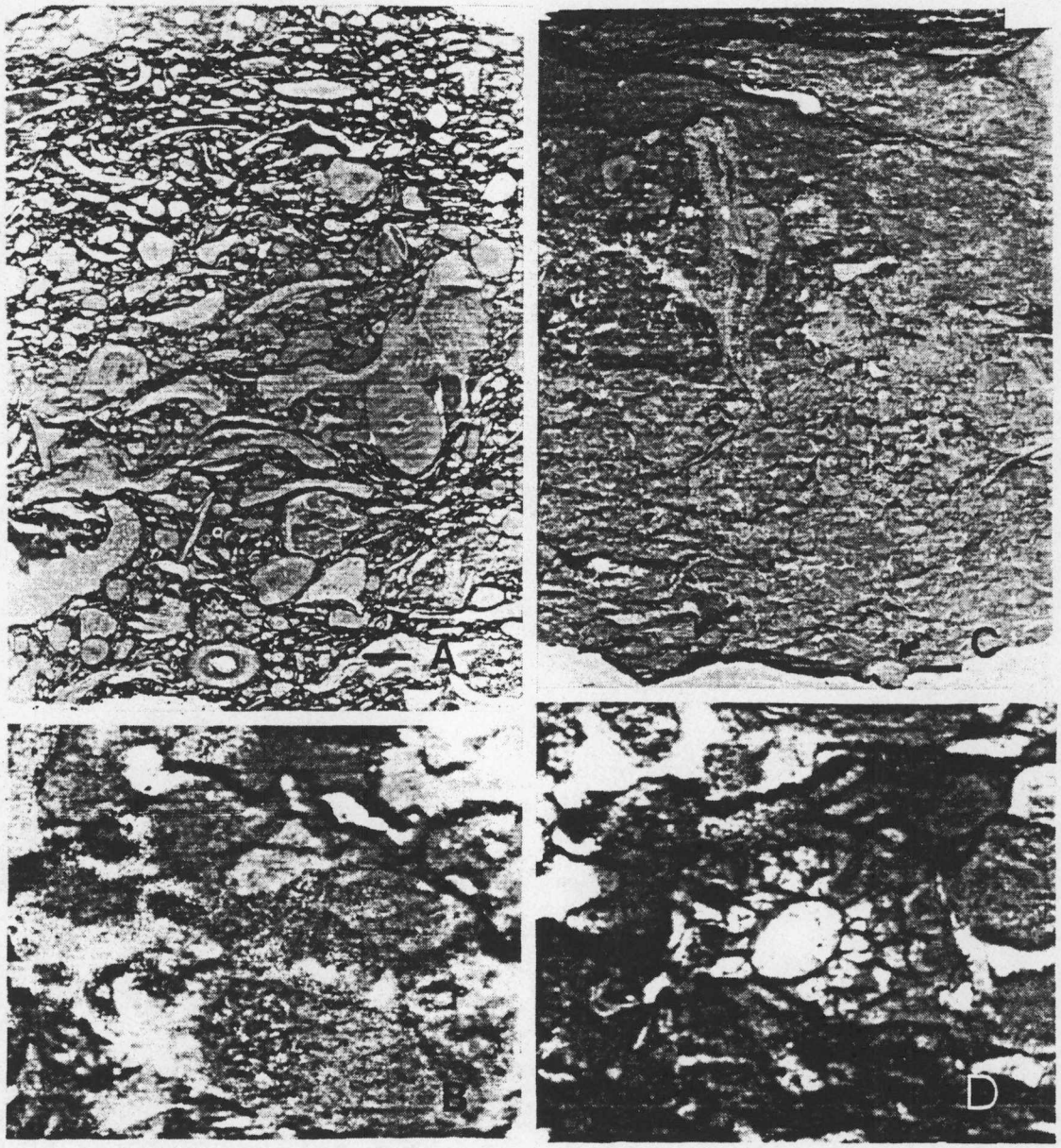


FIG. 22. Phases I and II of the mound. A. Thin section of the allochthonous terrigenous mudstone of Phase I (PQC1-I) showing graded bedding. Bar scale = 3 mm. B. Close-up of a crinoid ossicle from A showing heavily bored edges. Width of view = 1.5 mm. C. Vertical gradation of Phase II into intermound shale that draped onto mound (PQC2-F). Bar scale = 3 mm. D. Inset of C showing bryozoan encrusted cavity once occupied by alga. Diameter of cavity = 0.75 mm.

of the overlying strata within and adjacent to the mound and underlying strata of the Decatur Limestone. Fragments of once erect cryptostome bryozoans are the second most common constituent (9%). Other skeletal allochems include cystoporate bryozoan fragments (8%) and articulate brachiopod fragments (6%).

Compactional features such as intergranular pressure solution and grains broken in situ are common. The fossil allochems in the mudstone are graded to produce a fining-upward sequence, and rotated biogeopetal features (Clement, et al., 1987) are locally present. In core samples, Phase I only occurs under the mound (PQC 2) and is not traceable into the transition zone (PQC 3) or into the intermound area (PQC 1).

Phase II. Phase II consists of approximately 60 cm of gray echinoderm-bryozoan packstone (Fig. 22c). Echinoderm fragments (19% - 42%) are broken and angular but do not show bored surfaces like those of Phase I. The bryozoans consist mostly of fragmented cylindrical cryptostomes (10% - 11%) with some encrusting cystoporates (2% - 5%) and bifoliate cryptostomes (present, but not encountered in point counting). Cystoporates occur as encrustations on lithoclasts, voids once filled by algal tissue, and as flat, imbricated clasts. Brachiopod fragments are present

in small amounts (ranging up to 1%).

The amount of carbonate and terrigenous mud is much reduced relative to the underlying rocks of Phase I. Phase II consists of a series of fining-up sequences with shale draped surfaces separating individual sequences. Other structures include umbrella voids and bladed and equant calcite cement. Phase II grades vertically and laterally into the intermound lithology (Fig. 22c), but is distinguished from the latter by its lack of distinct bedding, greater bryozoan content, and greater mud content.

Phase III. Phase III consists of approximately 1.7 m of non-laminated, massive, greenish-gray, lime mudstone with the encrusting cystoporate bryozoan Buskopora being the dominant (11% - 20%) faunal element (Fig. 23a). Faunal diversity is lowest within this phase of the mound; other elements include echinoderm debris (5% - 6%), cryptostome bryozoans (up to 2%), brachiopods (less than 1%), and ostracodes (observed but not point counted). Buskopora colonies show highly contorted growth forms, commonly exhibiting growth directions toward the bottom of the mound. Commonly, influxes of mud interrupted the upward pattern of development of many colonies, which was later reestablished, resulting in an interbedded bryozoan-mudstone sequence (Fig. 23a).

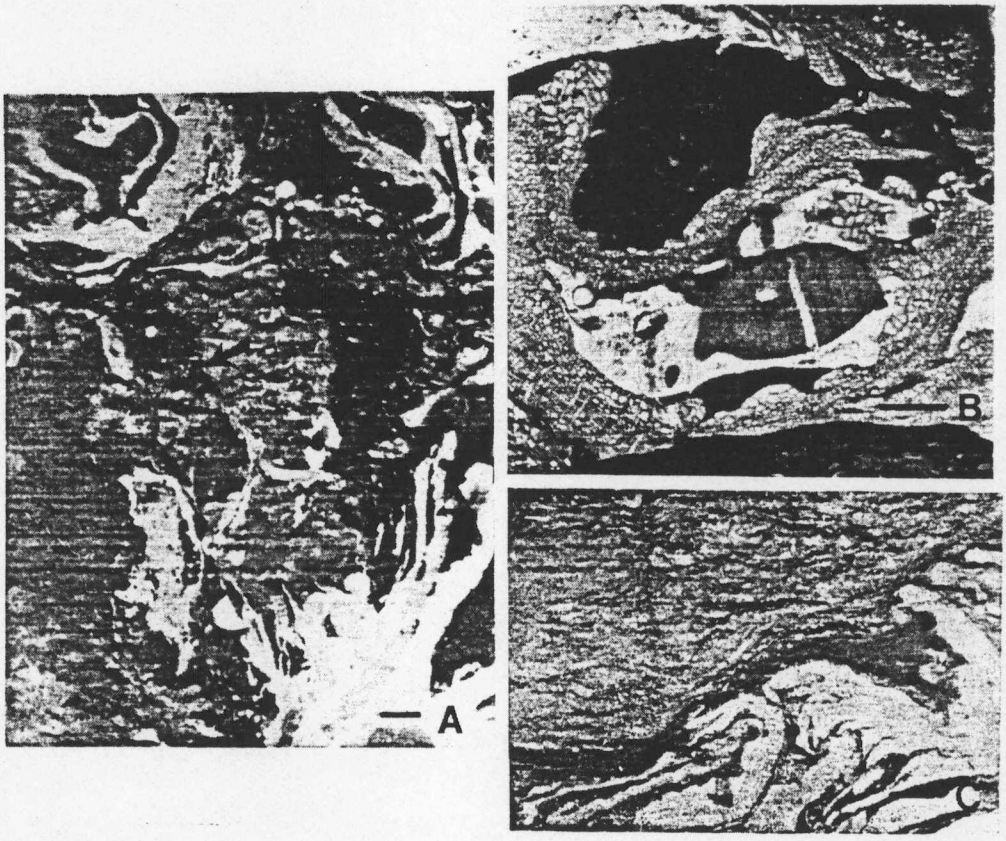


FIG. 23. Phases III of the mound. A. Thin section of PQC2-C showing the contorted nature of Buskopora growth. Bar scale = 3 mm. Large arrow points to a contact between two generations of mud. The darker colored mud is the first generation mud, whereas the lighter colored mud is a later generation. Small arrows point to Buskopora intergrowths on mud indicating syndepositional origin for much of the darker colored mud. Note the calcite-filled cavity with fragmented Buskopora colonies (bottom right of slide). B. Rare well developed stromatactis cavity lined by Buskopora with a crinoid holdfast encrusting the bryozoan. Bar scale = 5 mm. Note the smooth surfaced mud filling occuring in the bottom of the cavity and between the crinoid stolons suggesting syndepositional origin. C. Thin section from the edge of the mound showing intermound packstone interbeds and overturned Buskopora colonies with attached mud substrate (lower part of photo; PQC2-E). Bar scale = 3 mm.

Syndepositional cavities occur within the mudstone and are usually lined with coelobitic growths of Buskopora. Crinoid stoloniferous holdfasts are attached to the undersides of overhanging masses of Buskopora (Fig. 23b), and spar-cemented crinoidal debris occurs on the floors of cavities. Portions of Phase III occur as overturned or rotated blocks within intermound lithologies along the mound flanks (Fig. 23c). Locally, within this phase, colonies of Buskopora are broken as collapse fillings into cavities, where fragments of the colonies shelter voids.

The mudstone matrix consists of at least two generations of mud influx (Fig. 23a). The first generation contains fragments of bryozoan, echinoderm, brachiopod, and ostracode debris. It is usually darker gray than the second generation mud and locally exhibits a faintly clotted or laminar texture. This mud dominates the matrix and is bound by the colonies of Buskopora. The second generation of mud is less fossiliferous, usually lighter gray in color, and is most often observed perched on top of umbrella features or within cavities in the darker mud.

Phase IV. The final phase, Phase IV, consists of a gray echinoderm-bryozoan mudstone and wackestone (Fig. 24a) with packstone/grainstone lenses. This phase forms the top unit within the mound and is approximately 70 cm thick.

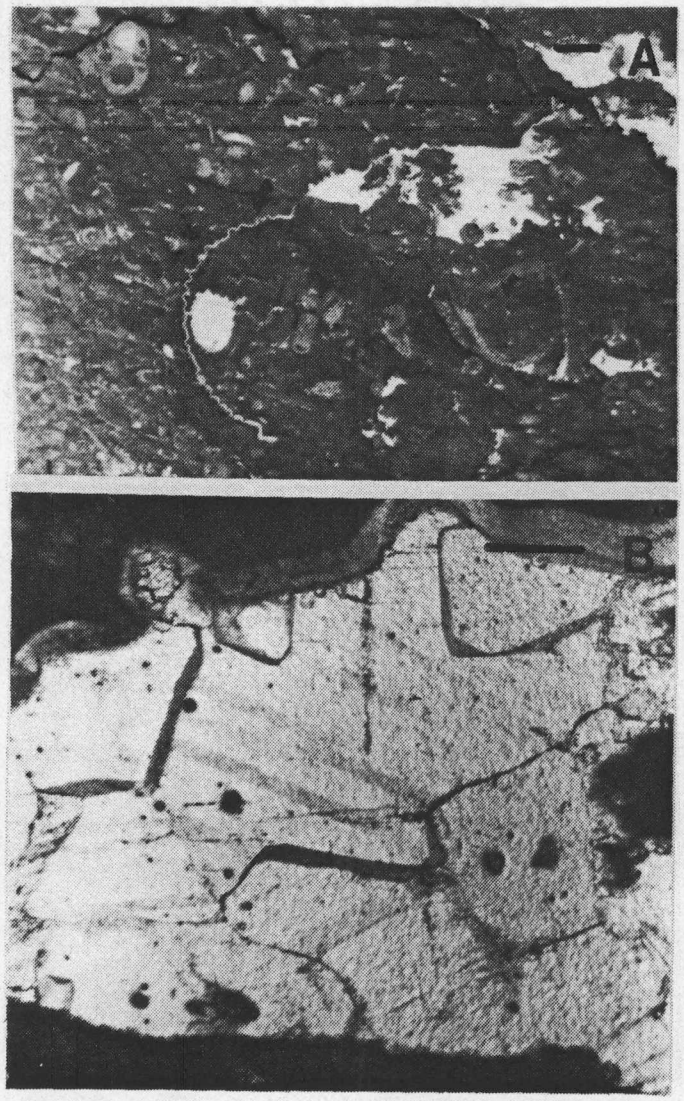


FIG. 24. Phase IV of the mound. A. Photomicrograph of the echinoderm-bryozoan mudstone/wackestone (PQC2-B). Note the fragmented trilobites (large arrows) and sponge spicules (small arrows). Bar scale = 3 mm. B. Enlargement of part of A showing trilobite shelter-void with spar cemented echinoderm debris in the bottom of the void. Bar scale = 0.5 mm.

Faunal diversity is significantly higher; the fauna consisting of echinoderms (10%), brachiopods (1% - 4%), cryptostome bryozoans (3% - 7%), Buskopora (1% - 3%), sponge spicules (up to 2%), and ostracodes and trilobites (observed but not encountered in thin sections).

The matrix seen in Phase IV samples largely consists of carbonate mud (65%) and void-filling spar (6% - 10%). Large patches of spar occur within umbrella voids that are sheltered mostly by skeletal fragments, including large trilobite exuviae (Fig. 24b).

Supra-mound Shale

Above the mudmound is a 5 to 10 cm thick, slightly fossiliferous, terrigenous mudstone that blankets the entire area. This unit is poorly exposed, usually is observed as small localized remnants on the surface of the bench, and normally is obscured by rubble along the base of the upper highwall. Above this mudstone, the upper part of the Rockhouse is dominantly an interbedded coarse-grained skeletal packstone and fossiliferous shale that becomes more shale-rich upsection, grading into the Birdsong Shale. The shale to limestone ratio increases upward, as does the thicknesses of the limestone beds. Other than bedding thickness, in general, the upper Rockhouse has the same

lithologic character as the intermound lithofacies of the lower Rockhouse (Broadhead et al., 1988).

Interpreted Sequence of Mound Development

The initial stages in the development of the mound are problematic. The overall depositional regime of the Decatur was a shallow subtidal, skeletal-rich carbonate shelf or bank that was maintained throughout its history in the zone of effective fairweather wave action (Reid, 1983; McComb, 1987). Thus, the skeletal sand deposits of the Decatur are relatively mud-poor due to current and wave activity. No features in the uppermost beds of the Decatur suggest environmental conditions that were appreciably different from those under which the lower part of the unit formed.

The base of each mudmound, as seen in outcrop cross section, exhibits a depressed lower surface, probably due to compaction subsequent to mound formation. Core PQC-2 contains the basal greenish gray skeletal-rich terrigenous mudstone (Phase I) that was not observed to extend into the surrounding intermound lithofacies (PQC 1, 3). This unit, however, may be more widespread than suggested by its distribution in the three cores, because Reid (1983) and Capaccioli (1987) reported a 5 to 10 cm shale bed at the

base of the Rockhouse elsewhere in Parsons Quarry and at Allan's Mill.

The mudstone of Phase I differs from other mud-rich lithologies within the Rockhouse by one or more of the following: (1) being terrigenous mud rather than carbonate mud, (2) containing broken and bored fossils, and (3) exhibiting graded bedding. These characteristics collectively indicate that the sediment of Phase I is allochthonous and probably resulted from massive, storm-generated influx of "old" skeletal debris and terrigenous mud. Under normal wave- or current-active conditions, this skeletal-rich mud would have been removed. However, a massive influx, such as that suggested here, that blanketed the area would most likely have been selectively removed, rather than being entirely stripped away. Storm-induced mud accumulations of this type have been noted by other workers on carbonate shelves during other times such as the Middle Ordovician of east Tennessee (Walker, 1974; Walker and Alberstadt, 1975) and the Middle Devonian of New York (Brett and Baird, 1985). Both of those types of mud incursions differ from that of the Rockhouse by not containing abundant skeletal material. Mud accumulations forming slightly elevated features relative to the surrounding seafloor or accumulating between stabilized megaripples of skeletal sand would

easily remain behind as isolated patches and be stabilized by algae and bacteria. Suspension feeding organisms could have colonized these patches, further stabilized them, and served as a sediment baffle.

The terrigenous mudstone was next covered by the skeletal sand of phase II. Graded bedding, shale drapes, and encrusted lithoclasts indicate a reworking of the Phase II sediment. The similarity of the fauna to that found in the overlying and adjacent lithologies and the lack of widespread breakage and boring suggests that many skeletal allochems were derived from the mudmound itself or the immediately surrounding seafloor. Although calcareous algae were not observed in thin sections, bryozoans encrusting spar- or micrite-filled circular cavities do occur (Fig. 22d, p.84). The cavities may have originally been uncalcified algae that decayed, leaving voids that later filled with mud or spar.

This phase represented the initial stabilization and patchy colonization phases of mound development (Alberstadt et al., 1974; Walker and Alberstadt, 1975). A mixture of hypoautochthonous skeletal debris and in situ organisms would have been present on the surface of the mound during Phase II. Much of the accumulation of skeletal sediment was probably strictly hydrodynamic (sensu Heckel, 1974), but the biota of the mound contributed both to the

accumulation of skeletal debris and, to a less obvious degree, to binding of the mound sediment. The mound at this point was higher than the surrounding areas. It was probably subject to gentle flushing by passing currents leading to enhanced marine cementation relative to the surrounding sediment (K.R. Walker, pers. comm., 1986). In contrast, the abundance of clear equant calcite cement in the intermound area suggests that this sediment did not lithify early (Broadhead et al., 1988). At this point, biotic diversity (assumed to be indicative of the indigenous biota) is relatively high in comparison to that of Phase III, but not as high as that of Phase IV.

During this portion of mound development, the amount of control the mound fauna exerted in the form of baffling and binding was not as great as in Phase III. The variety of organisms observed suggests that the developing mound presented surfaces on which a wide range of larvae could settle, and hydrodynamic conditions on and around the mound promoted the colonization by many types of sessile, suspension feeding organisms. The cystoporate bryozoan Buskopora first appears during this phase of mound development as fragmented parts of colonies. Rotated blocks of Buskopora with mud substrate attached further indicates that early cementation played an important role in stabilizing portions of the mound (Fig. 23c). Rapid

colonization of the sediment surface by Buskopora still further stabilized the sediment on the mound. During the earliest stages of Phase II colonization, hydrodynamic influences and localized substrate differences remained the controlling factor. By the end of Phase II, Buskopora encrustation had stabilized a large portion of the surface of the mound and may also have excluded most other suspension feeding organisms by virtue of its more rapid colony propogation. Periodically, influxes of terrigenous mud left accumulations in the surrounding intermound area but also encroached and covered portions of the mound, probably causing widespread mortality of mound inhabitants (see, e.g., the shale drape in Fig. 22, p. 84).

Phase III is the thickest part of the mound and the most distinctive of the four basic mound lithologies. It is dominated by Buskopora, which formed large and contorted encrusting masses on the carbonate mud substrate. This represents the domination phase of reef development (Walker and Alberstadt, 1975) in that the mound consists of a boundstone with relatively low species diversity and a clearly dominant organism, which is also an encrusting coelobite.

This phase of mound development is considered to be completely autochthonous. The carbonate mud matrix probably resulted from the in situ production of

fine-grained material by algae (the algae themselves are, however, not preserved), and stands in sharp contrast to associated intermound carbonate sediment, which continued to be well-washed skeletal sand. Tsien (1985a) cites (1) clotted or patched texture, (2) curved laminae, (3) spongy structure, (4) vague internal banding or zonation, (5) porcelaneous milky aspect, (6) variations in color, skeletal debris content and distribution, and (7) preservation of algal filaments as evidence for biogenic micrite and mud binding in Devonian mudmounds in Belgium. The mounds at Parsons Quarry exhibit the rare clotted texture, faint discontinuous vague banding locally, and variations in the color, skeletal debris content, and skeletal debris distribution.

Recognizable fossils considered to have been indigenous to Phase III include well-preserved, but small numbers of brachiopods, crinoids, ramose bryozoans, and other groups that were not completely preempted by Buskopora colonies for attachment sites on the mound surface. Encrusting colonies of Buskopora served a dual role as the predominant sediment binder and as coelobites within cavities. There probably was little influx of allochthonous skeletal debris, except as broken or disarticulated fragments trapped in the mud matrix, in

contrast to the abundant influx characteristic of Phase II deposition.

The cavity-rich nature of the upper portion of Phase III is indicated by primary void space (observed vertical height up to 3 cm) partly filled by encrustations of Buskopora and crinoid holdfasts (Fig. 23b, p. 87). Similar voids in the lower part of Phase III have been completely infilled with mud and debris. These cavity fills, however, are not the typical stromatactis of previously described Silurian and Devonian mudmounds (Burchette, 1981; Longman, 1981; Wilson, 1975; Wallace, 1987).

Stromatactis structures are masses of spar with smooth, usually mud-filled bases with digitate roofs and generally exhibit a reticulate pattern of development (Bathurst, 1980; Wallace, 1987). Most of the cavities in Phase III of the Parsons mounds are more irregular in shape, rather than reticulate, and are lined with bryozoan coelobites. Also, the Parsons mounds rarely exhibit the smooth floor and digitate roof pattern except in the uppermost part of Phase III.

It is possible, however, that the Parsons mounds shared a similar process for the early stage development of cavities to that associated with stromatactis in other Devonian mudmounds. The bryozoans clearly inhabited the cavities during their formation as exhibited by the

completely lined nature of many cavities, collapsed cavities with bryozoan debris in the bottoms of the cavities, and re-encrusted pendent micrite that covers some Buskopora colonies. These characteristics, along with the suspected presence of algae and bacteria, suggest a combination of coexisting inorganic and organic processes for the origin of the cavities of Phase III. The inorganic phase of formation was probably current scouring of less-well cemented mud (Bathurst, 1980, 1982; Burchette, 1981; Tsien, 1985b). The organic phase involved binding of the sediment by Buskopora and probably also by algae similar to the process described by Textoris and Carozzi (1964; binding by bryozoans and algae) or by Bourque and Gignac (1983; binding by sponges).

Wallace (1987) described stromatactic cavity development in the Rocky Camp Limestone (Lower Devonian) of eastern Victoria that resulted from a multi-step process of precursor erosion to form a cavity system and the redeposition of the mud to fill the cavities. This process created a series of upward progressing cavity systems in which the lower portions of the cavities became infilled with sediment, while the upper portions remained open. This resembles the Parsons mounds in that the greatest remnant cavity development, as indicated by spar filling, occurs in the upper portions of Phase III with more

sediment fill in the lower portions. The Parsons mounds differ, however, in that this process of cavity development occurs only within Phase III and halted by the time of Phase IV deposition.

Phase IV represents a deviation from the normal stabilization - colonization - diversification - domination sequence in reef development (Walker and Alberstadt, 1975). The domination stage of Phase III is succeeded by a breakdown in succession and a rediversification of the biota. Also, the completely autochthonous boundstone nature of the mound gives way to interbedded autochthonous echinoderm-bryozoan mudstone and packstone containing lenses of hypoautochthonous packstone and grainstone. This indicates a change in the biotic and physical structure of the mound reflecting less favorable environmental conditions for Buskopora that probably included an increase in water energy.

As already noted above, the Rockhouse Member is an interbedded carbonate-terrigenous sequence. The position at which Phase IV occurs coincides with the level at which the amount of terrigenous influx increases dramatically. Small mud drapes commonly extended onto the mound surface, severely limiting the development of low-lying sessile invertebrates, such as Buskopora colonies. This phase represents an ecological response, as reflected in

paleocommunity characteristics and paleocommunity development, to changing environmental conditions which basically returned the mound to an earlier stage of mound development that is similar, but not identical, to Phase II (community regression of Johnson, 1972).

The demise of the mound biota and end of mound growth was caused by the massive influx of terrigenous mud represented by the 5 to 10 cm thick shale that blankets the entire mound field. This type of episodic influx became a common feature in deposition of the remainder of the Rockhouse. Presumably these shale beds represent storm-mobilized sediment transported into the study area. They are probably similar in origin to that described for the basal terrigenous mudstone of Phase I. However, these shales usually differ significantly from Phase I by containing fewer but better preserved fossils.

Discussion

The cystoporate bryozoan-dominated mudmounds described here represent a significant type of buildup different from buildups usually encountered in other Lower Devonian rocks (Burchette, 1981; Longman, 1981). Small fistuloporid-dominated mudmounds have been described from the Silurian Rochester Shale of New York (Sarle, 1901; Hewitt and Cuffey, 1985), from the Silurian of Indiana

(Textoris and Carozzi, 1964), and from the Keyser Limestone of Pennsylvania (Cuffey et al., 1986), but these differ from the Parsons mounds in several ways. The Parsons mounds are much smaller in size than the Indiana mounds and did not develop in a dominantly quiet water, mud-rich environment of deposition, hence they are not encased in shale. These mounds also do not contain pervasive stromatactis structures, although analogous coelobite encrusted cavities are present during one stage of the mudmound. The fauna of the Parsons mounds consists predominantly of cystoporate bryozoans and crinoids as sediment binders and coelobites rather than being dominated by a stromatoporoid-coral assemblage. Bryozoans are generally considered an accessory element in most Paleozoic buildups (Cuffy, 1977; Cuffey and McKinney, 1979). However, Lees (1974), Textoris and Carozzi (1964), and Walker and Ferrigno (1973) have demonstrated that bryozoans, especially encrusting bryozoans, can be important components in carbonate buildups.

The Parsons mounds are also significant in that they offer an opportunity to view their three dimensional distribution. They represented a local development of topographically low buildups in which the binding organisms exerted sufficient control over the surrounding seafloor that the mounds grew upward with little lateral migration.

Mound growth did respond to the prevailing current direction by developing an elongate profile with the highest topographic development apparently being in the offshore direction as is typical of modern reefs. These patterns should prove useful in reconstructing their paleogeographic position at the time of mound development (Gibson et al., 1986).

The stable upward growth is surprising considering the presence of a relatively high energy regime indicated by the intermound lithofacies, and that the mounds lacked an abundance of "rigid" framework organisms. Early lithification of the mudmound sediment relative to the surrounding seafloor is indicated by the following relationships: (1) two generations of mud, (2) rotated and overturned Phase III blocks with attached substrate, (3) clotted textures in the mud matrix, (4) Buskopora and crinoid coelobites, (5) stromatactic development in the upper portions of Phase III, and (6) the stationary vertical development of the mudmounds. The early lithification probably resulted from algal binding, micrite cementation, and bryozoan binding as no other early cement is evident. The predominantly organic processes were responsible for initially stabilizing the muddy patches on the Decatur seafloor as well as maintaining the mud-rich subenvironment on the mudmounds. Without early

lithification, the mud of Phase I would probably have been removed by wave and current activity.

This type of synsedimentary substrate modification (sensu Walker and Diehl, 1985, 1986) is important because it can retard transportation and mixing effects (i.e. dampen hydrodynamic destruction) and facilitate biotic colonization and succession. Changes in sediment consistency, changes in substrate surface caused by colonization, and early lithification by cementation, or in this case, by algal binding, to produce patchy firmgrounds, contributed to the formation of the Parsons mounds. It is possible that this type of synsedimentary substrate modification is responsible for many of the smaller mudmounds described by other workers in moderate to high energy environments.

Lastly, these mudmounds contain organisms that not only lived on the mound surface and helped to maintain it in a current swept environment, but also encrusted cavities within the mounds. Although coelobites have been recognized as important in some modern environments, mostly under coral rubble (Ginsburg and Schroeder, 1973; Ginsburg and James, 1974; Choi and Ginsburg, 1983; Choi, 1985; Kobluk and Lysenko, 1987), their ecological role in Paleozoic buildups has been virtually unrecognized. The duality of roles played by Buskopora as both a sediment

binder and as a coelobite emphasizes the unique nature of the Parsons mudmounds. This appears to be the first time that an encrusting coelobite has been reported to be the dominant in a successional sequence as well as contributing to the primary "framework" growth of Paleozoic buildups.

Birdsong Shale Member

Purpose

The Birdsong Shale represents a period of time on the Ross Shelf characterized by a mixed carbonate-gray shale sequence. Although the fauna of the Birdsong has been collected for taxonomic study, paleodepositional studies have remained wanting. This sequence is abundantly fossiliferous and the fauna exhibits evidence of having inhabited both the muddy soft substrates represented by the shale and the coarser substrate represented by the limestones (Broadhead and Gibson, 1986). More importantly, the depositional setting promoted the development of a diverse epibiont-rich fauna that rivals the well known Silica Shale (Middle Devonian, Ohio) in epibiont content (Broadhead and Gibson, 1986). A more complete review of the previous studies of deposition in the Birdsong is given in Chapter 1.

The purpose of study of the Birdsong is to determine

the depositional history of this unit, especially the fossiliferous and epibiont-rich shales, within the context of the paleogeographic reconstruction of the Ross Shelf presented in Chapter 2. Emphasis is placed on the local sedimentary processes active during deposition of the Birdsong. The resulting depositional model will then be used to evaluate the faunal adaptations and biotic interactions represented in the epibiont-rich fauna and the environmental factors that influenced these interactions (see Chapter 4).

Methods

Rocks belonging to the Birdsong Shale were studied at two locations, McClanahan and Elkin's quarries (Fig. 1, p. 3). Bed-by-bed sampling of both the limestone and shale beds was made at McClanahan's Quarry (Appendix A, Fig. 25). The complete measured section consists of three offset sections along the highwall exposure. One sample was collected for each bed except in thick beds, where samples were collected at the top and bottom or top, middle and bottom depending on the thickness of the bed. Sixty-eight samples were collected from which 5 x 7.5 cm thin sections were prepared for 60. The combined potassium ferricyanide and alizarine red S staining technique described by Dickson (1965) was used to test for ferroan

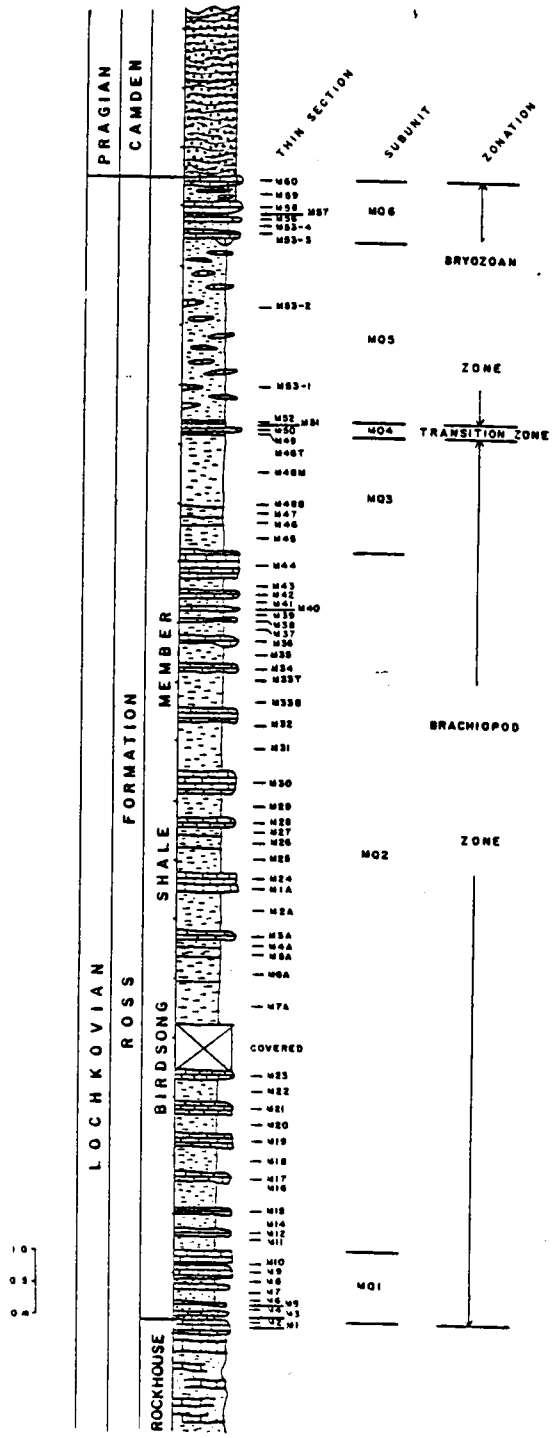


FIG. 25. Measured section at McClanahan's Quarry.

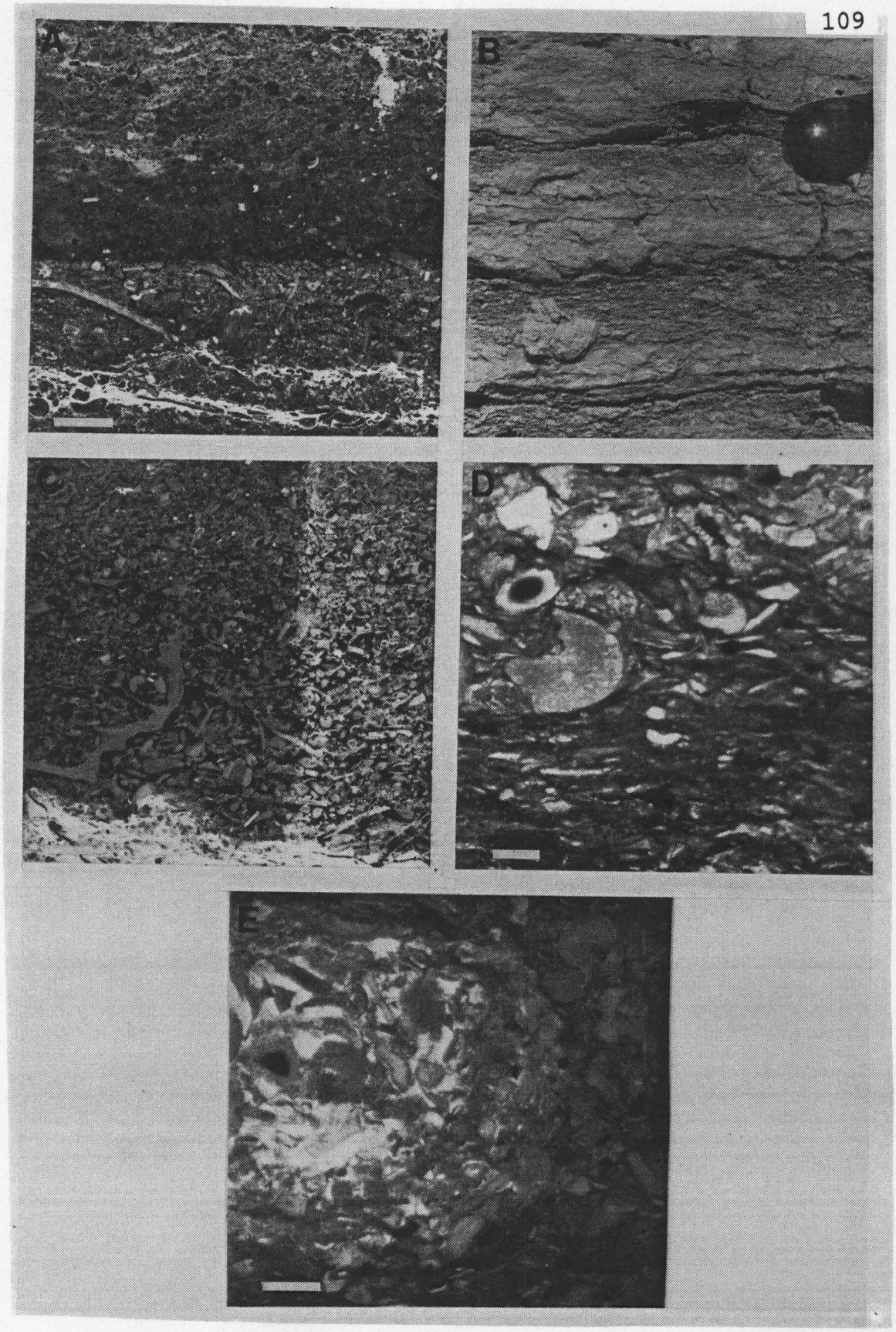
cements. Each thin section was point counted using 300 counts per slide (Appendix B). .Petrographic analysis resulted in the recognition of seven lithotypes in the Birdsong and one additional lithotype in the uppermost Rockhouse at McClanahan's Quarry.

Bed-by-bed collecting was not possible at Elkins Quarry due to the inaccessable nature of the highwall exposure; however, the quarry floor contains spoil and slump blocks of the Birdsong lithologies. The stratigraphic position of these blocks in the highwall was determined using bedding thickness, sequence of bedding occurrence, and weathering characteristics. The weathered nature of these spoil blocks made bedding-plane grid counting of the fauna possible. The section was measured by extending a tape down the highwall to measure the thickness of individual beds.

Lithotypes

Lithotype A. Lithotype A (thin section M1) is a thin- to medium-bedded, coarse-grained, echinodermal grainstone that fines upward to a thin- to medium-bedded, medium-grained echinodermal packstone (Fig. 26a). Glauconite-infilled echinoderm plates are common as is

FIG. 26. Lithotypes A and B. Stratigraphic up is to top of page. A. Photonegative of Lithotype A, echinodermal grainstone to packstone (M1) showing fining-upwards sequences and shale drape. Bar scale = 5.0 mm. B. Outcrop of Lithotype B showing repeated limestone-shale couplets. Note sharp lower contacts of limestone beds and more gradational limestone to shale contacts. C. Photonegative of Lithotype B (M13). Bar scale = 7.0 mm. Note sharp erosive contact with underlying shale, fining upwards bedding, shale drapes at top. D. Photomicrograph of shale to packstone transition in Lithotype B (M3). Bar scale = 1.0 mm. Note bedding parallel nature of allochems in shale, poor sorting and non-random orientations of allochems in packstone. E. Uncollapsed, spar-filled burrow in Lithotype B (M3). Bar scale = 1.0 mm.


A
B
C
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E

some silica replacement of echinoderm plates. Disarticulated, moderately abraded echinoderm plates are the dominant allochem (53%, total rock volume) and exhibit extensive clear syntaxial overgrowths (11%), with lesser amounts of drusy mosaic to equant interparticulate calcite cement (3%). This lithotype forms the last major limestone bed of the Rockhouse Limestone and is absent in the Birdsong Shale.

Lithotype A is interpreted to represent well-washed, skeletal sand reworked by moderate-energy current or storm activity which removed most of the mud. The waning of the scouring event produced the fining-up sequence, which also becomes more muddy upward. This lithotype is, in part, equivalent to Reid's (1983) subunit 4, which she noted showed considerable lateral variation from Parson's Quarry (wackestone) to Benton Quarry (grainstone) to Allan's Mill (packstone).

Lithotype B. Lithotype B (thin sections M3, 5, 11, 13, 19, 28) consists of fining-upward, medium- to coarse-grained, echinodermal and brachiopod grainstone to packstone with shale drapes at the tops of the fining upward sequences (Fig. 26b, c). This lithotype is thin-bedded with a succession of fining upward sequences (1-3 cm thick) capped by shale drapes that show irregular

gradational lower contacts and sharp, erosional upper contacts. The frequency of occurrence of shale drapes increases upsection. The basal portions of lithotype B begin either as grainstone (similar to lithotype A) or as packstone (Fig. 26d). Carbonate and terrigenous mud content increases upward in each fining-upward cycle. Well-developed, shell-filled and spar-cemented, horizontal burrows are common, and show little evidence of compaction, suggesting early lithification (Fig. 26e). Umbrella voids with perched sediment are also common. The grainstone beds generally overlie and are interbedded with terrigenous mudstone to green fissile fossiliferous shale (of lithotypes D, E, and F) with a relatively sharp, wavy contact that shows evidence of erosion (Fig. 26c). Upper contacts are more gradational and sometimes display slightly rippled surfaces. The fauna of lithotype B is identical to the fauna in the surrounding terrigenous rocks, only grain size differs.

Lithotype B is interpreted to represent storm winnowed distal "tempestites" like those described by Kreisa (1981), Aigner (1982, 1985), and Walker (1985). Passing storm waves or currents scoured the mud substrate, placing the mud into suspension and transporting it out of the immediate area, while the coarser bioclastic grains resettled in a graded fashion as the energy of the storm

waned. The idealized "tempestite" described by Aigner (1982), shown in figure 27, ranges in thickness from a few centimeters to a few decimeters. Individual beds have a basal contact that is sharp and erosive and are internally graded by either lithoclasts or bioclasts. Beds contain a basal shell lag that grades upward to laminated calcilutites. Bioclasts are typically imbricated, edgewise, or convex-down, but, in general, non bedding-parallel orientations dominate. The tops of individual beds occur either as gradations into the overlying shale, hardgrounds, or wave ripples.

The Birdsong Shale event beds closely resemble Aigner's (1985) descriptions, but all of the bedforms are not present, especially many of the upper bedforms. Repetitious fining upward sequences suggest repeated events with each succeeding event partially eroding the upper portions of the previous event.

Lithotype C. Lithotypes C, D, and E represent an intergrading continuum that is mutually interbedded and interbedded with other lithotypes (Fig. 28). Lithotype C (thin sections M8, 14, 20, 22, 31, 33B, 33T, 35, and 37) is a thin- to medium-bedded, fossiliferous, dark green, fissile shale. Fossils consist of very finely comminuted echinodermal and brachiopod debris; however, large

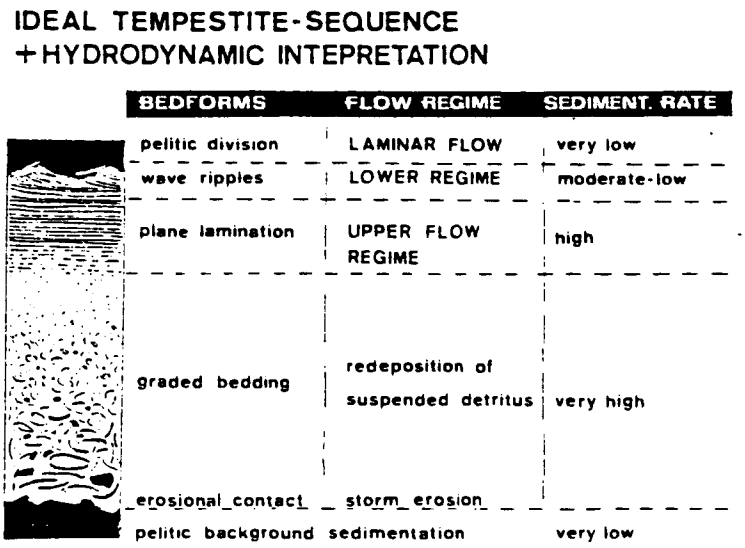
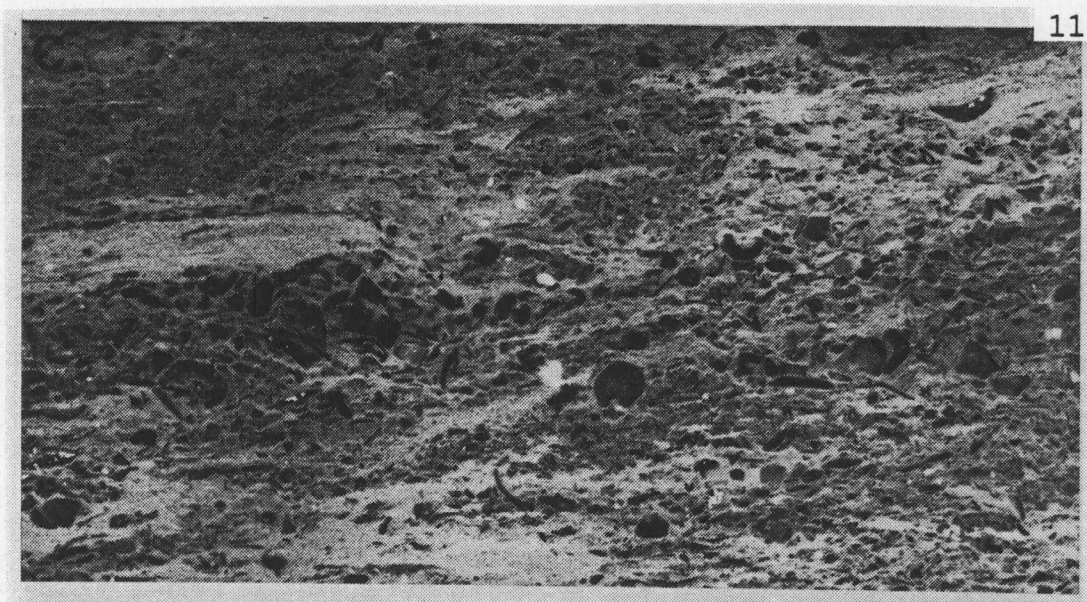
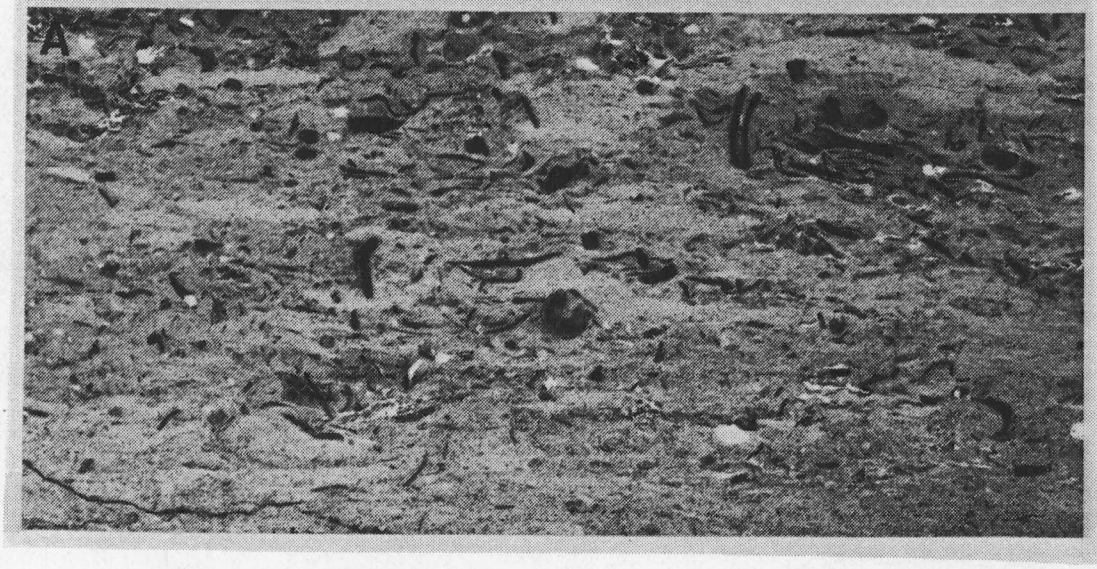


Fig. 27. Idealized tempestite sequence. Graded beds result from the winnowing of fine-grained material by passing currents during high energy events (from Aigner, 1982).

Fig. 28. Continuum of lithotypes C, D, and E. Field of view = 4 cm in all photonegatives. Stratigraphic up to the top of the page A. Fossiliferous shale of Lithotype C (M37) showing compacted burrows and finely comminuted debris in matrix. B. Shaly mudstone of Lithotype D (M26) showing overturned articulated Atrypa. C. Echinodermal packstone of lithotype E (M9) with shaly partings and poor to moderate sorting.




B

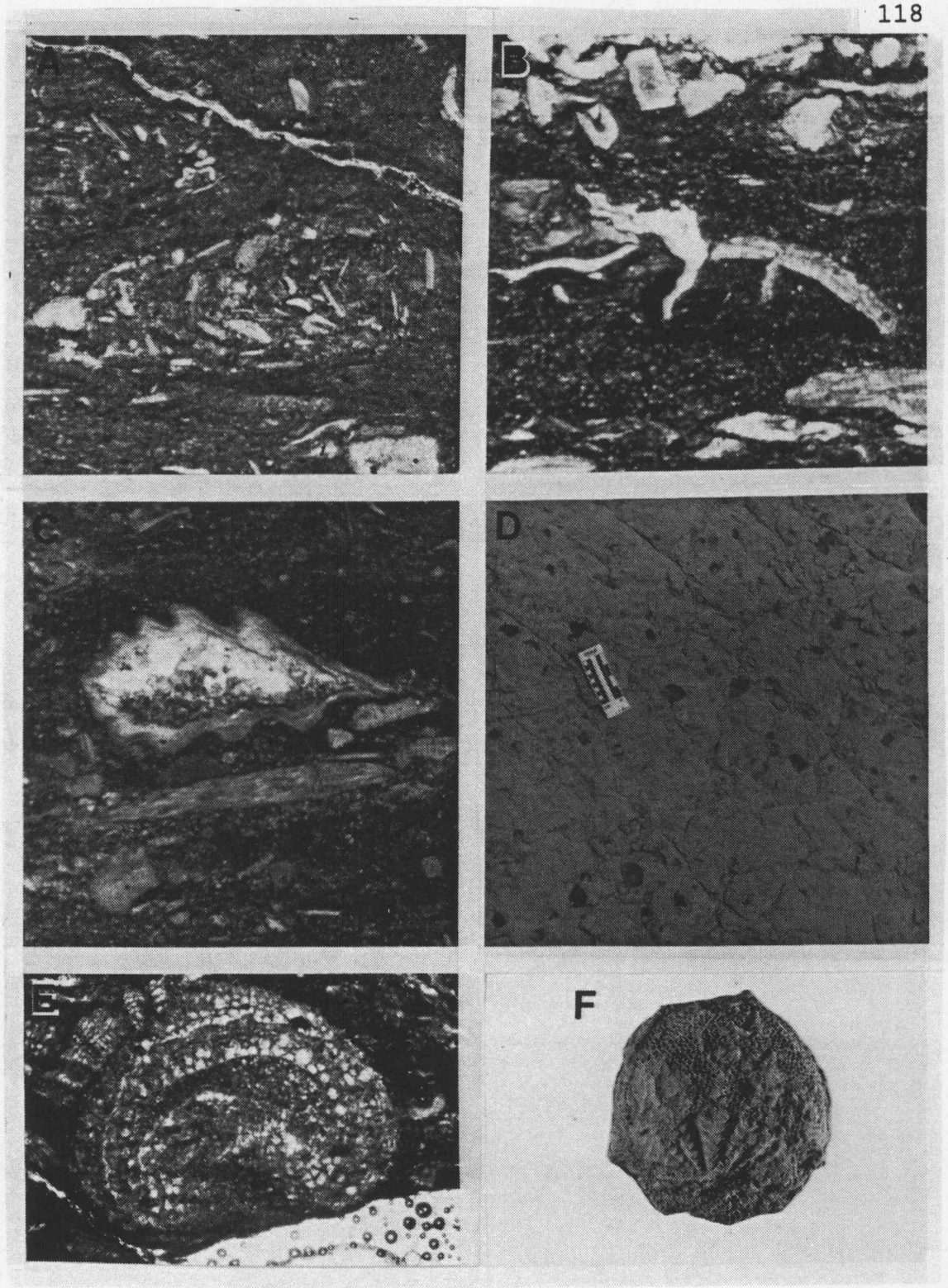

A

disarticulated and articulated mud-filled brachiopods also occur (Fig. 29c), making this lithotype poorly to moderately sorted. Orientations of valves range from completely random to bedding parallel. The shale is extensively burrowed. Burrows appear lense-shaped in transverse section, dark brown, compacted to diffuse, and exhibit a swirled fabric (Fig. 29a). Epibiont encrusted brachiopods are common.

The compacted nature of the diffuse burrows and fractured allochems (Fig. 29b) suggest extensive sediment compaction while the mud was still soft. Mixed burrow types (swirled textures to diffuse burrows) and overturned fossils suggest that this lithotype underwent dewatering, probably due to bioturbation, and sediment firming.

Lithotype D. Lithotype D (thin sections M7, 23, 26, 27, 32, 45, 46, 47, 48M, and 48T) is a fossiliferous terrigenous mudstone to shaly mudstone (Fig. 28b). It is dominated by echinoderms and brachiopods in the lower Birdsong sections, but becomes more bryozoan-rich in the upper Birdsong sections (as do all of the other lithotypes). This lithotype is similar to lithotype C in all other respects, except that it is the more massive endmember and contains a greater percentage of spar-filled articulated brachiopods.

Fig. 29. Features of lithotypes C and D. Stratigraphic up to the top of the page. A. Photomicrograph of compacted debris-filled burrow in Lithotype C (M27). Long diameter of burrow = 4 mm. B. Photomicrograph of fractured brachiopod fragments (M6B) in lithotype C. Bar scale = 0.5 mm. C. Geopetal infill in articulated brachiopod in lithotype C (M15). Brachiopod is 3 mm in diameter. D. Field photograph from Elkins Quarry showing bedding surface of Leptostrophia beckii (thanatocoenose) from Lithotype D. E. Photomicrograph of circumrotatory cystoporate bryozoan from Lithotype D (M59). Diameter of bryozoan = 4 mm. F. Circumrotatory bryozoan from Lithotype D showing the brachiopod Kozlowskiellina that served as the nucleus for bryozoan growth (X 1.5).

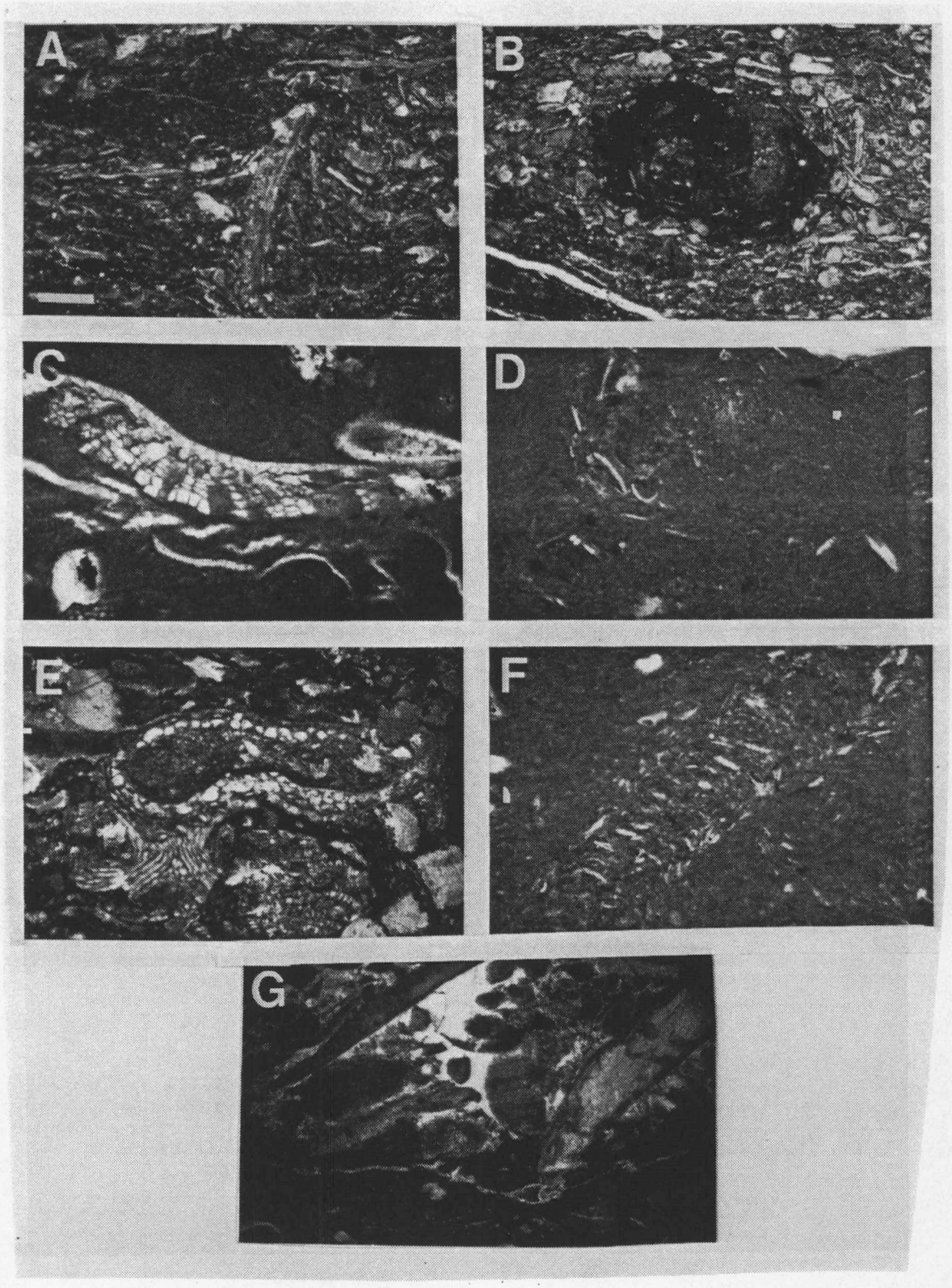

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The interval represented by thin sections M45 through M48 shows evidence of well developed mud firmgrounds. This interval contains: (1) circumrotatory bryozoans that grew by periodically rolling on the seafloor as zooids were added (Fig. 29e, f), (2) soft substrate, thin shelled brachiopods, such as Leptostrophia (Fig. 29d), and indistinct burrows mixed with pedunculate and heavy-umbo brachiopods and arborescent bryozoans, and (3) ripple-form lenses of abraided and rounded debris belonging to all types of fauna.

Lithotype E. Lithotype E (thin sections M9, 15, 6B, and 48B) is a fossiliferous echinodermal wackestone to packstone with thin- to medium-bedded shale interbeds and shale partings (Fig. 28c). This lithotype is highly variable in appearance with discontinuous zones rich in shale interbedded with packstone-rich zones that fine slightly upwards (Fig. 30a). Grain size ranges from fine to coarse and is poorly to moderately sorted. This lithotype represents the coarse-grained, less muddy endmember of the continuum (Fig. 28). This lithotype matches the descriptions of subunit 6 of Reid (1983) and occurs at the same stratigraphic level.

Lithotypes C-E are interpreted to represent the normal muddy bottom sediment of the Birdsong. The ultimate source

Fig. 30. Features of lithotypes E, F, G, and H. Stratigraphic up to the top of the page. A. Photomicrograph of gradational contact between fossiliferous shale and wackestone of Lithotype E (M9). Bar scale = 1 mm. B. Photomicrograph of burrow in Lithotype E. Note mud infill, coarse-grained allochem burrow wall and swirled nature of burrow infill. Diameter of burrow = 3 mm. C. Photomicrograph of calcareous mudstone to wackestone of lithotype F (M10). Note encrusting cystoporate bryozoan on brachiopods. Field of view = 6 mm. D. Photomicrograph of calcareous mudstone of Lithotype F with diffuse burrow swirls and randomly oriented debris (M10). Field of view = 6 mm. E. Photomicrograph of bryozoan packstone of Lithotype G (M53). Note circumrotatory cystoporate encrusting mud lithoclast and Ptylodictya base encrusting the cystoporate. Encrusted clast = 4 mm. F. Photomicrograph of skeletal-infilled burrow in Lithotype G calcareous mudstone. Field of view = 6mm. G. Photomicrograph of sharp erosive contact between shale and fining-upwards echinoderm packstone to grainstone of Lithotype H (M58). Field of view = 6 mm.


A
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G

of the terrigenous mud is problematic, especially because the surrounding land areas were not contributing great amounts of sediment to the western Tennessee area during the Early Devonian (Buschbach, 1986; Schwalb, 1983); however, the paleogeographic setting of the Ross Shelf in the western storm track system (see Chapter Two) suggests transport of the mud onto the shelf from the south. Subsequent storm activity continually winnowed and suspended mud which was then redistributed, along with finer-grained bioclastic debris. Lithotypes B-E produce the interbedded limestone-shale beds, which should be viewed as couplets in that they are genetically related. Periodic firming of the mud substrate produced a fine-grained equivalent to firm- or hardgrounds (Fig. 30b). The substrate was then periodically smothered by new incursions of mud, which were then recolonized by fauna and underwent compaction processes.

Lithotype F. Lithotype F (thin sections M10, 18, 24, 30, 38, and 44) is an echinodermal calcareous mudstone to wackestone with shale drapes. The rocks are very thin-bedded to thin-bedded and fine-upwards in 2-4 cm thick cycles. Mud content increases upward in each cycle. Concave-up disarticulated fossils are common and mostly bedding parallel (Fig. 30c). Umbrella voids and infilled

geopetal structures occur as do horizontal and vertical burrows that give the bed a mottled appearance (Fig. 30d).

Lithotype F is interpreted as a carbonate-rich counterpart to lithotype D, in which less terrigenous mud accumulated. Reid (1983) recognized this lithotype also (part of her subunits 6, 8, and 9).

Lithotype G. Lithotype G (thin sections 49, 50, 51, 52, 53#3, and 53#4) is best developed in the upper Birdsong. It consists of very thin-bedded, bryozoan and echinodermal wackestone to packstone with thick shale drapes which are also bryozoan dominated (Fig. 30e, f). The wackestone and packstone grades upward into fossiliferous shale. Other features observed in lithotype G are the same as those observed for lithotype E, including evidence of periodic firming of the substrate. Reid (1983) designated a seperate subunit (subunit 11) for the part of the section with the characteristics of lithotype G. She saw this as the stratigraphically highest subunit; however, at McClanahan's Quarry, another bryozoan-rich unit (Lithotype H) occurs above this lithotype.

Lithotype H. Lithotype H (thin sections M53#1, 53#2, 56, 58, 59, and 60) is a bryozoan grainstone to packstone

with shale drapes and shale interbeds. Each bed fines-upward, contains shelter voids, abraided grains, nested allochems, and generally has a gradational upper contact with the overlying shale and an erosive, sharply defined basal contact (Fig. 30g). Although some of the grainstone beds may have resulted from compaction, most show evidence of having been repeated winnowed to produce a graded sequence. Thicker beds contain repeated fining upward packstone to grainstone cycles. Bed thickness thins upward from medium- to very thin-bedded. Grain size varies from fine to coarse and is moderately sorted.

Lithotype H is interpreted to represent the same type of winnowed storm event as lithotype B and contains many of the same sedimentary characteristics. Lithotypes G and H are developed only in the upper Birdsong and occur interbedded with each other and with lithotypes C-E. They are interpreted to represent bryozoan-dominated equivalents to lithotypes B and C.

Birdsong Diagenesis

A detailed discussion of Birdsong diagenesis is beyond the scope of this study; however, certain syndepositional and diagenetic characteristics provide insight to the depositional history of the Birdsong. The generalized paragenetic sequence for the Birdsong Shale, beginning with

syndepositional events and continuing through diagenesis (Fig. 31), was determined using the criteria and methods described in Walker (1988), Choquette and James (1987), Walker and Diehl (1985, 1986), and Longman (1980).

First, micrite coatings are not developed on the allochems suggesting that microbial activity and destruction was minimal and that burial occurred rapidly, or at least burial events occurred frequently. Most abrasion and breakage resulted from physical reworking during storm events, disarticulation of skeletal parts, and biological abrasion.

Second, marine cements are conspicuously absent, except for some minor development as part of the "pseudoholotheca" of the favositid coral Favosites foerstei (see discussion in Chapter 4). Instead, compaction followed by meteoric clear, drusy to equant calcite and non-turbid syntaxial overgrowths were responsible for occluding porosity.

Third, late stage and deep burial diagenesis are only represented by: (1) finely disseminated microcrystalline dolomite in the shaly lithologies, (2) minor chemical compaction represented by microstylolites (grain contact, multigrain contact, and nodule banding types of Wanless (1979)), (3) silica replacement preferential for brachiopods with lesser amounts of echinoderm replacement.

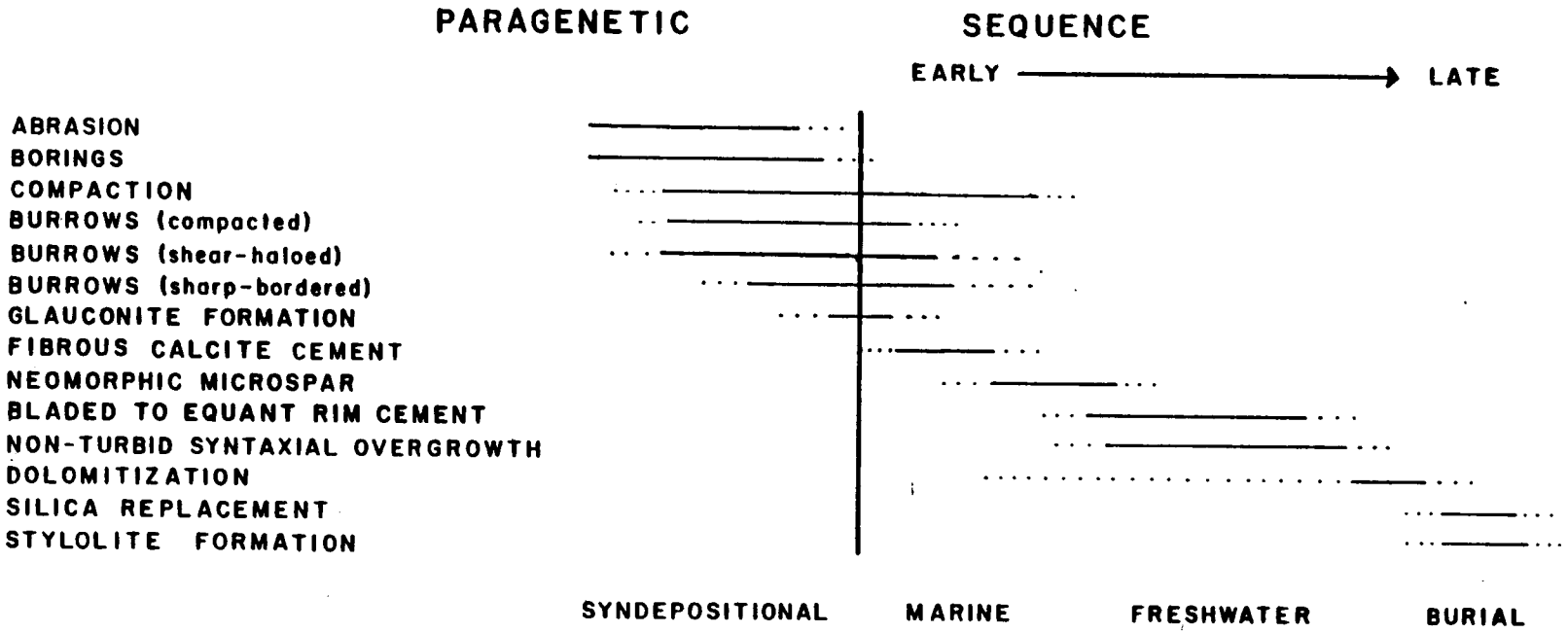


Fig. 31. Paragenetic sequence and syndepositional alteration of the Birdsong Shale.

The absence of iron rich cements in the Birdsong, usually interpreted in other sequences as being of burial origin, is an indication of the relative unimportance of burial diagenesis in these rocks. This suggests that porosity occlusion was complete prior to deep burial.

Most of the sediment alteration took place syndepositionally as a result of compaction and dewatering processes. The abundance of compaction features and equant calcite cement in the winnowed limestones suggests that the environment was too energetic and that sediment accumulation rate, in the form of steady, episodic mud incursions, was too quick to facilitate early cementation of the seafloor. Alternatively, as suggested by Walker (1988), the Silurian-Devonian may have been a time of reduced marine cementation generally, because of the composition of seawater during that interval. The firmgrounds produced in the muddier lithologies are attributed to compaction and dewatering processes, rather than cementation.

Depositional Phases in the Birdsong

The thickest known section of the Birdsong Shale occurs at McClanahan's Quarry (19.4 m; Fig. 25, p. 106), and the thinnest known complete section occurs at Elkins Quarry (4.5 m; Fig. 32) to the east. At both locations,

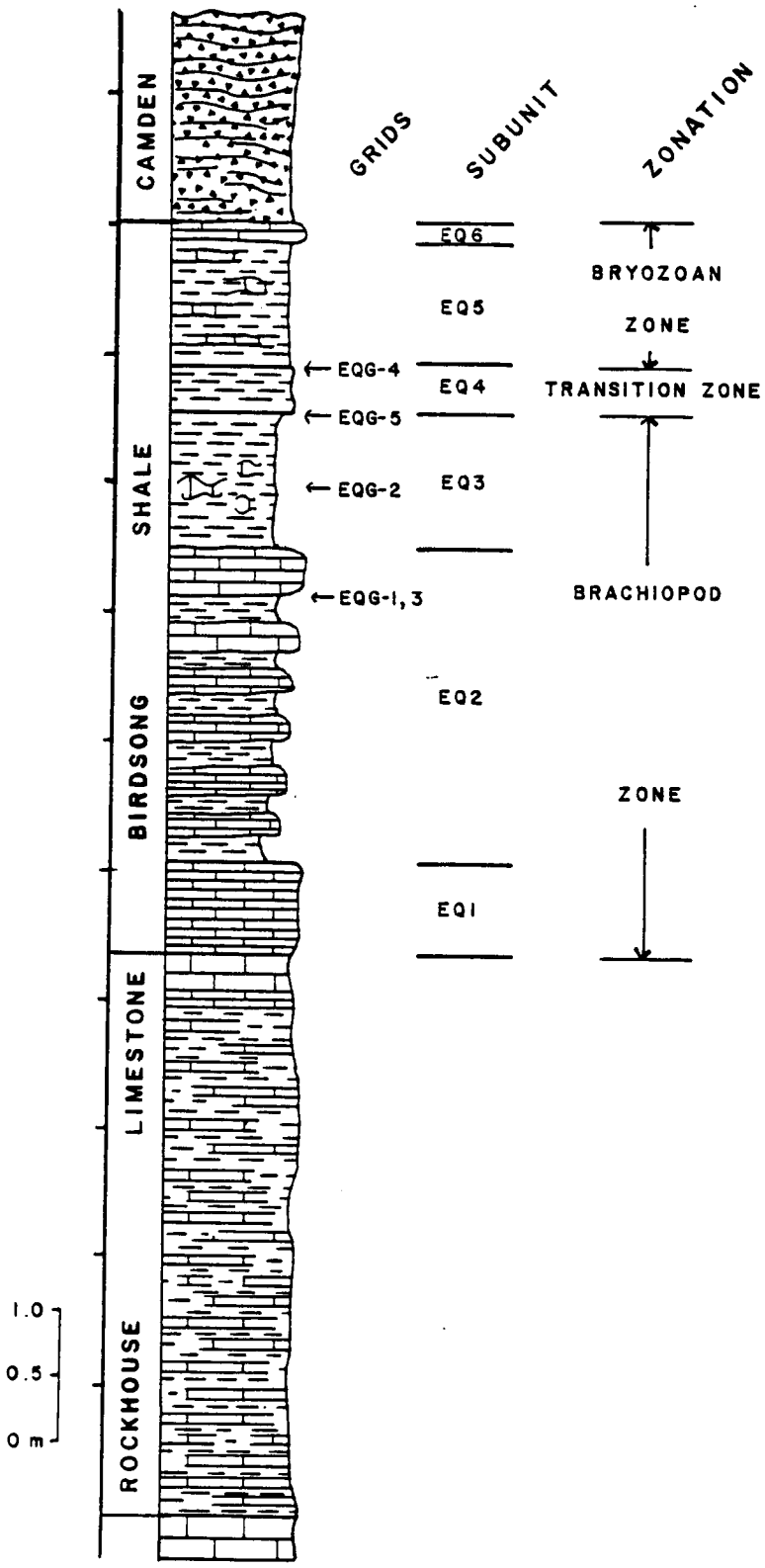


Fig. 32. Measured section at Elkins Quarry.

the Birdsong can be subdivided into six subunits that are composed of various combinations of and amounts of the seven lithotypes described above. Therefore, Elkins Quarry is believed to represent a complete, but condensed, section, which is summarized below.

The lowest subunit (MQ1, 1.2 m thick, and EQ1, 0.5 m thick) is a thin-bedded, interbedded crinoidal wackestone to packstone and fossiliferous shales of lithotypes B, C, D, and E. This subunit is roughly equivalent to Reid's (1983) units A-, B-, and P-5.

Subunit MQ2 (11.8 m) and EQ2 (1.9 m) is a thick sequence of interbedded mudstone, shale, and limestone belonging to lithotypes B, C, D, E, and F described above. This suggests that the Birdsong thins to the east. In general, the sequence consists of shaly packstone and wackestone with a lower abundance and diversity of fauna than MQ1 and EQ1. The shalier beds in MQ2 and EQ2 increase in thickness upsection, but generally remain thinner than the interbedded limestone beds. Subunits MQ1 and EQ1 represent an increase in the influx of terrigenous mud onto the Ross Shelf, relative to the underlying MQ1. This subunit is roughly equivalent to Reid's (1983) AM-, BM-, and PQ-6, 7, and part of 8).

The uppermost bed of MQ2 is a thick resistant calcareous mudstone (thin section MQ44) that grades upward

to echinodermal grainstone and packstone. This bed marks the end of predominantly interbedded shale and skeletal limestone sedimentation and the beginning of a thick mudstone and shaly mudstone interval (MQ3 and EQ3).

MQ3 (1.9 m) and EQ3 (0.8 m) are the uppermost units in the echinoderm-brachiopod dominated part of the Birdsong. This subunit is a thick sequence of lithotype D. Nodular mudstone to wackestone occurs near the central parts of individual thick mudstone to shaly mudstone beds. This unit shows abundant evidence of repeated modification from a soft substrate characterized by a soft substrate adapted fauna to a firmground. This subunit is roughly equivalent to the uppermost part of Reid's (1983) AM-, BQ-, and PQ-8.

Subunit MQ4 and EQ4 is a transition zone rich in horizontal trace fossils, especially Planolites, and is nearly devoid of other macrofossils (Fig. 33, 34). At McClanahan's Quarry, this zone consists of a calcareous mudstone to wackestone 2.5 m thick similar to lithotype G. However, at Elkins Quarry, this transition is entirely terrigenous shale. Below this zone, the Birdsong is brachiopod and echinoderm dominated; above the trace fossil zone, the Birdsong is bryozoan and echinoderm dominated (Fig. 34). This transition marks the beginning of the upper bryozoan-dominated Birdsong of Reid (1983).

MQ5 and EQ5 consist of lithotypes G and H

Fig. 33. Outcrop photograph of Planolites-rich bedding surface of the transition zone between the lower and upper Birdsong.



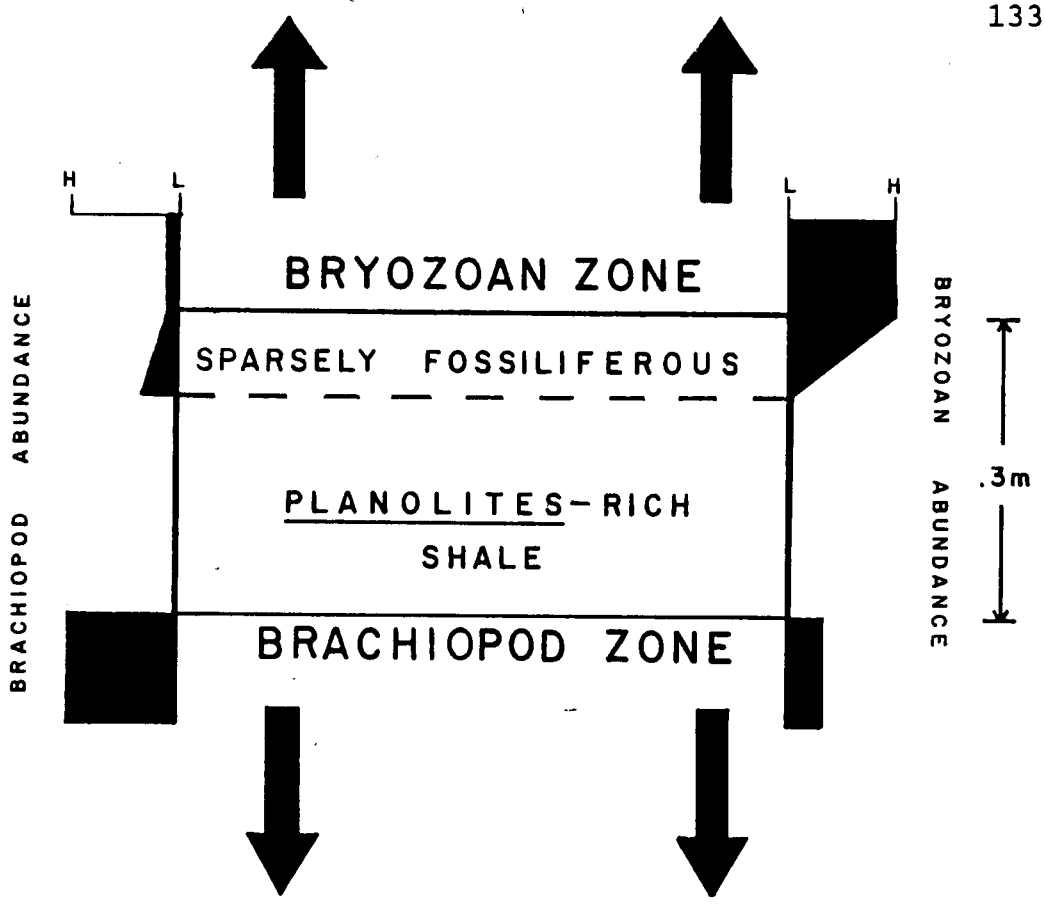


Fig. 34. Transition zone between lower and upper Birdsong. Lower Birdsong is brachiopod-dominated whereas the upper Birdsong is bryozoan-dominated. Transition zone consists of a Planolites-rich interval that gives way to a sparsely fossiliferous shale.

and are dominated by ramose cryptostome bryozoans and large echinoderm stems. Firmground development of the muddy substrate is indicated by swirled to distinct walled burrows, mixed soft and hard substrate adapted fauna, abraded skeletal debris occuring as lenses in the mudstone, and circumrotatory bryozoans. This subunit is equivalent to Reid's (1983) AM-, BM-, and PQ-10.

MQ6 and EQ6, equivalent to Reid's (1983) unit 11, is a very thin- to thin-bedded packstone (lithotype H) with thin shale drapes. Ramose bryozoans and very large stoloniferous crinoid stems dominate the fauna. In places the substrate is encrusted by small (few tens of centimeters) patches of encrusting bryozoans that formed small topographic mounds on the seafloor.

The last known bed of the Birdsong at McClanahan's Quarry consists of an echinoderm-rich terrigenous mudstone. The Camden bedded chert (representing dissolved and replaced limestone, possibly including some of the Birdsong; see Chapter 1) caps the entire Birdsong at both quarries.

Mixed Carbonate - Shale Deposition

The interbedded skeletal carbonate, calcareous mudstone and shale, and noncalcareous terrigenous mudstone and shale of the Birdsong Shale and the Rockhouse Limestone

can be classified as a mixed carbonate-siliciclastic sequence. Mount (1984) described four general types of processes by which such mixed sequences can be produced (Fig. 35).

The mixed sequences of the Birdsong occur on two scales, intrabedded mixtures and interbedded mixtures (Fig. 36). The intrabedded mixtures in the Birdsong Shale and Rockhouse Limestone are best explained by the Punctuated Mixing Model of Mount (1984). In this model, sediment is transferred between contrasting environments during rare, high intensity, sedimentation events. The storm track, within which the Ross Shelf was situated during the Early Devonian, provided the mechanism for mobilizing fine grained sediment and leaving behind winnowed bioclastic accumulations (the limestone-shale couplets described). The frequent occurrence of siliciclastic beds in the Birdsong suggests that the high energy events on the Ross Shelf were probably not rare events; rather, they probably constituted a normal depositional regime. This type of disturbance-driven regime is common in storm track depositional systems (Kelling and Mullin, 1975; Markello and Read, 1981).

In addition to the intrabedded mixing discussed by Mount (1984) interbedded mixing (carbonate-shale cycles of Brett and Baird, 1985) can occur, along with the

Type of mixing	Process	Environment
Punctuated	Transfer of sediment between contrasting depositonal environments during rare, high intensity sedimentation events	Erosion of peritidal carbonates or nearshore belt and tidal flat siliciclastics. Deposition in subtidal, carbonate or terrigenous mud-dominated environments below fairweather wave-base. Erosion of shallow subtidal sediments and deposition on tidal flats and in shoals or reefs may also occur
Facies	Mixing of sediments occurs along the diffuse borders between contrasting facies	Mixing along interface between nearshore siliciclastic belt--tidal flat facies and offshore carbonates. Reef or shoal-derived carbonates and tidal flat carbonates mix with subtidal, back-reef, fore-reef and tidal channel siliciclastics. Eolian sands mix with nearshore and tidal flat carbonates
In Situ	Mixing occurs through the autochthonous generation of carbonate material within siliciclastic sediments	Mixing takes place dominantly in subtidal, terrigenous mud-dominated environments where productivity is high. Also formed in subtidal to intertidal environments by algal binding and by inorganic precipitation of carbonate
Source	Erosion of uplifted carbonate source terranes. Admixtures of clastic carbonates with siliciclastic material	Occurs in marginal marine and nearshore environments that are proximal to exposed carbonate source terranes

Fig. 35. Genesis of mixed siliciclastic-carbonate sequences (from Mount, 1984).

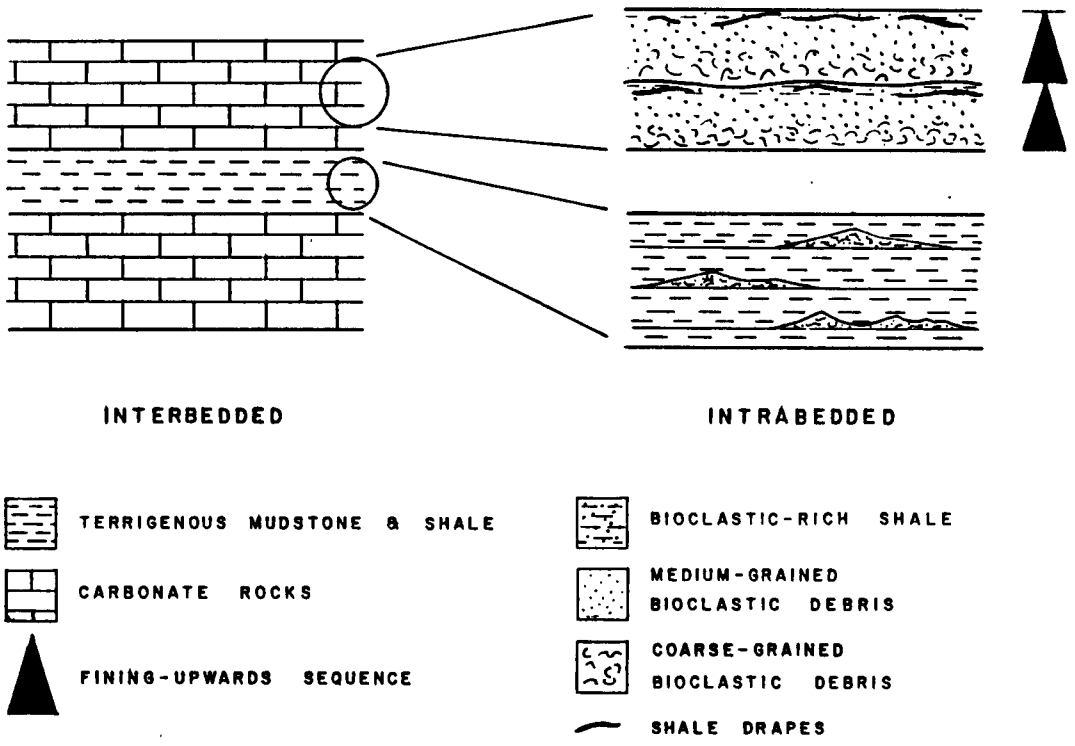


Fig. 36. Schematic diagram showing two styles of mixed sequences present in the Birdsong. Intrabedded sequences contain carbonate and terrigenous clastics within individual beds. Interbedded sequences have individual beds that are either pure carbonate or pure terrigenous (limestone - shale couplets).

intrabedded mixing, making the distinction difficult to discern. This occurs in the Rockhouse and Birdsong formations. Many workers attribute interbedded cycles to sea level changes (Read, 1982; Mount, 1984; Brett and Baird, 1985; Einsele and Seilacher, 1985). Johnson and Murphy (1984) recognized transgressive-regressive cycles spanning the Silurian to Devonian boundary in the western United States. Johnson et al. (1985) discussed post-Lockov transgressive-regressive cycles, concluding that they occurred in response to eustatic sea level fluctuations, possibly caused by glaciation of Gondwanaland. Crowley et al. (1987) modeled paleoclimate for the Early Devonian of Gondwana and indicated that glaciation would have probably covered up to two-thirds of Gondwanaland. Such extensive glaciation could have caused the fluctuations in sea level suggested by the other authors.

Interbedded mixing can be formed by means other than transgressive-regressive events also. Walker and Parker (1975) and Walker, Shanmagam, and Ruppel (1983) described the development of interbedded shale and limestone from the Ordovician of eastern Tennessee. In their interpretation, the limestone represents the slow accumulation of skeletal debris associated with ecological succession of the biota that inhabited the seafloor. The shales represented influxes of storm-mobilized muds that blanketed the

seafloor and punctuated the succession causing the seafloor to become a soft mud bottom substrate and was accompanied by a corresponding change in biota to that of a soft bottom fauna. This differs from the Birdsong interbedded sequence primarily in the formation of the limestone beds, which are storm winnowed accumulations (i.e., events) rather than slow accumulation.

Each of Mount's (1984) processes for the formation of mixed carbonate-siliciclastic sequences shares certain central characteristics. First, a separate source for the carbonate and terrigenous component is the usual case. In the case of the punctuated storm deposited beds of the Birdsong, the muds were transported onto the shelf from the south (making up the transported-in event sedimentation), while the fining upward skeletal beds represent skeletal accumulations (background accumulation) derived mostly from the storm-winnowing of muds (although some longer period skeletal accumulation beds are present). A second characteristic is an efficient and commonly complex hydrodynamic regime that transports, winnows, segregates, and concentrates the components. Storms crossing the Ross Shelf accomplished these functions resulting in the mixed intra- and interbedded carbonate-siliciclastic sequences (limestones with shale drapes and limestone-shale couplets). Third, nearly all of the mixing of deposits

occurs either in shallow waters offshore or in nearshore basins. Storm deposits are the notable exception. Finally, most of the occurrences are within tropical to temperate climatic regions, as was the Ross Shelf. This presumably coincides with carbonate production requirements.

The combined effects of possible global sea level changes, in conjunction with the demonstrated structural tilting or movement of the Ross Shelf (see Chapter 2), were responsible for the Ross Shelf being below normal wave base, and local deposition processes (dominated by event stratification producing processes) is the most likely explanation for the Rockhouse-Birdsong depositional sequence. The result was the formation of a drowned platform (terminology of Read, 1982), rich in terrigenous sediment.

CHAPTER 4

PALEOECOLOGY AND BIOTIC INTERACTIONS

General Introduction

An integral part of any paleoenvironmental reconstruction is the recognition and interpretation of the biotic constituents preserved within the sediment of that environment. Traditionally, paleontologic information derived from this type of analysis has been used to correlate laterally contiguous rock units, establish the ages of the rocks, and determine the subenvironments within the overall depositional setting. Detailed paleoecologic reconstructions have concentrated on discerning recurrent paleocommunities that can then be used to aid in the interpretation of the depositional environments. Such reconstructions have been based primarily on larger biotic components, such as brachiopods, bryozoans, and mollusks (e.g. Weidner and Feldman, 1985; and Wiedman, 1985), and have provided little documentation of less conspicuous biotic elements, such as epibionts and endobionts. The associations among endo- and epibionts and their relationships to "host" organisms remain a little-explored

component of paleocommunity analysis (however, see Vogel et al., 1988).

Two aspects of paleoecologic reconstructions that remain poorly understood, but have received much attention in recent years, are biotic interactions and animal-sediment relationships (see McCall and Tevesz, 1982; Tevesz and McCall, 1983). Both of these general topics are intimately interrelated because complex relationships exist among the organisms themselves and between the organisms and the environments in which they live. Direct interactions such as predation, competition, symbiosis, parasitism, ammensalism, mutualism, and toleration are common and fundamental focal points in most modern ecologic studies (e.g., Ache, 1974; Muscatine and Porter, 1977; Vance, 1978; Scanland, 1979; Osman and Haugsness, 1981; and Keough, 1984), but have received considerably less attention in paleoecologic studies. This is probably due to the difficulty in recognizing these types of interactions in the fossil record and the generally poor state of taxonomic understanding of most of the epibiont organisms.

The goal of this part of the study is to: (1) describe the general paleoecological characteristics of the Birdsong Shale, with emphasis on the animal-sediment relationships, (2) evaluate the adaptations of the major organisms to

their environment and to each other, (3) measure the paleobiotic diversity, abundance, and dispersion of endobionts and epibionts on fossil hosts (hereafter, the term "epibiont" is used to include endobionts), (4) place the paleoecology of the fauna within the depositional framework established in Chapter 3.

The Birdsong Shale is an ideal unit for this type of study for several reasons: (1) The Birdsong contains an abundant and diverse shelly macrofauna, major aspects of which (e.g., brachiopods and trilobites) have been studied by previous workers. (2) Larger skeletal fragments from the Birdsong, especially brachiopod valves, are abundantly encrusted and bored, and exhibit a diverse assemblage of epibiotic taxa. (3) The shaly nature of the Birdsong facilitates collection, cleaning, and subsequent study of both epibionts and the "host" shells. (4) Most other studies of symbiosis, commensalism, etc. have been conducted on rocks of Silurian and Devonian age, and therefore, serve as appropriate comparisons for this investigation.

Methods

General Paleoecology

The paleodepositional setting of the Birdsong was

established in Chapter 3 and serves as the basis for interpreting the paleoecology of the Birdsong. This portion of the study is in two parts. The first part concentrates on the adaptations of the larger, more conspicuous, members of the fauna to their environment. Two of the more abundant groups of organisms in the Birdsong, brachiopods (solitary organisms) and favositid corals (colonial organisms), will be used to illustrate organism-substrate relationships and the adaptive responses of representatives of these two groups to local environmental conditions. Colonial organisms show a tremendous range of adaptive strategies to their environment; therefore, the adaptations of the Birdsong favositids to soft substrates are compared to soft substrate adaptations of favositids from the Waldron Shale (Upper Silurian, Newsom Station, TN; Fig. 1, p. 3) to evaluate the range of adaptive responses of corals to substrates of variable consistancy and to sediment accumulation rate in the Birdsong.

General paleoecological characteristics were determined by evaluating the biotic composition and morphological adaptations of the biota that occurred in the lithotypes and subunits described in Chapter Three. Biotic abundance was determined from point count data (Appendix B) and grid count data (Table 1). A 0.5 m^2 acetate quadrat

Table 1. Grid count data from Elkin's Quarry. Stratigraphic location of grids is shown in figure 32. Values represent numbers of individuals per 0.5 m^2.

ALLOCHEMS	GRID (EQG-#)				
	1	2	3	4	5
Rhipidomelloides	7	4	2	23	1
Gypidula	0	10	4	0	3
Macropleura	5	0	2	0	1
Atrypa	0	5	10	0	0
Rhyncospirina	2	1	4	0	8
Leptaena	11	8	20	0	0
Kozlowskiellina	2	0	8	0	0
Obturamantella	1	8	3	4	6
Leptostrophia	0	5	7	0	0
Strophodonta	0	1	0	0	0
Renssellarina	0	4	0	0	0
Stalked Echinoderms	37	3	19	18	7
Arborescent Bryozoan	11	0	4	0	11
Encrusting Bryozoan	1	0	14	0	0
Fenestrate Bryozoan	7	3	5	0	0
Huntonia	1	0	2	0	0
Phacops	1	0	1	0	0
Rugose Coral	2	0	2	0	0
Favosites conicus	0	1	1	0	0
Pleurodyctium	0	0	0	0	1
Gastropod	2	0	1	0	0
Cephalopod	1	0	0	0	0
Spirorbis	2	1	2	0	0
Sponge	0	0	1	0	0
Burrows	0	7	0	95	0
Conchostracan	1	0	0	0	0
Unidentified Debris	151	60	178	0	16
TOTAL	245	121	290	136	54

was placed on bedding surfaces, and all fossil allochems counted. Although the larger biotic constituents were easily counted and identified, the smaller, comminuted debris was often obscured by shale drapes; therefore, the percentage of unidentifiable debris determined from grid counting shale surfaces is probably underestimated. This problem was partly circumvented by supplementing the grid count data with the thin section abundances determined petrographically. Organism-substrate relationships were evaluated using field evidence and thin sections.

Analysis of Biotic Interactions

The second part of this chapter deals specifically with analyzing the biotic interactions represented in the Birdsong. This was accomplished on two levels. First, host-epibiont relationships were documented. Second, epibiont-epibiont relationships were documented.

Specimens for the biotic interaction analysis were collected using two methods. In the first, blocks of fossiliferous shale, from known positions in the sequence, were collected at the time of section measuring in McClannahan's Quarry. At Elkins Quarry, surfaces of shale blocks contained condensed accumulations of fossils due to selective removal of the shale matrix by weathering. These surfaces (Fig. 37) were scraped to collect the fauna from

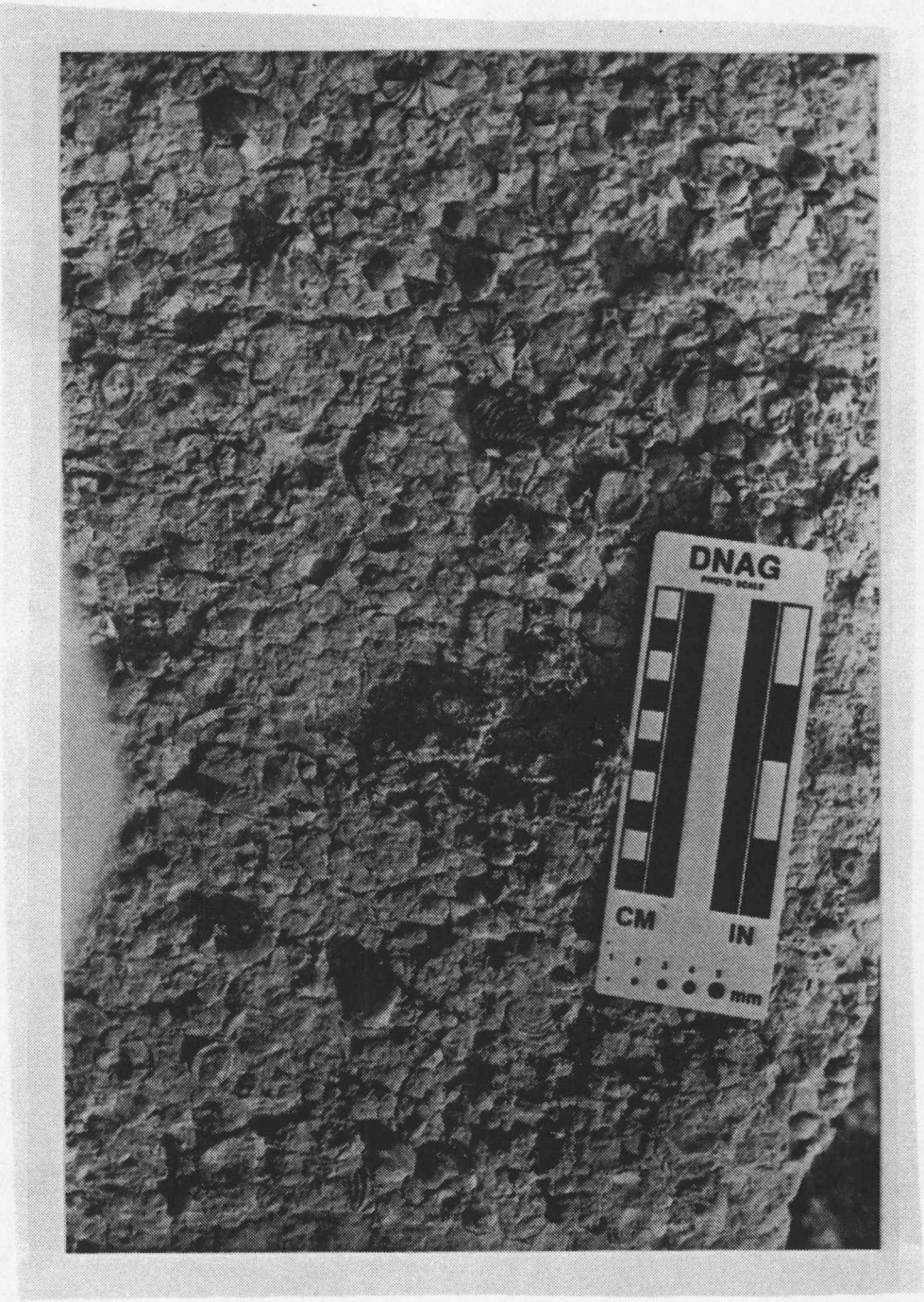

DNAG
CM
IN
mm

Fig. 37. Surface of shale block in Elkins Quarry. Shale blocks have weathered to produce in situ condensed accumulations of fossils on exposed bedding surfaces.

that interval. The amount of condensation could be determined by comparing the thickness of the interval sampled on the weathered slab to that of an unweathered slab. In no case was such a condensed interval that represented more than 4 cm of original rock thickness sampled.

In the laboratory, the shale blocks were disaggregated and matrix removed from the fossils by boiling them in the surfactant Miramine OC-ES. The specimens were run through a Number Five sieve to collect the coarser fraction.

An electronic digitizer interfaced with an IBM PC computer was used to map the distribution and record the abundance and diversity of epibionts on individual hosts. The digitizing apparatus and program are discussed more fully in Appendix C. Once collected, the data were transformed to CMS SAS format and transferred onto a mainframe computer for statistical analysis.

General Paleoecology

Brachiopod Paleoecology

The depositional environment of the Birdsong is characterized by mud-rich substrates that ranged in consistency from soft to firm. Deposition of these substrates was interupted by periods of coarse-grained

bioclastic accumulation that resulted from current winnowing of the muddier sediment (see Chapter 3). The mode of preservation and adaptive morphology of the Birdsong fauna reflects the variable conditions present during deposition of the Birdsong Shale, and is indicative of a substrate that was constantly being modified.

The lower Birdsong is brachiopod-dominated (Dunbar, 1919; Reid, 1983). The shale and mudstone are highly burrowed and the majority of the faunal elements display adaptations for soft substrates. Brachiopods are the best known of the Birdsong fauna and are also the best studied in terms of their adaptations to substrate. Richardson (1985) summarized the adaptations of recent brachiopods to substrate consistency. He noted that most mud- and other fine-grain sediment dwelling brachiopods have pedicles that atrophied and are almost useless for attachment to large, stable substrates. Rather, these brachiopods rely on size, shape, and shell thickness of the lower valve to maintain stable feeding positions (Richardson, 1985). Bioclastic or terrigenous silt and sand, on the other hand, are better colonized by brachiopods with small pedicles that tether and fasten the brachiopod to a clump of sediment or to particles of sand. In addition, silt- and sand-dwelling brachiopods generally have thickened umbo regions (i.e., are posteriorly weighted) in the pedicle valve to help

stabilize the shell in the sediment and aid in resisting scour. Also, the posterior weighting helps to keep the commissure oriented upwards into the water column.

Bassett (1984) has summarized the life strategies of Silurian brachiopods from Gotland, emphasizing organism-substrate relationships (Fig. 38). Burrowing brachiopods, such as Lingula, are very rare in the Birdsong. Only one specimen of questionable identity has been found and none has been reported previously from the Birdsong.

Quasi-infaunal (= semi-infaunal of most other workers) brachiopods were adapted for sinking slightly into the substrate or were partly buried (Rudwick, 1970; Bassett, 1984) after a period of initial attachment to some hard object. These brachiopods are typified by concavo-convex to plano-convex shell shapes, large surface areas, and reduced or atrophied pedicles. Usually, the pedicle valve is slightly thickened for secondary stability. Bassett (1984) noted that a saucer-shaped upper valve, typical of strophomenids, was an adaptation to keeping the mantle edge and commissure above the substrate. In the more extreme form, this adaptation leads to geniculation, such as in Leptaena. Some biconvex brachiopods also lived quasi-infaunally in an umbo-downward position (Cooper, 1977; Bassett, 1984).

CATEGORIES OF LIFE STRATEGIES		NATURE OF SUBSTRATE with comment on changing habits through life
BENTHIC BRACHIOPODS	**ENDOFAUNAL HABITS**	
	Burrowing	soft-bottom
	Quasi-infaunal	initial pedunculate attachment to hard-bottom with subsequent partial 'burial' in soft-bottom
	? Interstitial	pedunculate attachment to hard-bottom within voids of uncompacted sediment
	EPIFAUNAL HABITS	
	FIXOSESSILE	
	Encrusting	hard-bottom
	Umbonally cementing	hard-bottom, some forms becoming detached and supported on hard- or soft-bottom
	Plenipedunculate	hard-bottom, some forms becoming recumbent and supported on hard- or soft-bottom
	Rhizopedunculate	soft-bottom or hard-bottom
	? Epiphytic	plants
	LIBEROSESSILE	
	Ambitopic	initial pedunculate attachment to hard-bottom, becoming recumbent and detached on hard- or soft-bottom
	Cosupportive	initial pedunculate attachment to hard-bottom, becoming detached with mutual support in dense clusters
? PLANKTIC OR PSEUDOPLANKTIC BRACHIOPODS		no evidence for primary planktic life: pedunculate and encrusting forms possibly drift from bottom on detached plants or buoyant shells

Fig. 38. Categories of life strategies for Silurian and Devonian brachiopods (from Bassett, 1984).

The majority of the Birdsong brachiopods were quasi-infaunal, including Leptostrophia, Leptaena, Gypidula, Strophodonta, Schuchertella, Atrypa, and Atrypina. Bedding planes of in situ quasi-infaunal brachiopods are common. These bedding planes are generally preceded and followed by thin, relatively unfossiliferous shale blankets that contain very finely comminuted skeletal debris. These blankets represent periodic influxes of mud deposited over large areas of the seafloor. The finely comminuted debris served as sites for larval settlement for the soft-bottom adapted brachiopods that initially colonized the substrate.

Some Birdsong brachiopods, for example, Atrypa, display other morphological adaptations for living on soft substrates. Most of the Atrypa have flange-shaped or upturned margins. Bassett (1984) interpreted this adaptation as evidence of ambitopism. Ambitopic brachiopods are those brachiopods that are attached to some hard object as juveniles, but become free-living (i.e., liberosessile) as adults. The upturned flange is an adaptation to increase surface area and keep the commissure above the substrate in soft sediment (Cooper, 1977; Bassett, 1984). Cooper (1977) noted that Atrypa displays a highly variable range of morphological features, many of which are adaptations to soft substrates.

Epifaunal brachiopods include encrusting and strongly pedunculate types (Bassett, 1984). Fixosessile brachiopods are those forms that cement directly to the substrate, whether that substrate is the seafloor or another organism throughout its ontogeny. The Birdsong fauna contains two such brachiopods, Crania and Liljevallia. Both occur as epibionts on brachiopods and the stems of crinoids, adapted for soft substrates themselves indicating a specialized approach to avoiding the otherwise unfavorable substrate. The adaptation was to develop a commensalistic relationship with another brachiopod or crinoid that was already adapted to cope with the substrate.

Plenipedunculate brachiopods are those in which the pedicle is a single unbranched stalk. Bassett (1984) interpreted most plenipedunculate brachiopods as inhabiting hard substrates. This is consistent with observations of recent brachiopods in which the strongly developed pedicle serves two functions (Richardson, 1985). First, the pedicle anchors the brachiopod to the substrate. Second, the pedicle muscles provide the brachiopod with the ability to rotate or turn in response to current direction or to shake off sediment. Presumed plenipedunculate brachiopods are less common in the Birdsong than the other forms; and probably include orthids such as Rhipidomelloides. Atrypa may have also relied on its pedicle for attachment to hard

objects (Cooper, 1977) during the less muddy periods of Birdsong deposition or during periods of firm mud substrates.

Rhizopedunculate brachiopods are those brachiopods that "root" into soft substrates using a byssus-like arrangement of pedicle threads (Rudwick, 1970; Bassett, 1984). In larger brachiopods, this adaptation is better suited for living on unconsolidated or mobile sediment (bioclastic sands) and muddier substrates. Curry (1981) suggested that this pedicle type allowed the brachiopod to exploit a wider range of substrate types, making a more generalized adaptation. In the Birdsong brachiopod fauna, it may have also allowed them to exploit substrates that were modified due to compaction and dewatering or received mud influxes or was scoured to produce packstone to grainstone substrates. Bromley and Surlyk (1973), Curry (1981), and Bassett (1984) noted that this adaptation is particularly well developed in recent terebratulids. It is possible that the Birdsong terebratulids, such as Rensselaerina, had this adaptation also.

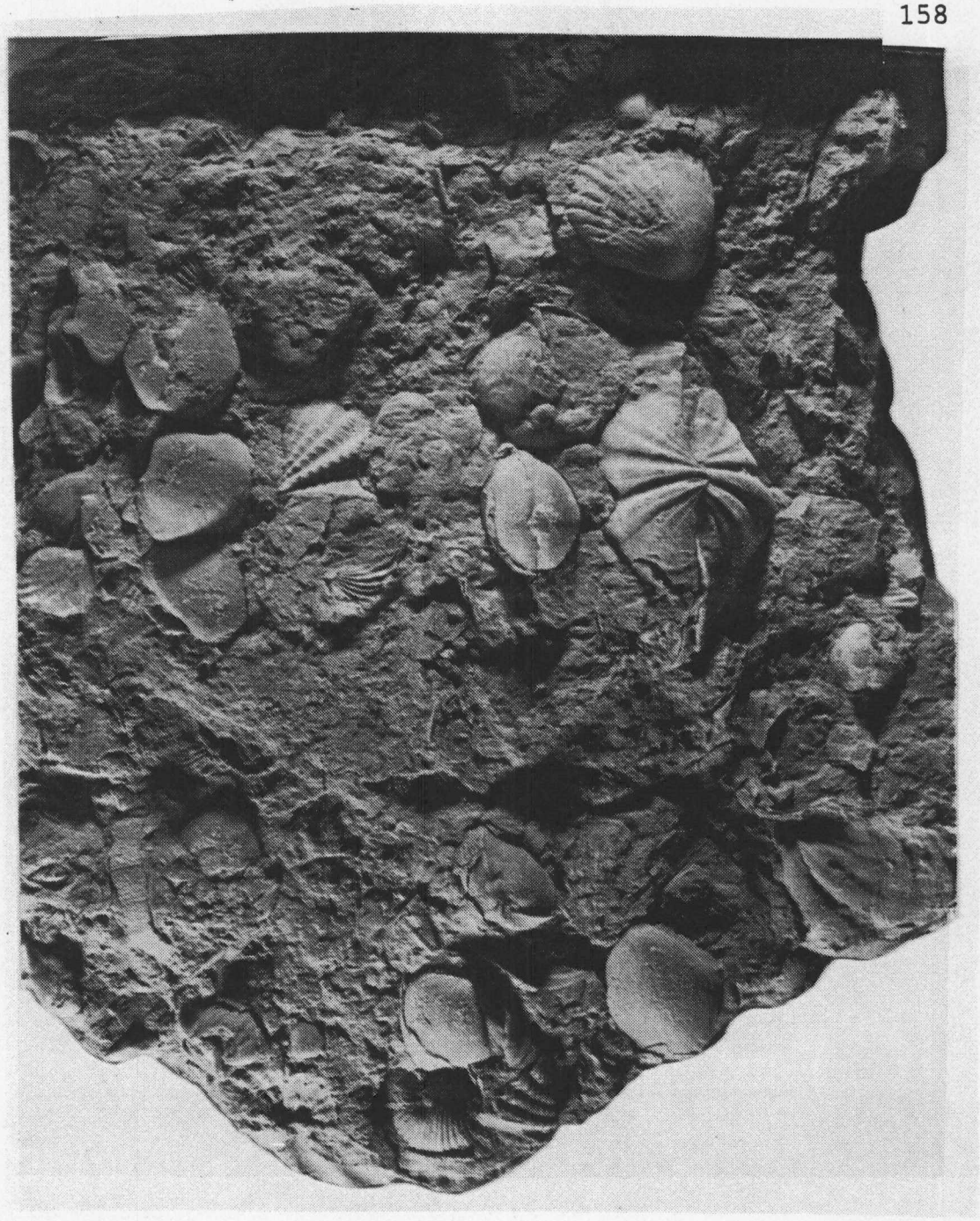
Ambitopism is a primary adaptation to living on soft substrates (Bassett, 1984). Retarding sinking, by providing greater surface area, and hence, developing a snow-shoe effect (Grant, 1981; Thayer, 1975; Rhoads, 1970; Rudwick, 1970), can not only be developed in the

quasi-infaunal brachiopods, but can also be achieved in epifaunal spiriferids by increasing the surface area of the interarea (Rudwick, 1970; Bassett, 1984). The increased interarea provided a platform on which the shell rested. Wings in spiriferids served a similar area maximizing function (Bassett, 1984). Winged brachiopods in the Birdsong with large interareas include Macropleura and Kozlowskiellina. As noted above, most of the Birdsong brachiopods were probably ambitopic.

The shaly beds of the Birdsong, which represented the normal mud-rich bottom of the seafloor, commonly contain bottom fauna smothered by rapid sediment influx that preserved a partial biocoenose. In situ brachiopods (Fig. 39) and rotated coral colonies surrounded by shale drapes attest to the periodic influxes of mud that inundated the indigenous fauna from time to time.

The upper Birdsong contains most of the same characteristics as the lower Birdsong; however, it differs in two respects. First, the fauna contains a higher percentage of ramose (cryptostome and fenestrate) bryozoans. Second, it contains a greater proportion of skeletal-rich beds, especially in the uppermost meter. As noted earlier, the fauna contains a mixture of soft-substrate adaptations (Leptostrophia and Leptaena) and hard substrate adaptations (arborescent bryozoans,

Fig. 39. Brachiopods in living position. Undersurface of shale bed showing articulated beaks of Sphaerirhynchia lindenensis, Gypidula multicostata, and Macropleura macropleura, x 1.5.



circumrotatory bryozoans) occurring together as abraded and fragmented debris accumulated in shell bed lenses.

Deposition of the upper Birdsong occurred during the waning of the mud-rich terrigenous input phase of deposition on the Ross Shelf (see Chapter 2) during which time the seafloor was characterized by longer periods of coarse-grained substrate separated by less mud influx.

Species-Specific Growth Response of Birdsong Favositids

Colonial organisms, such as bryozoans and corals, have evolved a considerable range of morphologies, both on the level of the individual and on the level of the colony, many of which are adaptive responses to different environmental settings in which these organisms live. Paleozoic corals, in particular, show a tremendous range of growth forms. The colonial (or compound) corals have a variety of shapes for the entire corallum, many of which are analogous to those of solitary rugose corals (Hill, 1981), but are more complex because of the numerous additional forms and relationships that can also exist among the individual corallites of a corallum. The variety of growth patterns in colonial corals results from the development of the colony (astogeny) in response to both genetic and environmental stimuli (Oliver, 1968). Oliver (1968) described astogenetic patterns in terms of four

features: form, increase, overall pattern, and individual corallite shape. Philcox, (1971) studied favositid corals from reefs of the Gower Formation (Upper Silurian) and emphasized the paleoecological importance of growth forms suggesting that sedimentation rates exerted a primary control on the form of the corallum. Pandolfi (1984) reached a similar conclusion for favositids from the Windom Shale Member of the Moscow Formation (Middle Devonian).

The purpose of this section is to describe in detail the resultant growth responses of three species of favositid corals (Favosites conicus Hall, F. foerstei Dunbar from the Birdsong, and for comparison, F. forbesi Milne-Edwards & Haime from the Waldron Shale) to a similar environmental problem. The problem was survival on a mud-rich substrate. These three species of favositids exhibit species-specific growth forms that evolved in response to the consistency of the substrate. This resulted in colony forms that allowed these corals to live on top of (F. conicus, partially buried within (F. foerstei), and above the substrate (F. forbesi).

As noted above, mud substrates can be detrimental to the survival of larvae that require a firm substrate for initial attachment and development. However, early dewatering of the mud to form a firm or thixotropic surface or the presence of suitable 'islands' of hard substrata,

such as shelly macrofauna, enhance the environment for larval recruitment. Once established, colonial organisms may have been more likely to survive than some solitary forms because of the plasticity of colony form and the ability to rapidly dominate any available substrate (Jackson, 1977, 1979, 1985; Coates and Jackson, 1985). Colonial organisms, as a group, have a greater variety of ways to cope with some unfavorable conditions such as soft bottom substrates. The term `substrate-starved' (Broadhead and Gibson, 1986) can be used to represent settings in which the availability of sites for larval settlement or for epizoan attachment is limited.

Material. Specimens used in this study include 135 coralla of Favosites conicus Hall and 62 coralla of F. foerstei Dunbar, collected from exposures of the Birdsong Shale at Parsons, Benton, and McClanahan's quarries (Fig. 1, p. 3). F. forbesi is represented by 21 coralla from collections of the Waldron Shale fauna housed at the University of Tennessee, Knoxville. These specimens were collected from the quarry at Newsom Station, Tennessee. All specimens were prepared by boiling in the surfactant Miramine OC-ES to remove attached argillaceous matrix. Thin sections were prepared to examine internal structures.

Favosites conicus Hall. F. conicus colonies are

hemispherical with a flat to slightly undulose holotheca-covered base (Fig. 40a, b). Increments of growth of the holotheca (Fig. 40b), and hence the colony, are evident as a series of fine, slightly wrinkled, concentric bands of the holotheca (regarded as normal growth) separated by fine concentric grooves which represent periods of reduced or interrupted colony expansion. Individual corallites are arranged radially from the center of the base of the corrallum (Fig. 40d), increasing outward both in number and in diameter ("radial" growth pattern of Philcox, 1971; "massive" pattern of Oliver, 1968).

Size frequency distribution of the maximum width of coralla of F. conicus (Fig. 41) exhibits a mode at the 15.0 - 17.5 mm size class and a mean of 18.2 mm (SD = 5.1). The leptokurtic shape of the graph, which includes immature coralla, and small maximum size (35.0 mm) of coralla suggests that there was a limit to maximum size (= approximate age) of this species. Vojnovskiy-Kriger (1970) and Leleshus (1985) interpreted a similar pattern observed in other favositids to represent determinant growth. They believed that once the colony became sexually mature, growth ceased, gametes were shed, and the colony died soon after. The occurrence of encrusting bryozoans on the upper surfaces of several specimens of F. conicus (Fig. 40c) lends further support to the hypothesis that colonies of

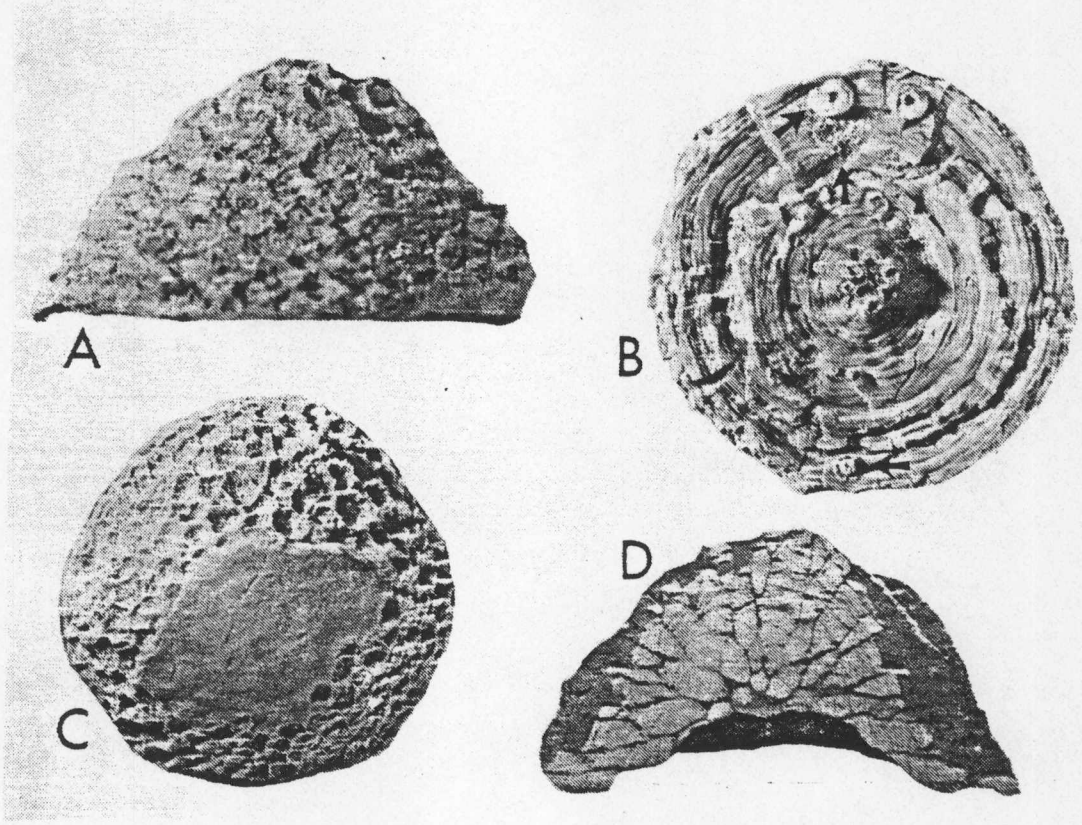


Fig. 40. Favosites conicus Hall. A. Side view of domal corallum (USNM 424444), x 2.5. B. Underside of corallum showing finely rugose holotheca with epibiotic (possibly cryptic) spirorbid worm tubes (top arrow) and two types of bryozoans (middle and bottom arrows) (USNM 424445), x 2.5. C. Upper surface of corallum with encrusting colony of cystoporate bryozoans (USNM 424446), x 2.0. D. Longitudinal thin section of specimen shown in A exhibiting radial growth pattern (USNM 424444A), x 2.5.

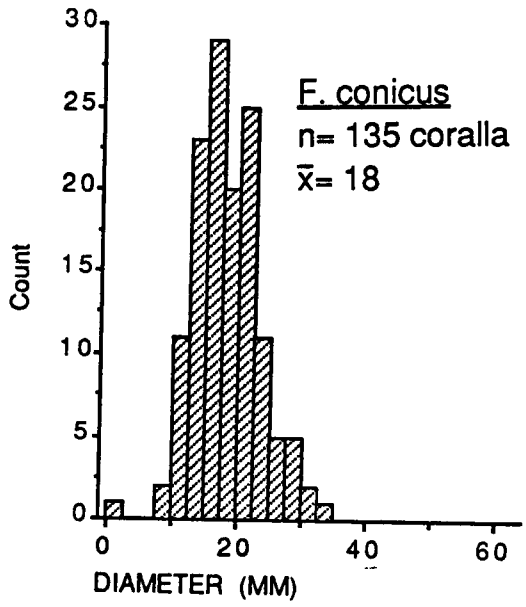
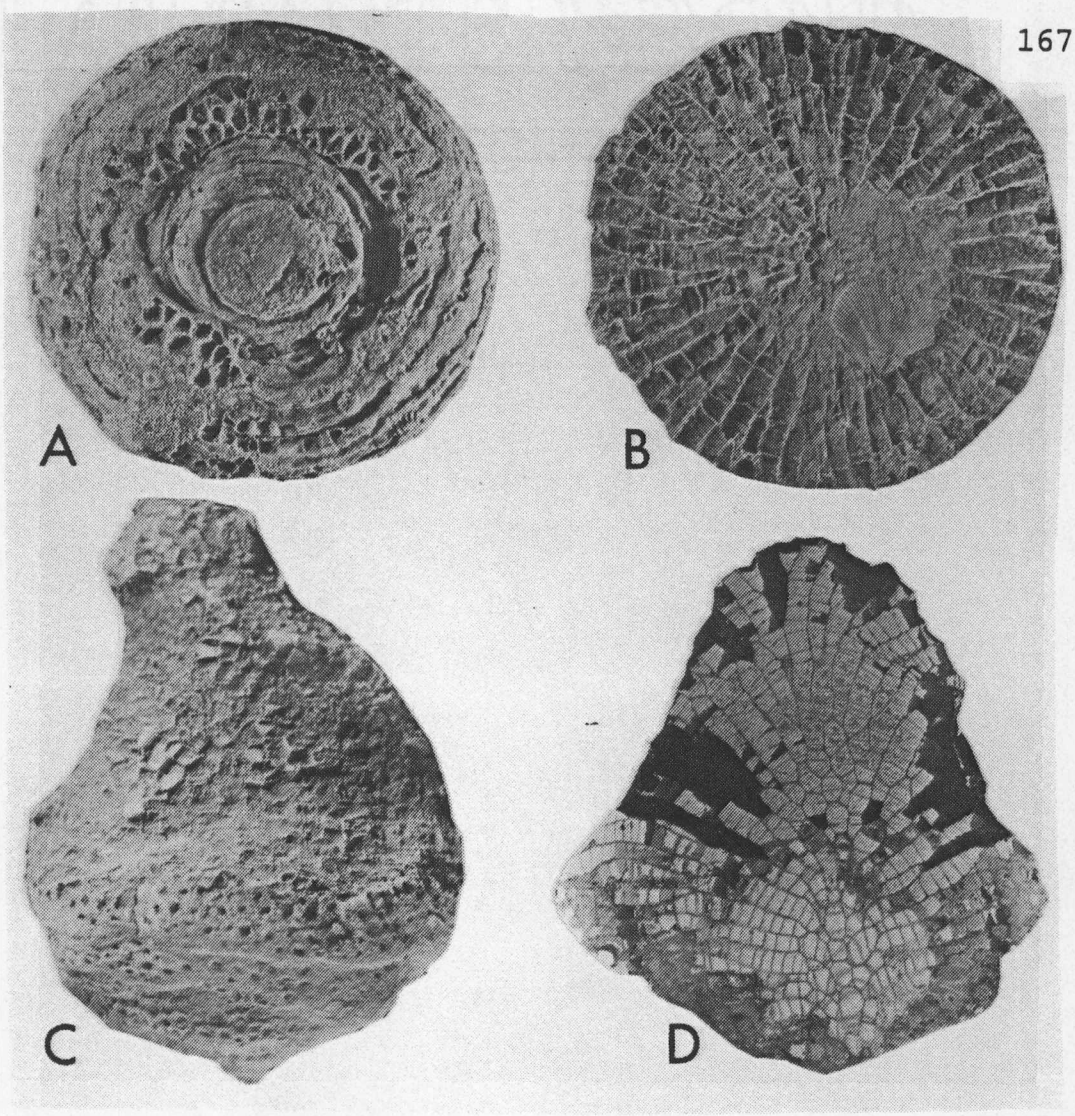


Fig. 41. Size frequency distribution of coralla of Favosites conicus. Maximum diameter was measured across the base of the corallum.

this species characteristically died, for whatever cause, at a small size. Encrustation must have taken place after the death of the coral and prior to burial, otherwise the bryozoan larvae would have been fended off or eaten by the polyps. Thus, it is possible that following the achievement of maximum size, the colony underwent sexual reproduction, died, and then became a substrate or 'island' for larval attachment. If F. conicus colonies survived to only produce gametes once, it would be considered to be a monocarpous species (sensu Leleshus, 1985), although such a phenomenon has not been documented in living scleractinians (J.E. Sorauf, pers. comm., 1988).

Favosites foerstei Dunbar. Coralla of F. foerstei are characterized by a conical to convex, "pseudoholotheca"-covered base (Fig. 42a) (The term "pseudoholotheca" describes an outer covering of early marine fibrous calcite cement on and within the lowermost corallites of the corallum. It superficially resembles the finely rugose holotheca of other favositids (Broadhead et al., 1988b); the upper surface has an irregular elevated profile (Fig. 42b, d) unlike the hemispherical form of F. conicus and is usually incomplete owing to preburial erosion (Fig. 42b, c). Upper surfaces are usually flat to slightly concave. Rare specimens are found in which the upper surface of the colony being is along the lateral

Fig. 42. Favosites foerstei Dunbar. A. Bottom view of corallum showing convex, pseudoholotheca-covered base (USNM 424447), x 1.5. Note the coarsely rugose nature of the pseudoholothecal bands. B. Side view of a corallum showing the convex base with pseudoholotheca. Irregular profile of upper part of corallum may represent partial erosion or inconsistant growth rates of adjacent corallites (USNM 424448), x 1.3. C. Top view of specimen shown in A, exhibiting eroded, flat to concave surface lacking epibionts but containing mud-infilling at center, x 1.5. D. Longitudinal thin section of corallum similar in shape to that shown in B (USNM 424449), x 1.3. Axial growth center extends from base to top; corallites extend outward in lower part of corallum and upward and outward in upper part. Gray, indistinct area at base is pseudoholothecal covering and infilling of early marine cement.


A
B
C
D

margins with a low hemispherical dome of corallites located at the center. In these specimens, corallites can be traced horizontally from their origin near the center of the colony (axial growth center of Krasnov & Preobrezhenskiy, 1972) outward to its periphery, especially where the corallites of the colony edge are strengthened by an overgrowth of pseudoholotheca or by encrusting bryozoans. Coral growth above the pseudoholotheca never extends laterally beyond the maximum width of the lower part of the colony. The result is a taller corallum in which the living portion extends several centimeters above the upper extent of pseudoholothecal growth, which represented the level to which sediment had accumulated around the corallum.

F. foerstei coralla exhibit a much broader range of sizes in a right skewed distribution and a larger maximum observed diameter (122.5 mm) (Fig. 43) than those of F. conicus. This suggests that it did not have determinate growth, and colonies probably lived to varying ages, which are represented by the differing sizes of the coralla. According to the terminology of Leleshus (1985), F. foerstei may have been a polycarpous species, capable of many successive cycles of sexual reproduction, as is also indicated by the occurrence of bands of closely spaced

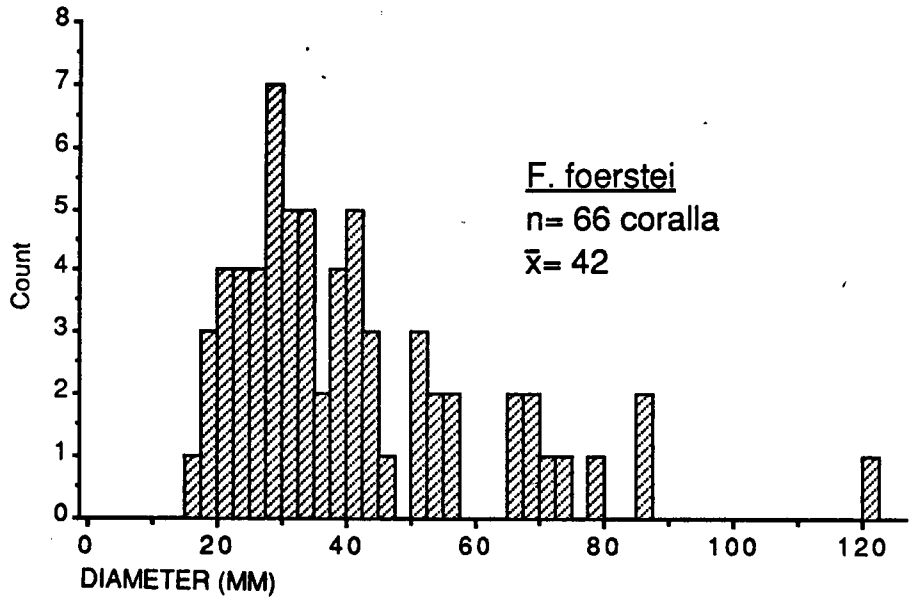


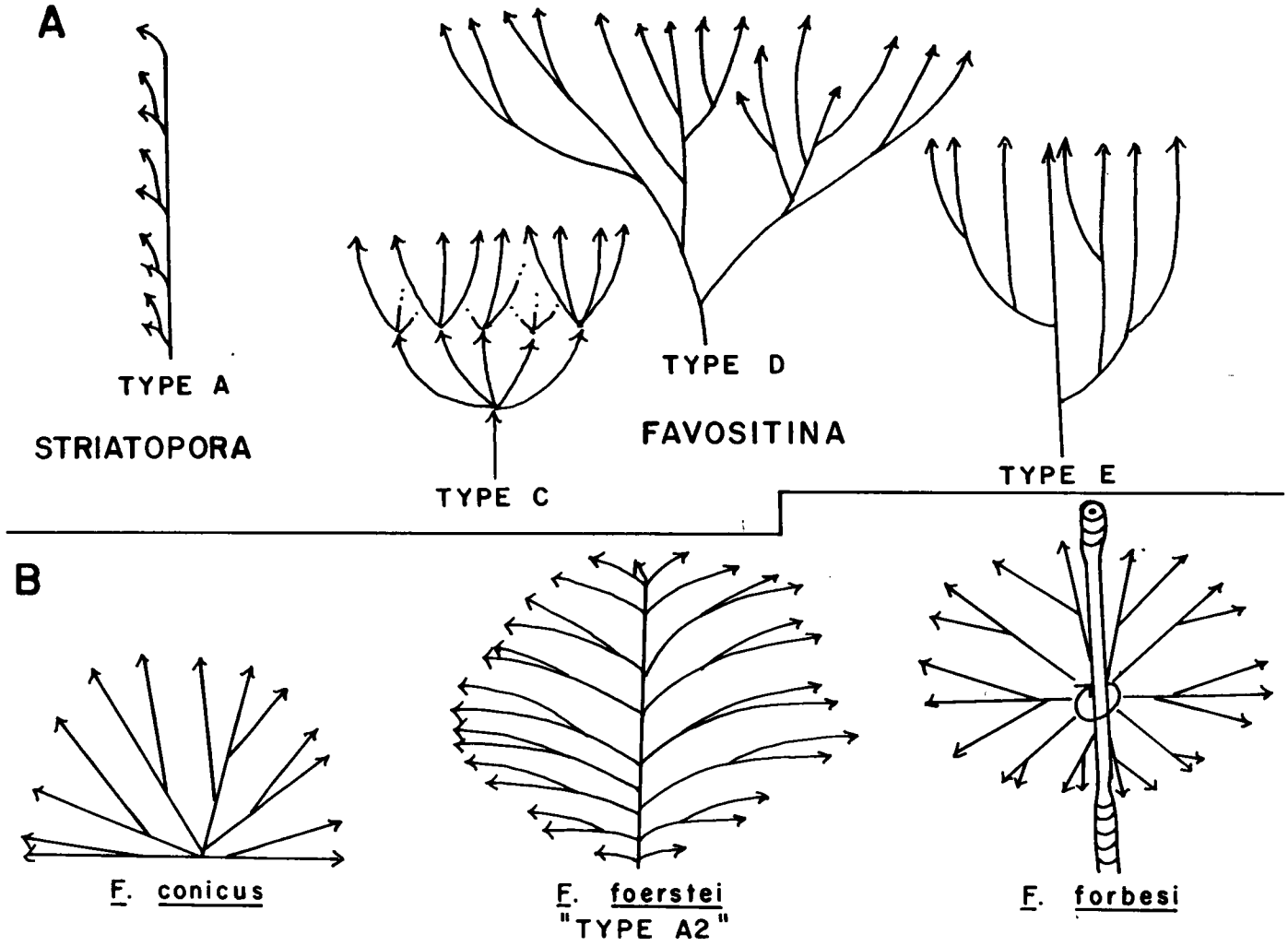
Fig. 43. Size frequency distribution of coralla of Favosites foerstei. Maximum diameter measured across the base of the corallum.

tabulae, and therefore would fit the usual pattern for favositids.

Individual corallites originate at the center of the corallum (axial growth center), from which they extend upward a short distance, and then recurve sharply, extending subhorizontally to the lateral margin of the corallum (Fig. 43d). Additional corallites bud within a zone largely restricted to the central half of the corallum. The lateral margins of the colony are circlets of corallites that progressively extend outward over earlier circlets, expanding the colony diameter as growth proceeds. The resulting pattern is one of a series of successive horizontal rings or circlets of corallites, in groups of two or three over-riding circlets. This pattern results in a broadly conical base to the corallum.

This pattern does not exactly match one of the nine basic colony form patterns described by Oliver (1968) for tabulates; it most closely approximates type A, which describes growth in a slender branching corallum (Fig. 44a). The primary difference between Oliver's type A, typified by Striatopora, and the growth pattern of F. foerstei is that the latter expands rapidly outward from a central point forming a low but wide pattern (Fig. 44b) rather than a tall almost cylindrical pattern. This pattern is not simply a very rare modification of Oliver's

Fig. 44. Branching patterns of selected tabulate corals. A. Colony form patterns recognized by Oliver (1968). Types C, D, and E represent common patterns recognized in favositids; type A is recognized from the pachyporid genus Striatopora. B. Colony form patterns recognized for species of Favosites examined in this study. Although patterns shown by F. conicus and F. forbesi are modifications of one of the basic types of favositid patterns, the pattern shown by specimens of F. foerstei is more similar to the Type A of Oliver, but differs primarily by being more rapidly expanding in an unbranched corallum.


A
TYPE A
STRIATOPORA
TYPE C
TYPE D
FAVOSITINA
TYPE E
B
F. conicus
F. foerstei
"TYPE A2"
F. forbesi

type A, rather, this pattern represents an additional tenth type, A2.

Favosites forbesi Milne-Edwards and Haime. Specimens of this species from the Silurian Waldron Shale were studied in conjunction with the Birdsong species to determine if there were other adaptations to soft substrata that were not seen in the Birdsong species. F. forbesi occurs as irregular to globose masses completely surrounding pluricolumnal segments of crinoid stems (Fig. 45a) and as small coralla cemented to brachiopod fragments (Fig. 45b). Coralla associated with crinoid stems do not exhibit a holotheca, whereas those attached to brachiopods have a rugose holothecal covering of the small, upright coralla. The pattern of arrangement of corallites generally is radial (Fig. 45c) in both the globose, crinoid associated coralla and upright forms. Corallites of globose forms represent larval settlement on the erect stalks of crinoids, and Kissling (1973) noted that this form is distinct from, but superficially similar to the circumrotatory growth patterns exhibited by some corals. Longitudinally sectioned coralla containing an axial crinoid stem (Fig. 45c) show that corallite lengths were longer on one half of the corallum than on the other. The side with longer corallites was probably directed upward, as indicated by geopetal mud infillings in the corallites.

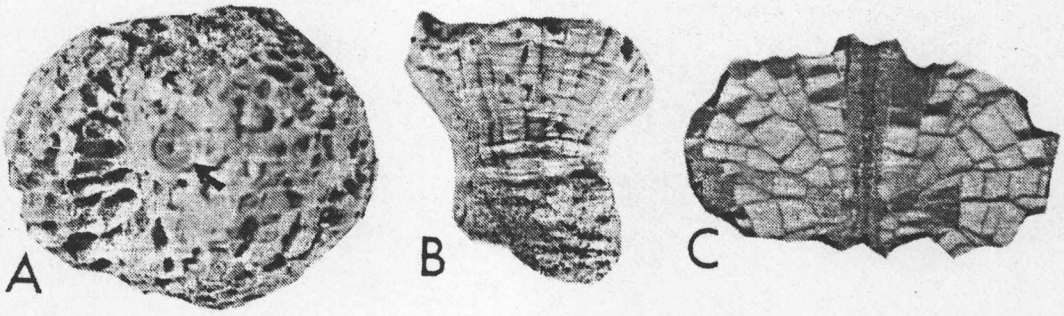


Fig. 45. Favosites forbesi Milne-Edwards and Haime. A. Globose corallum grown around a crinoid stem (arrow) (USNM 424450), x 1.8. B. Lateral view of upright corallum showing holotheca (USNM 424451), x 2.0. C. Longitudinal thin section of globose corallum surrounding crinoid stem. Widening of stem away from site of colony initiation indicates continued growth of stem, and hence a symbiotic relationship. Orientation is based upon our assumption that dominant growth direction of corallites was upward (USNM 424452), x 2.0.

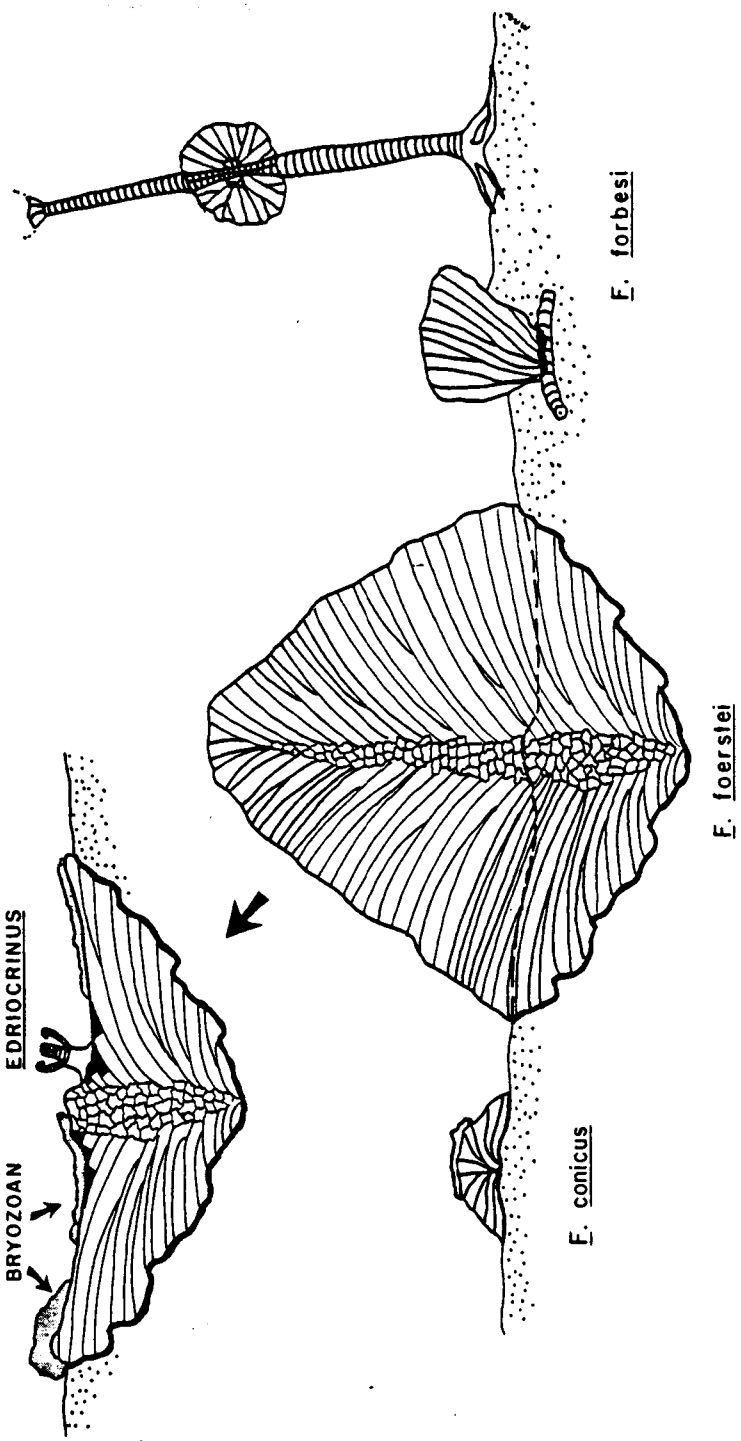
The small number of specimens of F. forbesi (13 globose, 8 upright) does not permit an evaluation of limits of growth, but the generally small size of coralla in the collection at hand suggests that there was a maximum limit to size. Globose coralla range in diameter from 12 mm to 31 mm, and upright coralla range in height from 9 mm to 29 mm with summit diameters ranging from 11 mm to 38 mm.

Autecology

The growth forms described above for Favosites conicus, F. foerstei, and F. forbesi represent distinct growth responses of these species to the consistency of substrate. Each growth form can be viewed as a combination of one or more of the following factors: (1) pattern of colony growth as determined by the arrangement and budding pattern of corallites within the corallum, (2) interfacial material (holotheca or pseudoholotheca) that separates the lower corallites of the corallum from direct contact with the substrate, and (3) biotic association that removed the colony from proximity to the substrate.

Favosites conicus was adapted to living on top of the substrate during times when the sediment was relatively firm and there was little or no net sediment accumulation (Fig. 46). The low domal profile of the corallum was hydrodynamically stable, and there is little evidence of

Fig. 46. Suggested life orientations of Favosites conicus, F. foerstei, and F. forbesi. Note that, although F. conicus and F. foerstei were sympatric, F. forbesi occurred geologically earlier. F. foerstei is shown both as a complete living colony and as the commonly preserved form with epibionts encrusting the postmortem eroded summit.


EDRIOCRINUS
BRYOZOAN
F. conicus
F. foerstei
F. forbesi

extensive disruption or overturning. The flat, holotheca-covered base helped to prevent subsidence ("snowshoe effect"). Philcox (1971) reported flat bases for reef-dwelling favositids, which he interpreted as having formed over periods of several years without net sediment accumulation around the colony (Fig. 47). Philcox's interpretation of an average growth rate of 2 cm/year, when compared to our size distribution data for F. conicus, supports our interpretation that colonies did not survive longer than about one year (because no bands of closely spaced tabulae occur), when sexual reproduction occurred. That this time of sexual reproduction was a yearly event is indirectly supported by the paleogeographic location of this area in a storm-influenced subtropical depositional regime located 25° to 30° south paleolatitude (Gibson et al., 1988).

The presence on the holotheca of small, single-layered, sheet-like bryozoan colonies and spirorbid worm tubes with appertures facing the outer margin of the corallum suggest that localized scouring around the outer margins of the corallum created small refugia for cryptic epibionts (Fig. 40b). Both the flat form of the holotheca and the presence of cryptic epibionts suggest that the substrate, although mud-rich, was not extremely soft or mobile. Under these conditions the success of F. conicus

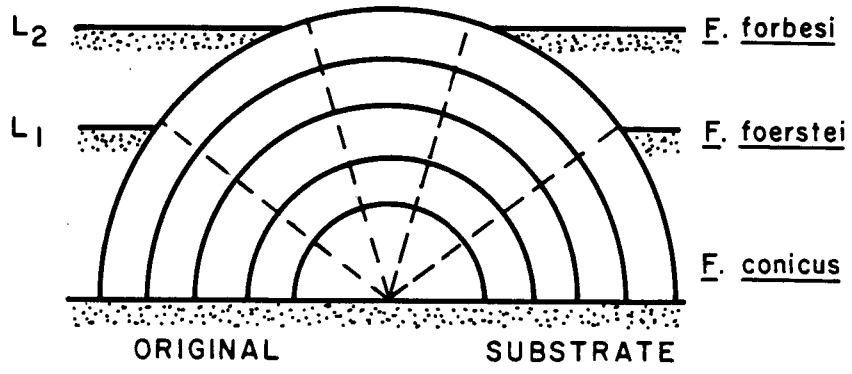


Fig. 47. Relationship between rates of coral growth and of net sediment accumulation as reflected in profile of the base of the corallum (modified from Philcox, 1971). Concentric lines represent schematic growth increments, and are not intended to reflect measured rates of growth.

was due to a combination of factors a and b - growth geometry plus the presence of holotheca.

Favosites foerstei ensured its survival on the muddy bottom of the seafloor by maximizing its surface area in contact with the seafloor as indicated by the rapidly expanding nature of the corallum. This type of 'snowshoe' adaptation to soft substrates occurs in many groups of organisms such as brachiopods (Grant, 1981; Thayer, 1975; Rhoads, 1970; Rudwick, 1970), bivalves (Jablonski and Bottjer, 1983; Thayer, 1975; Rhoads, 1970), and bryozoans. Indeed, many of the other organisms found along with F. foerstei are characterized by such a flat, expansive form, such as the brachiopods Leptostrophia and Leptaena.

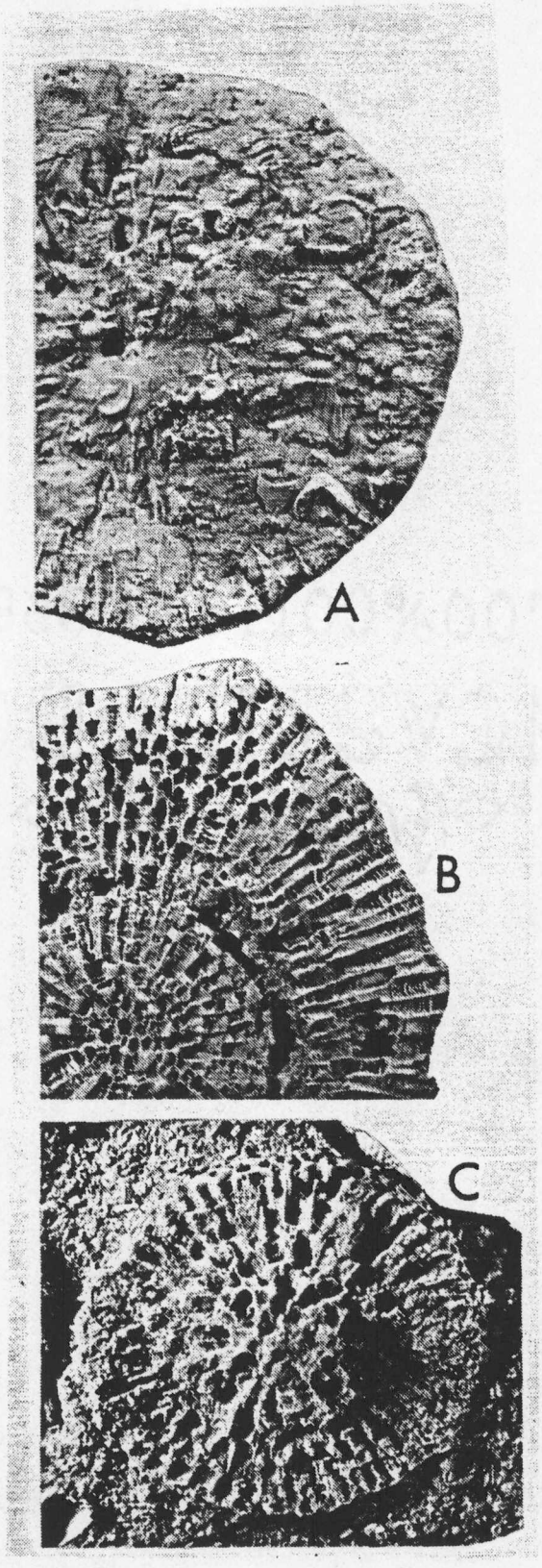
The convex base of the corallum results from two factors related to growth. First, the central portion of the corallum contained the greatest density of corallites and hence was heavier. As the corallum increased in size, the colony settled into the substrate, compacting and firming the underlying sediment, while the outer margin of the colony continued normal upward and outward growth at the sediment - water interface. Second, this upward and outward pattern of corallite growth progressively widened the base of the corallum, and allowed the colony to cope with small net amounts of sediment accumulation. For both factors, as the colony grew larger, the snowshoe effect

retarded sinking. The overall pattern is similar to that shown by Philcox (1971) for reef-associated favositids in settings where a convex base to the corallum resulted from the ability of the colony to maintain a growth rate that moderately exceeded the net accumulation of sediment (Fig. 47).

The convex conical shape of the corallum allowed the colony to rest nestled partially within the muddy substratum. This is an extremely stable position for a colonial coral because the colony would not easily have been overturned and a considerable amount of cohesion would have developed between the coral and the underlying mud making scouring difficult. This may also have been coupled with a low broad upper corallum, further stabilizing the coral on the substrate by providing a low center of gravity at or slightly below the level of the substrate. This stability is additionally supported by extensive epitaphic (i.e. postmortem) epibiont assemblages on the eroded concave upper parts of coralla indicating long periods of exposure (Fig. 48a).

The upper surfaces of coralla usually are concave or flat partly due to the way in which F. foerstei grew and partly due to taphonomic processes. New corallites originated in an axial growth region that formed a small domical region near the center of the upper surface of the

Fig. 48. Favosites foerstei exhibiting postmortem features associated with erosion and exposure of the corallum. A. Flat to gently concave eroded surface heavily encrusted by bryozoans and a crinoid holdfast indicating lengthy preburial exposure (USNM 424453), x 1.2. B, Gently concave eroded surface lacking epibiont encrustation. Concentric eroded zone (arrow) possibly represents a change in skeletal density associated with annual growth (USNM 424454), x 1.2. C. Small corallum with domal center suggesting resistance to erosion in the axial growth region (USNM 424455), x 1.8.


A
B
C

corallum. As corallites grew, they recurved sharply outward from the near vertical orientation in the axial region to a horizontal orientation. The horizontal portions of the corallites usually have widely to closely spaced tabulae, which are thinner than the corallite walls. Erosion after the death of the colony differentially eroded the summit of the corallum (Fig. 48c). There was a greater concentration of closely spaced corallite walls in the vertical-growing portion of the corallum, which often was more resistant to erosion after death of the colony, explaining the occurrence of some specimens with small domal centers (Fig. 48b). The lateral margins were reinforced by pseudoholothecal bands, and often epibiont overgrowths, which made this region less susceptible to erosion.

F. forbesi commonly grew on the upright stalks of living crinoids, resulting in a symbiotic relationship, i.e. the two organism simply lived together. There is very little benefit that the crinoid host could have gained from this relationship. In fact, the crinoid possibly suffered somewhat as a result of the stress added to the stem by the weight of one or more colonies. Sections of the stalk that were encrusted by colonies of F. forbesi were rendered immobile, although it is not clear whether this localized loss of flexibility would have been harmful to the crinoid.

It is also likely that the coral would have provided an additional attraction for predators thereby making the crinoid host more conspicuous also.

The coral did benefit from the relationship. First the crinoid provided the coral with a favorable substrate and habitat above the muddy sediment. Presumably, this resulted in less turbid waters passing over the coral, hence increasing the efficiency of the coral food gathering system by reducing the quantity of non-food material in the vicinity of the corallum, as well as providing a more constant supply of zooplankton. Second, the relationship enabled the coral to maximize the growth of living corallites in a spherical arrangement, thus providing a greater feeding and reproductive surface while maintaining a small corallum. If the crinoid hosts were gregarious, the coral also benefitted from having a localized gene pool for sexual reproduction and from the additional camouflage afforded by the thicket. This one-way benefit does not mean that the relationship was parasitic, but was commensalistic, and only potentially could cause harm to the host.

Specimens of F. forbesi that encrusted brachiopod valves and exhibit an upward growth pattern and a holotheca (Fig. 45b) probably represent an alternative ecophenotypic form that resulted from successful larval recruitment on

the seafloor. When viewed in terms of the growth forms discussed by Philcox (1971), the upright, slender growth of the corallum suggests a setting in which the rate of colony growth only slightly exceeded the rate of sediment accumulation.

Species-specific or Ecophenotypic Response?

Adaptations such as the ones described in this paper can result from two mechanisms, one primarily genetically constrained and one primarily ecologically constrained (Fagerstrom, 1987). First, observed morphology can be the result of evolved species-specific adaptations in which the genetic makeup of the species is responsible for colony form. Such species-specific adaptations tend to show discrete and consistent forms: that is, they tend not to vary in response to local environmental differences. These adaptations are characterized by a narrow range of variability so that individuals, or colonies, additionally show no clinal variation.

Where a species is less tightly constrained genetically, individuals and colonies respond to local environmental conditions by displaying a range of morphologies that permit the individual, or colony, to cope with these environmental differences. Such a morphological response is said to represent ecophenotypic variation. The

resulting forms usually can be placed within a spectrum of morphology that often corresponds to environmental gradients. Hence, there may be a topoclinally varying series of possible morphologies, as shown, for example, by modern species of Acropora in response to differing hydraulically induced stesses (Grause et al., 1977). Favosites conicus is the one species considered here in which the general corallum form appears to have been most strongly genetically constrained. Hall (1874) originally described F. conicus from specimens from New York and Maryland on the basis of corallum size, shape, and the presence of a flat basal holotheca in addition to corallite size, shape, and distribution of mural pores and tabulae. The radial arrangement of corallites, centered near the point of origin of the corallum, virtually limits the shape of the corallum to one with a domical summit. Departure from a relatively smooth contour has not been observed. The characteristically flat base also is probably directly related to the radial pattern of astogeny. Although a few slightly convex examples have been observed, the development of strongly convex bases may not have been possible. These rare convex forms could be due to lateral growth of lowermost corallites being only slightly more rapid than sediment accumulation or to sediment accumulation around the colony occurred at a constant

Coralla of Favosites forbesi show the largest degree of morphologic variation, being represented by two discrete forms. Although astogeny of F. forbesi is essentially radial, bottom-dwelling colonies characteristically originated on shell debris and formed steep-sided erect coralla. In contrast, other colonies were symbiotic on the erect stalks of crinoids and formed globose coralla. Although these technically represent ecophenotypic responses, each is a discrete form adapted to a distinct substrate. No continuous variation would have existed between these two forms. Although it might be argued that these represent two distinct species, colony form alone is usually an insufficient criterion for species-level discrimination.

Discussion

The depositional regime for the Birdsong was one of episodic (although probably frequent) occurrences of higher energy conditions and mud influx that continually modified the nature of the existing seafloor. The biota were adapted to the changing nature of the substrate; however, the resulting assemblages changed composition depending upon the frequency, type, and severity of the depositional disturbance. During any particular phase of Birdsong deposition, the environment can be said to have been

uninterrupted rate nearly identical to the rate of colony growth, which was unlikely.

Favosites foerstei was described by Dunbar (1920) from specimens from the Birdsong Shale and Ross Limestone in western Tennessee using the same emphases and features as Hall had used in describing F. conicus. F. foerstei is not known to be so geographically widespread as F. conicus, but nonetheless appears to exhibit little intraspecific variation. The axial growth region of F. foerstei produced a consistently, although not necessarily evenly contoured, domical summit. The convex base also is logically produced by this pattern of astogeny, in which corallites grow upward within the axial zone and then turn outward. Slight variation in the degree of convexity of the base or the eccentricity of the basal apex resulted from a combination of substrate consistency and fine differences in the pattern and rate of sediment accumulation. Growth of colonies of F. foerstei was dominantly genetically constrained, but allowed for a slight degree of ecophenotypic variability. It is worth noting, however, that the axial pattern of budding in F. foerstei (Fig. 42d) is generally similar to that of branching tabulates (e.g., Striatopora). Thus, a branched corallum is theoretically possible for F. foerstei, but its absence suggests additional genetic constraint.

"disturbance-driven" (White and Pickett, 1985: Pickett and White, 1985; Sousa, 1984, 1985; Probert, 1984). Soft-bottom fauna are commonly influenced by disturbances or develop in response to disturbances (McCall and Tevesz, 1985; Probert, 1984; Woodin, 1978).

Modern ecologic communities are defined as local populations of organisms that live at the same time, within the same general habitat (although the habitat can overlap with other communities), are dynamic in nature, and the biota either interacts or has the potential to interact. Most authors emphasize the importance of biotic interactions in determining and modifying community structure. Dayton (1979) suggested that the key to understanding the structure, at least of intertidal communities, is to identify the prevailing biotic interactions that occur <u>after</u> larval settlement.

Two types of interactions that have been considered to have the greatest primary structuring influence on marine community organization are competition for such resources as space (Woodin and Jackson, 1979; Jackson, 1977; Connell, 1961) and predation (Russ, 1980; Menge and Sutherland, 1970; Paine, 1966; Connell, 1961). Interactions such as symbiosis, parasitism, amensalism, etc. have received considerably less attention with respect to the marine environment (however, see Jackson, 1979; Aller and Dodge,

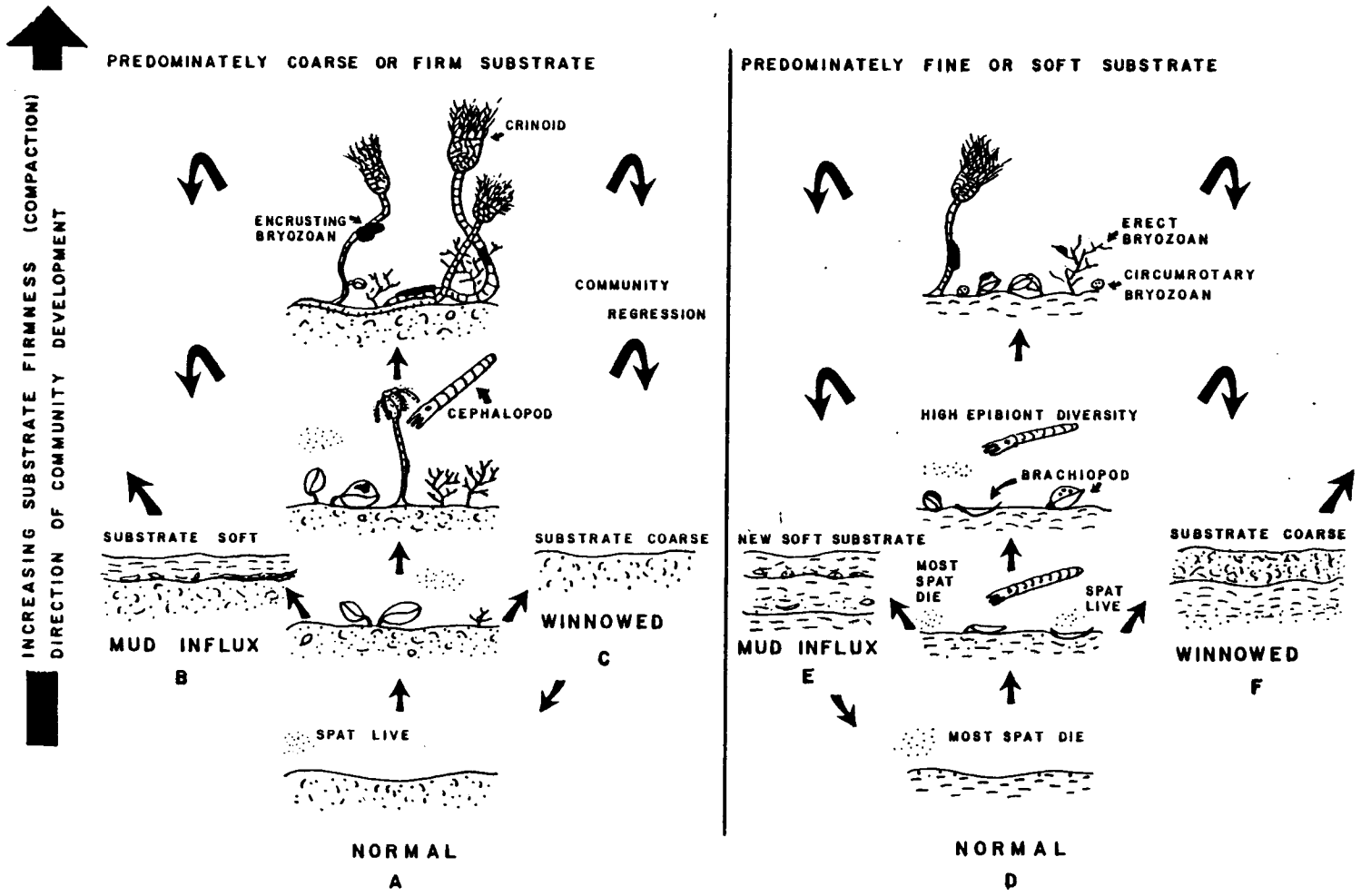
1974). In recent years, the importance of abiotic factors such as disturbances or perturbations has been recognized as also being able to affect the structuring of modern marine communites (Sousa, 1984, 1985; Probert, 1984).

All of these factors affect the organisms once they are established and clearly direct the structure of the community to varying degrees at varying times. However, the initial larval recruitment of the earliest members also plays a very important role in how the community will develop because it controls which organisms will be present to interact.

The model explained below (Fig. 49) describes the possible developmental pathways of assemblages common in the Birdsong (as well as those not well represented in the Birdsong) in response to the depositional regime and substrate modification at the time of larval recruitment. As used herein, developmental pathways differ from stages of succession (sensu, Walker and Alberstadt (1975)) in that there is no specified sequence of development that is taken (e.g., colonization - stabilization - diversification - domination) as is suggested by the term `succession'. Any combination of pathways, or regressions along pathways and redirections to other pathways, are possible.

The model has two primary controls, one biological and one environmental. The biological control is the temporal

Fig. 49. Developmental pathways for invertebrate communities in the Birdsong Shale. Pathways begin with a barren substrate (A or D) and can become modified along any of three pathways leading to either a soft mud substrate, a coarse-grained substrate, or a firm mud substrate. At any point in a pathway, depositional processes can reset or redirect the development. Spat arrival may be limited seasonally or by biological processes that are determined by which spat settle a substrate first. The stage of development of communities depends upon the original substrate characteristics, timing and composition of larvae, nature and frequency of disturbances, and biotic interactions between adults and larvae, larvae and larvae, host and epibiont, and in established communities, competition for resources, predation, etc.


INCREASING SUBSTRATE FIRMNESS (COMPACTION)
DIRECTION OF COMMUNITY DEVELOPMENT
PREDOMINATELY COARSE OR FIRM SUBSTRATE
CRINOID
ENCRUSTING BRYOZOAN
COMMUNITY REGRESSION
CEPHALOPOD
SUBSTRATE SOFT
SUBSTRATE COARSE
MUD INFLUX
B
WINNOWED
C
SPAT LIVE
NORMAL
A
PREDOMINATELY FINE OR SOFT SUBSTRATE
ERECT BRYOZOAN
CIRCUMROTARY BRYOZOAN
HIGH EPIBIONT DIVERSITY
BRACHIOPOD
NEW SOFT SUBSTRATE
SUBSTRATE COARSE
MOST SPAT DIE
SPAT LIVE
MUD INFLUX
E
WINNOWED
F
MOST SPAT DIE
NORMAL
D

variability and composition of larval recruitment. The environmental control is the nature of the substrate, including grain size, substrate mobility, and consistency. At any stage, one of three things can occur. First, an established community, regardless of its initial substrate of development, can continue to add shelly material to the substrate to produce and maintain an essentially coarse-grained substrate (A, but D can also accumulate bioclastic debris to evolve into a coarse-grained substrate). At this point, substrate ceases to be limiting and community development occurs like that described for the coarse-grained substrate. Second, an influx of mud can smother and "reset" the system to an earlier stage of development (E) or redirect it along a different path (B). Third, a storm event can winnow mud from the substrate and produce a graded packstone to grainstone substrate in which larval settlement sites are not limiting (C and F).

Assuming that oxygen, temperature, salinity, etc. are all within the living limitations of the larvae, then the nature of the substrate becomes the most critical factor in community establishment. Larvae require a firm substrate for attachment. If grain size is coarse enough (and not too mobile) attachment can occur almost anywhere (Fig 49). In other words, initial settlement sites may not be limiting.

Once the organisms are established, their competitive abilities take over and the traditional interactions such as competition, predation, etc. can develop and influence the development of community structure. The essential point is that the nature of the sediment is less important in coarse grained environments and the seasonality of spat arrival will remain the controlling influence (Gaines and Roughgarden, 1985; Humphries, 1973). Earlier arriving spat can conceivably dominate and exclude later spat. Viewed at this scale, larval recruitment determines which organisms will be present to dominate the community. Examples of recruitment-determined dominants in coarse grained environments range from the rocky intertidal (Gaines and Roughgarden, 1987; Connell, 1985; Sousa, 1979; Osman, 1977) to sandy substrates (Woodin, 1976) to artificial substrates (Sutherland and Karlson, 1978).

The developmental pathways model begins with a substrate initially barren of benthic life immediately after some disturbance such as a massive sediment influx. It should be noted that periodic sediment influxes in the marine environment are common occurrences on varying scales (see Sousa, 1985; Probert, 1984 for a summary of the varying types of disturbances recognized in the recent marine environment). Grain size and consistency are variable in the model.

On mobile substrates, larval survival is minimal and establishment is not possible; therefore, community development is impeded. Once the substrate becomes stabilized, the importance of consistency and grain size of the sediment becomes important. At this point, community development can proceed along two routes. On coarse grained sediment, attachment sites for larvae are plentiful. Also, early cementation of carbonate-rich substrates can decrease the effect of sediment type by creating continuous firm grounds. Although this was not important in the Birdsong, dewatering of the terrigenous sediment probably had much the same effect. Therefore, the source of the parent population or composition of the spat combined with the seasonality of larval release will determine which organisms will colonize the new substrate. Once this initial community is established, its persistence and direction of change will be determined by the more traditional biotic interactions of predation and competition for food, space, nutrients, mates, etc. or can be reset or redirected by subsequent periodic disturbances.

In the Birdsong, coarse grained substrates resulted from storm-winnowed accumulations of skeletal debris. The community that developed on this substrate was dominated by stoloniferous and rooted crinoids, pedunculate brachiopods, and encrusting and arborescent bryozoans. All of these

organisms are epifaunal suspension feeders. This community type is typical of the Paleozoic and has been considered the 'norm' (e.g. Sepkoski, 1979); however, in the Birdsong, it develops on event-produced coarse-grained substrates rather than slowly accumulated debris.

The second route for community development is best shown in the interbedded shale of the lower Birdsong. The shale represents initially very soft muddy substrates. The spat (no matter what their composition) would perish if they settled into the soft mud. In this situation, the available suitable attachment sites were either eliminated or consisted of only rare living biota or finely comminuted debris. The larvae could colonize only as epibionts or as epitaphic encrusters. Although seasonality of larval recruitment would have been an important factor in recruitment here also, the only organisms to survive on the soft substrate would be those that were adapted to soft substrates as adults (i.e., ambitopic). The shales, indeed, are dominated by these types of organisms such as strophomenid and atrypid brachiopods and stalked crinoids (Broadhead and Gibson, 1986).

Once this initial fauna was established, the substrate was effectively modified by providing isolated "islands" for larval attachment (living and dead substrates). Recruitment space, at this point, was still highly

limiting. Colonial organisms such as favositid and auloporid corals, bryozoans, and other epibionts such as spirorbids, cornulitids and inarticulate brachiopods became common. Competition for space dominated the community development process as evidenced by (1) the high ratio of epibionts and endobionts on both live and dead hosts, (2) numerous overgrowths among epibionts, (3) obvious changes in growth directions around existing epibionts and (4) reoccurring symbiotic relationships between certain epibionts and hosts (Broadhead and Gibson, 1986). The epibiont fauna that became established then controlled the further development of the community by either facilitating the recruitment of some larval types or eliminating others, (i.e., adult-larval interactions structured the community along with epibiont-epibiont interactions).

Comparison To Other Areas

The Birdsong fauna is comparable to large faunas (open shelf) discussed by other workers. Makurath (1977) recognized an open shelf lithofacies in the Keyser Formation (Upper Silurian-Lower Devonian) of the eastern United States composed of mixed carbonates and fine siliciclastics. He also recognized changes in substrate conditions, similar to those described for the Birdsong, by studying brachiopod pedicle adaptations and shell form.

The Birdsong differs from the Keyser, however, by not having nearshore lithofacies (tidal flats, etc.). The Keyser also has a more diverse biota that consists of stromatoporoids and algae.

Koch (1981) recognized six communities, arranged in an onshore-to-offshore, pattern from the Onandaga Limestone (Middle Devonian) of eastern North America. Two of his more nearshore shelf to slope associations, the Atrypid-Kozlowskiella community and part of the Atrypid-Levenea community, are similar to the Birdsong fauna in overall composition. Koch (1981) interpreted these two communities to have developed near the shelf margin under medium to high energy conditions. The Onandaga contains few shale interbeds.

Feldman (1980) recognized three associations from the Middle Devonian of New York State: (1) a Leptaena-Kozlowskiella association, (2) an Atrypa association, and (3) an Atrypa-Kozlowskiella association. All three developed within the presence of variable amounts of mud on the shelf, which were produced by cessation of coarse carbonate production rather than by clastic influx until the onset of Marcellus Shale deposition. As with the previous studies, Feldman interpreted the community pattern to have developed in response to distance from shore. All three communities were classified as "middle neritic" in

terms of depth and showed strong correlation with substrate conditions.

These studies illustrate the point that where a fauna developed in a depositional setting characterized by mixed carbonate-siliciclastic deposition, it was heavily influenced by the consistency of the substrate at various times during deposition and by the presence and severity of higher energy events.

Biotic Interactions

Previous Studies Of Biotic Interactions In The Fossil Record

The study of biotic interactions in the fossil record has a long history. The earliest in depth study in North Americas was by Clarke (1908), who documented various biotic associations for Paleozoic organisms (mostly Silurian and Devonian), which he interpreted to represent dependent associations (which he termed symbiotic). He later (1926) expanded his study of interactions to include Precambrian to Mesozoic organisms and postulated on the origin and significance of dependent associations, as well as the origin, expression, and significance of disease in the fossil record.

Yakovlev (1926) recognized three kinds of biotic

associations from the Russian Paleozoic (mostly Devonian) in an often cited study. His three associations were: (1) myzostomid parasites on crinoids, (2) platycerid commensals on the anal opening of crinoids, and (3) a symbiotic relationship between auloporid corals and various species of brachiopods. Later, Dunbar (1928) described encrusting bryozoans on an ammonite, which he concluded were commensal, because the ammonite shell partly covered the bryozoan colony.

Predation, as a biotic interaction, took on importance with the recognition of the common occurrence of borings in Paleozoic fossils (Clarke, 1908, 1926; Fenton and Fenton, 1931, 1932a, b). Clarke (1908) and Fenton and Fenton (1932a, b) also noted that some borings were not predatory in nature but, were the result of sponges in which the borings represented domiciles. Clarke (1908) named these Clionolithes and attributed them to the work of sponges similar to the modern Cliona.

From the 1930's to the 1950's, only a few scattered studies of biotic interactions were published. Most notable among these was a study of spirorbid encrustations on non-marine bivalves from the Carboniferous, in which Trueman (1942) argued for a commensal relationship, rather than a parasitic relationship. Teichert (1945) described parasitic worm borings in Devonian brachiopods and

bivalves. Shou-Hsin (1959) described the occurrence of Aulopora on the Devonian brachiopod Mucrospirifer, which he interpreted was mutualism. Seilacher (1960) was one of the first to use epizoans as a paleoecological tool to interpret the ecology of various types of host by plotting the preferred orientations and slope distributions of epizoans.

Ager (1961, 1963) profoundly influenced the way in which biotic interactions were viewed in the paleontological community. Drawing heavily from modern associations identified by Clarke (1954), Ager concentrated on describing and interpreting diversity of epibionts that occurred on Devonian brachiopods (Ager, 1961) and analyzing the role of relationships between species (Ager, 1963). Biernat (1961) described borings, which he attributed to a parasitic polychaete worm on Atrypa and noted that the borings were species-specific. Hoare and Stellar (1967), Schumann (1967), and Seilacher (1968) described various endobionts and epibionts and used the distributions on the host shells to determine the autecology of the host.

Cameron (1967) described a soft-bodied, limonite-replaced, spionid polychaete worm from the Devonian, which he compared to the recent boring polychaete Polydora. He also described a new serpulid worm from the Hamilton of New York State (Middle Devonian) and suggested

a commensal relationship with it's bivalve host (Cameron, 1968).

Carriker and Yochelson (1968) compared borings made by recent gastropods to those found in fossils, and the importance of boring organisms to paleoecology and interpreting environments of deposition has since increased tremendously. Carriker and Smith (1969) edited a volume devoted to the recognition and interpretation of boring organisms and borings in all calcareous substrates. This volume is still a basic reference for the study of boring organisms and contains many examples from the fossil record (e.g., Cameron, 1969; Seilacher, 1969; Sohl, 1969). Most of the newer studies involving boring organisms are of a more interpretive nature, rather than simply descriptive, attesting to the usefulness of studying borings (e.g., Boekschoten, 1966; Lawrence, 1969; Taylor, 1982; Pickerill and Harland, 1984; Lambers and Boekschoten, 1986; Liljedahl, 1985, 1986; Vogel et al., 1987).

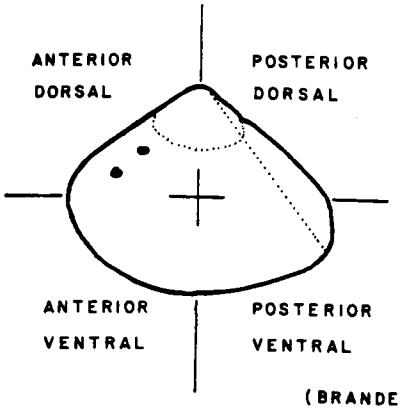
By the 1970's, and into the 1980's, studies of epibiont (and endobiont) paleoecology were common; however most studies were concerned only with describing diversity on single host individuals or species (Kesling, et al., 1980; Brett and Cottrell, 1982), specificity of epibionts to particular hosts (Brett, 1978; McNamara, 1978; Brett and Cottrell, 1982), or suggesting possible commensal

relationships with single specimens or species of host (Chatterton, 1975; Pitrat and Rogers, 1978).

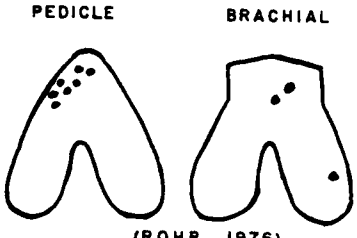
Several important studies contributed greatly to the development of techniques for analyzing the distribution and orientation of epibionts on hosts. Numerous methods have been devised for plotting the distribution of epibionts, depending on the preference of the different investigators (e.g., Rohr, 1976; Sparks et al., 1980; Zumwalt and Delacea, 1980; Kesling et al., 1980; Brande, 1982; Sando, 1984). Most of the more recent attempts use some form of overlay grid system (Fig. 50).

There have been few attempts to synthesize the information gleaned from all of the different studies of biotic interactions in the fossil record. Most such attempts have concentrated on: (1) particular groups of host or epibiont (e.g., Taylor, 1979, 1984; Oliver, 1983; Meyer and Ausich, 1983; Spjeldnaes, 1984), (2) distribution within particular environments of deposition (e.g., Kauffman and Sohl, 1974; Rodriguez and Gutschick, 1975; Thomsen, 1977; Watkins, 1981), (3) the effects of biotic interactions on sediment production and accumulation, or the patchy development of organisms on the substrate (e.g., Bottjer, 1982; Liddell and Brett, 1982; Pestana, 1984; Coates and Jackson, 1985; Miller and Alvis, 1986), or (4) identifying particular types of interactions recognized

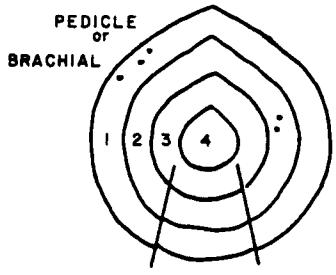
Fig. 50. Examples of the various systems used to plot the distribution of epibionts.



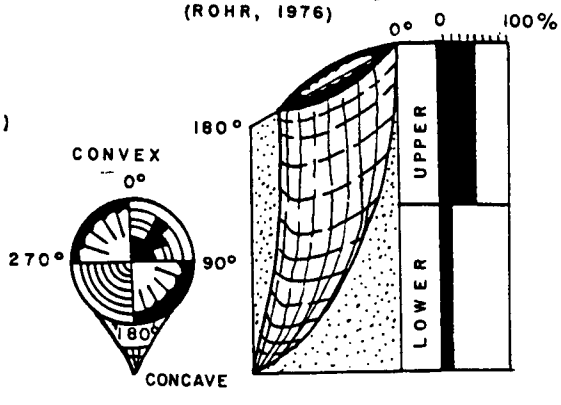
(BRANDE, 1982)



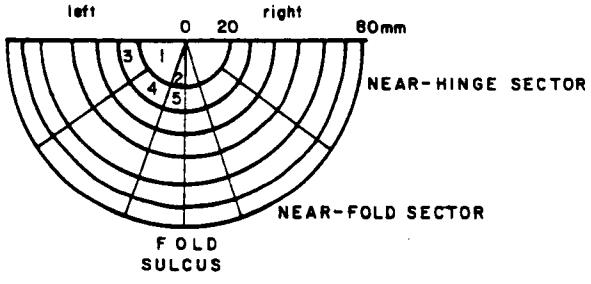
(ROHR, 1976)



(ZUMWALT & DELACEA, 1980)



(SANDO, 1984)



(SPARKS, HOARE, & KESLING, 1980)

within a particular species or individual (e.g., Newell, 1970; Blind, 1970; Peterson and Hoare, 1973; Newman and Ladd, 1974; Hurst, 1974; Richards, 1974; Warn, 1975; Welch, 1976; Pitrat and Rogers, 1978; Morris, 1981; Reid and Broadhead, 1983; Franzen, 1984; Werle et al., 1984; Duringer, 1985; Elias, 1986; Nield, 1986; Alvarez and Taylor, 1987).

Definitions

A biotic interaction is defined as the effect one organism has on another organism (Woodin, 1983). In the more general sense, biotic interactions refer to any relationship that exists between two or more organisms. This is true regardless of whether or not the relationship is obligate (required for the existence of at least one of the participants) or facultative (occurs by chance), direct (one organism physically encounters another) or indirect (one organism affects another through a series of intermediate stages or associations). In a more restricted usage, biotic interactions refer to unpatterned relationships between coexisting individuals or species-specific relationships in which the cooperative or antagonistic nature of the association, or the relative cost or benefit of the relationship, can be determined or inferred (Clarke, 1954; Ager, 1963; Woodin, 1983). The

definition of biotic interaction used in this study follows the more restricted usage. In this way, true biotic interactions in the fossil record (in which benefit or cost must be inferred from indirect evidence) can be distinguished from non-interactive associations.

Non-interactive associations are associations in which two or more organisms show some type of physical relationship (i.e., occur together), but did not interact with one another (usually because one of the organisms was not living). Among fossils especially, non-interactive association can be confused with true biotic interactions because of the difficulty in determining whether or not both members of the association were living at the same time. A useful term to describe this type of association is epitaphism (Stellar, 1965; Morris and Rollins, 1971; Sparks, et al., 1980), which is the occurrence of an epibiont attached to the shell of an organism that was not living at the time of attachment.

There has been considerable confusion in the literature concerning terminology and definitions applied to the study of biotic interactions, both in Recent studies (Cheng, 1970; Starr, 1975; Lewin, 1982; Goff, 1982; Woodin, 1983) and in studies in the fossil record (Ager, 1963). Most studies of biotic interactions in the fossil record invariably refer to Ager's (1963) classification, which was

modified from Clarke (1954), and in which the definitions of many of the types of interactions differ considerably from their original usage. Starr (1975), Lewin (1982), and Goff (1982) have summarized the nomenclatural problems that have arisen over the years, especially with the use of term "symbiosis". In the course of this study, a review of the paleontological literature revealed that there was no consensus on the usage of terminology used to describe fossil interactions. This is probably because nearly all studies of fossil interactions refer to Ager's (1963) definitions, or to some other study that drew heavily from Ager's work.

Symbiosis was originally defined by de Bary (1879) to describe two organisms that simply "lived together", regardless of whether the association was harmful or beneficial (Lewin, 1982). As a result of Clarke's (1954) definitions, which were in the basic ecology textbook of that time, symbiosis has taken on a more specific meaning, namely, the term implies benefit to <u>each</u> participant (Lewin, 1982). Goff (1982) recommended usage of the original, less specific definition, under which different categories of symbiosis could be recognized that reflect the types of coexistent relationships between two organisms.

Using symbiosis to mean "living together" is more

appropriate for paleontological studies because, even though it can usually be established with reasonable certainty that two organisms lived together, the relative cost or benefit of the relationship can rarely be determined with confidence (only inferred using common sense). Clearly, a hierarchical system of classification of interactions that reflects the degree of certainty of the type of relationship that existed between the two organism is more suitable to the study of biotic interactions in the fossil record and is more in keeping with the original intended usage of the terms. The suggested hierarchical classification and definitions of biotic interactions that should be applied to the fossil record is given in Table 2.

Results

The surfaces of 371 digitized specimens, belonging to 13 species of host, contained 1786 epibionts (Appendix D, E). The Birdsong Shale fauna is rich in epibiont diversity; 39 different species of epibionts and endobionts were recognized (Table 3). A plot of the frequency of occurrence (total epibionts per host) of all epibionts on individual hosts (Fig. 51) shows that the Birdsong epibionts exhibit no clearly definable host preference (i.e., the relationships are not taxon-specific),

Table 2. Suggested Hierarchical Classification Of Biotic Associations As Applied To The Fossil Record. Relative Benefit Of The Association Is Given By: + = Gain, - = Loss, 0 = Neutral.

INTERACTIVE ASSOCIATIONS: Both members living at the time of the interaction.

1. Antagonistic Association: One species suffers through the actions of another.
   - A. Defense Action (0,-) or (-,-): Short duration act of warning or means of avoiding predation (bites, scrapes).
   - B. Predation (+,-): Deliberate, exploitative interaction of short duration in which one organism benefits from the association by deriving nutriment, resulting in the death of the other organism.
2. Competitive Association: Species contend for resources.
   - A. Direct Competition (-,-): Two or more organisms physically compete for resources.
   - B. Indirect Competitiion (-,-): Competition for resource in which there is no direct contact between participants.
3. Symbiotic Association: Species live together.
   - A. Non-cooperative Symbiosis: One or both participants suffer from the relationship.
     1. Parasitism (-,+): Long term exploitative relationship in which the parasite benefits at the obvious detriment of the host.
     2. Amensalism (0,-): (= Antibiosis) Interference phenomenon resulting from one member inhibiting another in an attempt to avoid interacting.
   - B. Neutral Symbiosis (0,0): (= Toleration) Technically not an interaction by definition, but differs from epitaphism in that both organisms are living at the time of the association.
   - C. Cooperative Symbiosis: One or both members benefit, but neither is harmed.

NON-INTERACTIVE ASSOCIATIONS: Association characterized by a lack of interactions between physically contacted species or individuals.

1. Epitaphism: Association in which the host was not living at the time of the association.

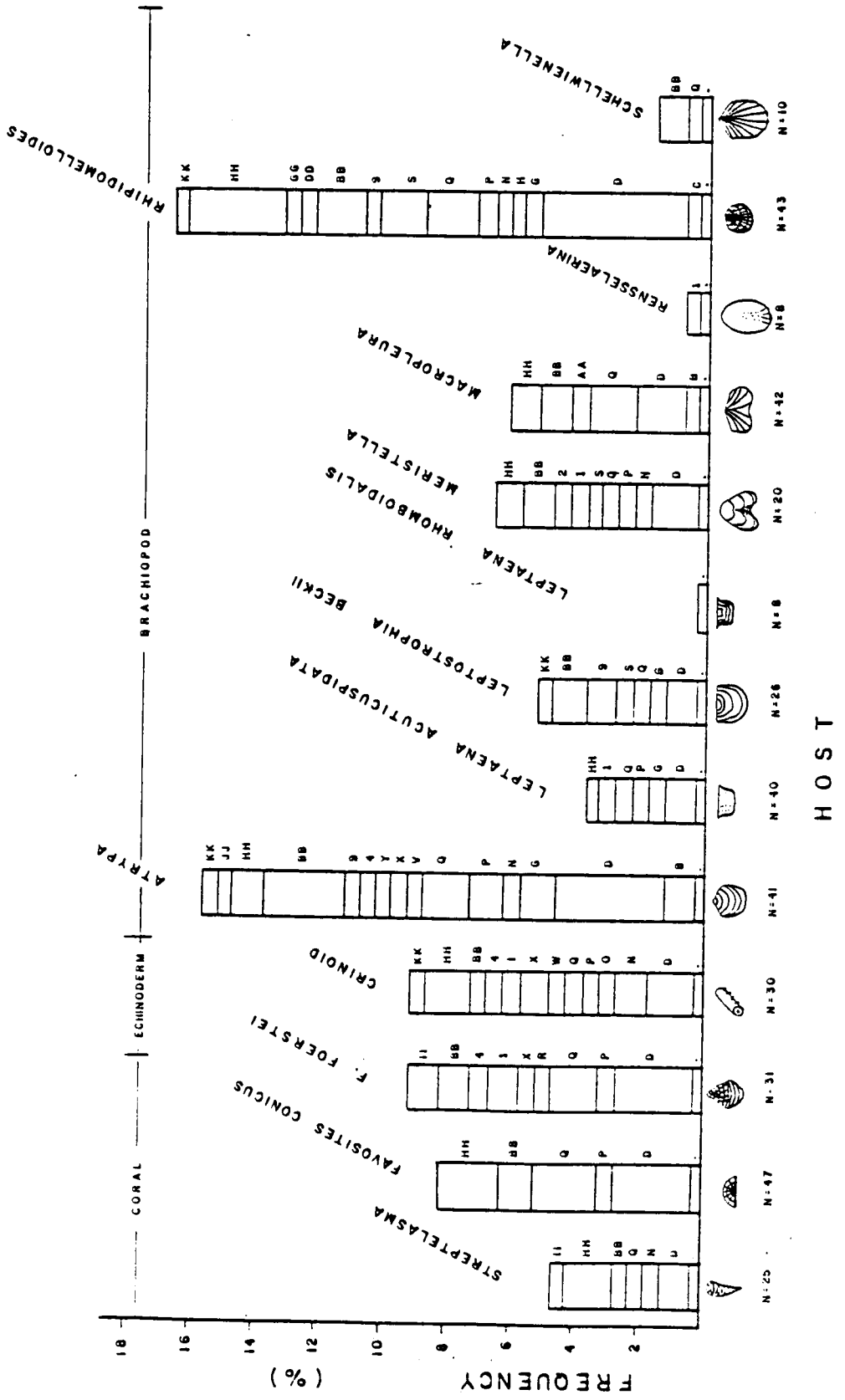
Table 3. List Of Epibionts In The Birdsong Shale. Codes Refer To CMS SAS Output Designations Used In Figures 54 And 55.

EPIBIONT	CODE
CORALS	
Aulopora schohariae	9
Pleurodictyum lenticulare	A
Favosites sp.	C
BRYOZOANS	
Botryporella sp.	B
Eliaspora stellaria	-
Hederella sp.	J
Ceramopora cf. *parvicella*	Q
Fistulipora cf. *unilinea*	Y
F. cf. *maculosa*	W
F. sp. A	X
F. sp. B	V
Buskopora sp.	U
Eridopora sp.	-
Lichenalia cf. *lerialis*	-
Ptylodictya tenuis	T
P. tenuis bases	S
Intrapora puteolata	2
Leptotrypa cf. *spinifera*	N
Leptotrypella sp.	O
Eridotrypa sp.	P
Lioclema cf. *pulchellum*	1
Monotrypa cf. *tabulata*	-
Phaenopora sp.	R
Flabellotrypa sp.	M
Stomatopora sp.	L
Bryozoan bases	HH
Unidentified	B
BRACHIOPODS	
Liljevallia adnascans	4
Crania sp.	3
Unidentified articulates	5

Table 3 (Continued)

EPIBIONT	CODE
ECHINODERMS	
Edriocrinus adnascans	-
BORINGS	
Irmena sp.	II
Dendrina sp.	GG
Clionoides sp.	DD
Vermicuformis sp.	F
WORMS	
Spirorbis laxus	D
Cornulites sp.	C
Other	E
OTHER	
Pyrite crusts or tubes	0
Bite marks	H
Black organic tubes	I

Fig. 51. Distribution of epibionts on hosts. Frequency percent is the percentage of the total population of digitized epibionts on that host. Letters and numerals refer to epibionts (see Table 3). Lower block designated with a "." represents the sum total of all other epibionts on that particular host.


SCHELLWIENELLA
RHIPIDOMELLOIDES
RENSSELAERINA
MACROPLEURA
MERISTELLA
RHOMBOIDALIS
LEPTAENA
BECKII
LEPTOSTROPHIA
ACUTICUSPIDATA
LEPTAENA
ATRYPA
CRINOID
F. FOERSTEI
FAVOSITES CONICUS
STREPTELASMA
BRACHIOPOD
ECHINODERM
CORAL
HOST
FREQUENCY
(%)
18
16
14
12
10
8
6
4
2
N=10
N=43
N=8
N=42
N=20
N=8
N=26
N=40
N=41
N=30
N=31
N=47
N=25

regardless of the mode of life of the host. The most common epibionts occurred on representatives of nearly all thirteen host species. Omissions can be easily explained as reflecting the low numbers of host specimens digitized for those particular hosts. The most common epibiont species was the solitary annelid Spirorbis laxus (22% of the total epibiont population) followed in decreasing abundance by Ceramopora cf. parvicella, unidentified bryozoan zoaria, bryozoan basal attachment points, Leptotrypa sp., Fistulipora sp. A, Ptylodictya tenuis bases, and Eliaspora stellaria (Fig. 52). The more common members of the Birdsong fauna have the greatest numbers of epibionts and the greatest diversity of epibiont types. This can be due to two causes. First, the more common hosts have a greater chance of being encrusted by a greater number of epibionts. Second, the less common hosts are not as well represented in the digitized data; therefore, the lower numbers of epibionts might be an artifact of collection rather than a real pattern in epibiont abundance on those hosts.

Host-Epibiont Associations

There is a wide range of structural and behavioral relationships that can be identified among epibionts and hosts in the Birdsong fauna. These associations can be

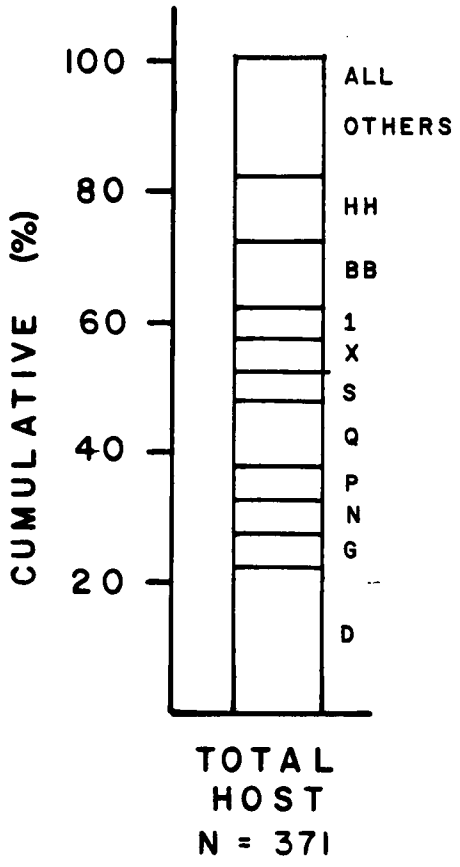


Fig. 52. Cumulative abundance (%) of Birdsong epibionts showing the ten most commonly occurring species. See Table 3 for key to letters and numerals.

divided into host-epibiont (Fig. 53, 54) and epibiont-epibiont associations (Fig. 55). In spite of the large data set of digitized epibionts, the low frequency of occurrence of many epibiont species on some hosts makes interpretations of recurrent distributions and possible associations speculative at best; therefore, only the most common and obvious epibiont associations will be discussed.

Spirorbis laxus does not show any particular host specificity, nor does it show much preference for a region on most hosts (Fig. 56, 57). For example, although S. laxus appears to be more common in region three on Atrypa reticularis (Fig. 58), that region covers a greater area of the shell. When looked at proportionally with respect to region, S. laxus shows no preference for any region on A. reticularis. This same observation holds true for the brachiopod hosts Leptaena acuticuspidata, L. rhomboidalis, Leptostrophia beckii, and Rhipidomelloides oblata, which are all characterized by low surface ornamentation (see below).

S. laxus does show a preference for region in two of the brachiopod hosts, Meristella atoka and Macropleura macropleura. On M. atoka, S. laxus exhibits a weak preference for region five (Fig. 57) which is the fold and sulcus region (Fig. 56) and is more common on the pedicle valve. M. atoka has a heavy umbo with a small pedicle and

Fig. 53. Host-Epibiont Relationships - I. A. Epitaphic association of Ceramopora cf. parvicella encrusting interior (and exterior) surface of abraded spiriferid, x 3.0. B. Commensal relationship between Meristella atoka and unidentified bryozoan, x 1.0. Note that the bryozoan has encrusted both valves, but that the bryozoan colony remained broken across the commissure of the host indicating that the encrustation was not lethal. Arrow points to a epizoitic brachiopod completely overgrown by the bryozoan. C. Rhipidomelloides oblata with Aulopora schohariae, Cornulites sp., Ptylodictya tenuis base, and Spirorbis laxus, x 1.4. Note the lack of competitive interactions and the offset of the younger corallites of the auloporid across growth increments of the host (arrow) so that the coral could remain along the commissure of the host, indicating a commensal relationship. D. Epitaphic association of auloporids and bryozoans on pedicle valve of ?Orthostrophia strophomenoides, x 1.0. E. Oriented Aulopora schohariae commensal on Schellwienella sp., x 1.0. F. Fistulipora cf. maculosa on Atrypa reticularis, x 2.0. G. Epitaphic bryozoan encrusting across the commissure of Leptaena rhomboidalis, x 1.0. H. Leptostrophia beckii with epitaphic Aulopora schohariae that was overgrown by a fistuliporid bryozoan, x 1.0. I. Surface of Streptelasma strictum showing Irmena borings, x 10.0. J. Epitaphic encrustation of Leptotrypa cf. spinifera on crinoid columnal, x 38.

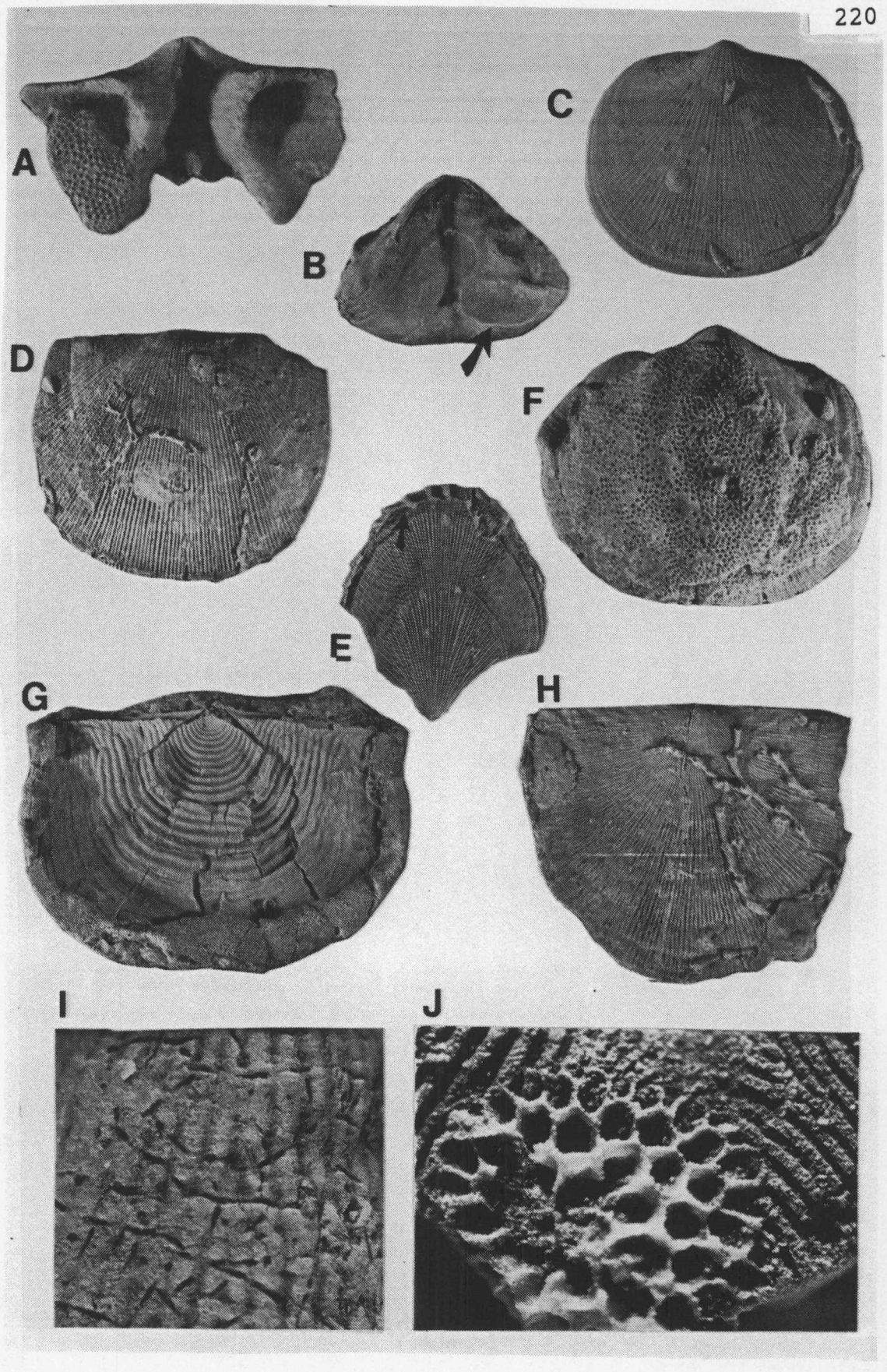

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Fig. 54. Host-Epibiont Relationships - II. A. Atrypa reticularis with completely encrusted brachial valve, x 3.0. B. Pedicle valve of A showing bryozoan encrusting commissure of brachiopod suggesting either an epitaphic relationship or a symbiotic relationship that continued after the death of the host, x 3.0. C. Atrypa reticularis with encrusting Pleurodictyum lenticulare, x 2.0. D. Atrypa reticularis with oriented auloporid in sulcus and large Spirorbis laxus near the umbo, x 2.0. Large crystal next to spirorbid is pyrite. Note the upturned flanges of the host; an adaptation to soft substrata. E. Rynchospirirna globosa with commensal Leptotrypa cf. spinifera that grew to the commissure of the brachial valve but did not cross it, x. 3.0. F. Brachial interior of Rhipidomelloides oblata with epitaphic bryozoan, Hederella sp., x 2.0. G. Stoloniferous crinoid stem with smaller parasitic crinoid (note gall material secreted by the host) which was later encrusted by Leptrotrypa cf. spinifera. Note that the parasitic crinoid changed growth direction upon comming into contact with the stoloniferous side of the host, which would have been the side attached to the substrate, x 2.0. H. Macropleura macropleura with bite mark (arrow) and bryozoan basal atachments, x 1.0. I. Eliaspora sp. on R. oblata showing stolons connecting zooids, x 15. J. Epitaphic fistuliporid bryozoans, Spirorbis laxus, and Clionoides on Atrypa reticularis, x 3.0.

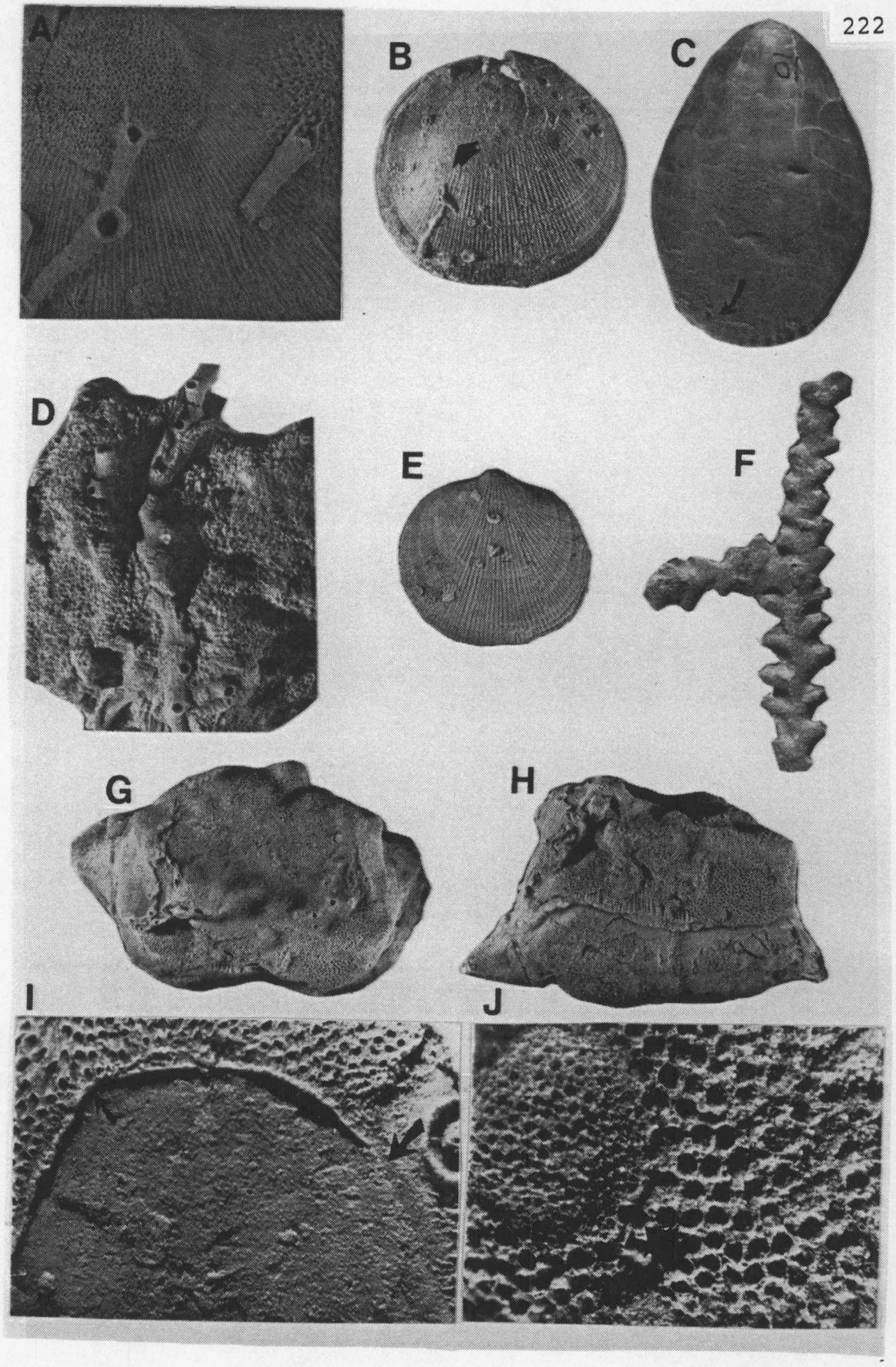

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Fig. 55. Epibiont-Epibiont Relationships. A. Leptostrophia beckii showing epitaphic overgrowth of fistuliporid overgrowing earlier formed corallites of Aulopora schohariae, x 1.0. B. Auloporids, spirorbids, and Eliaspora on Rhipidomelloides oblata with pyritized encrusting sponge (arrow) that originally overgrew a spirorbid and part of the Eliaspora colony, x 1.25. C. Rensselaerina medioplicata with two encrusting bryozoans over commissure, x 1.6. Note that part of one bryozoan has actively grown towards the other bryozoan (arrow). D. Auloporid-bryozoan commensalism (ramose variety) embedded in an encrusting Leptotrypa cf. spinifera, x 1.0. Note that the corallites remained open. E. Auloporid-bryozoan commensalism showing regular arrangement of corallite branching, x 1.5. F. Example of a "typically" encrusted specimen of R. oblata showing lack of substrate competition between the epibionts, x 1.0. G. Auloporid-bryozoan symbiosis (massive variety). View from top, x 2.0. Note open corallites (arrow). H. Side view of G showing intergrowth of bryozoan and coral. I. Ceramopora cf. parvicella on brachiopod valve showing marginal zoarium growth to form an upturned fringe against an unidentified soft-bodied encruster. Note response of brachiopod to the soft-bodied encruster (large arrow). The bryozoan also redirected growth around the obstruction (small arrow), x 15. J. Competitive interaction between one bryozoan (round massive colony) on top of a sheet-like bryozoan, Leptotrypa cf. spinifera. Note that the zooids of L. cf. spinifera remained open (arrow) as the second bryozoan grew around it., x 16.

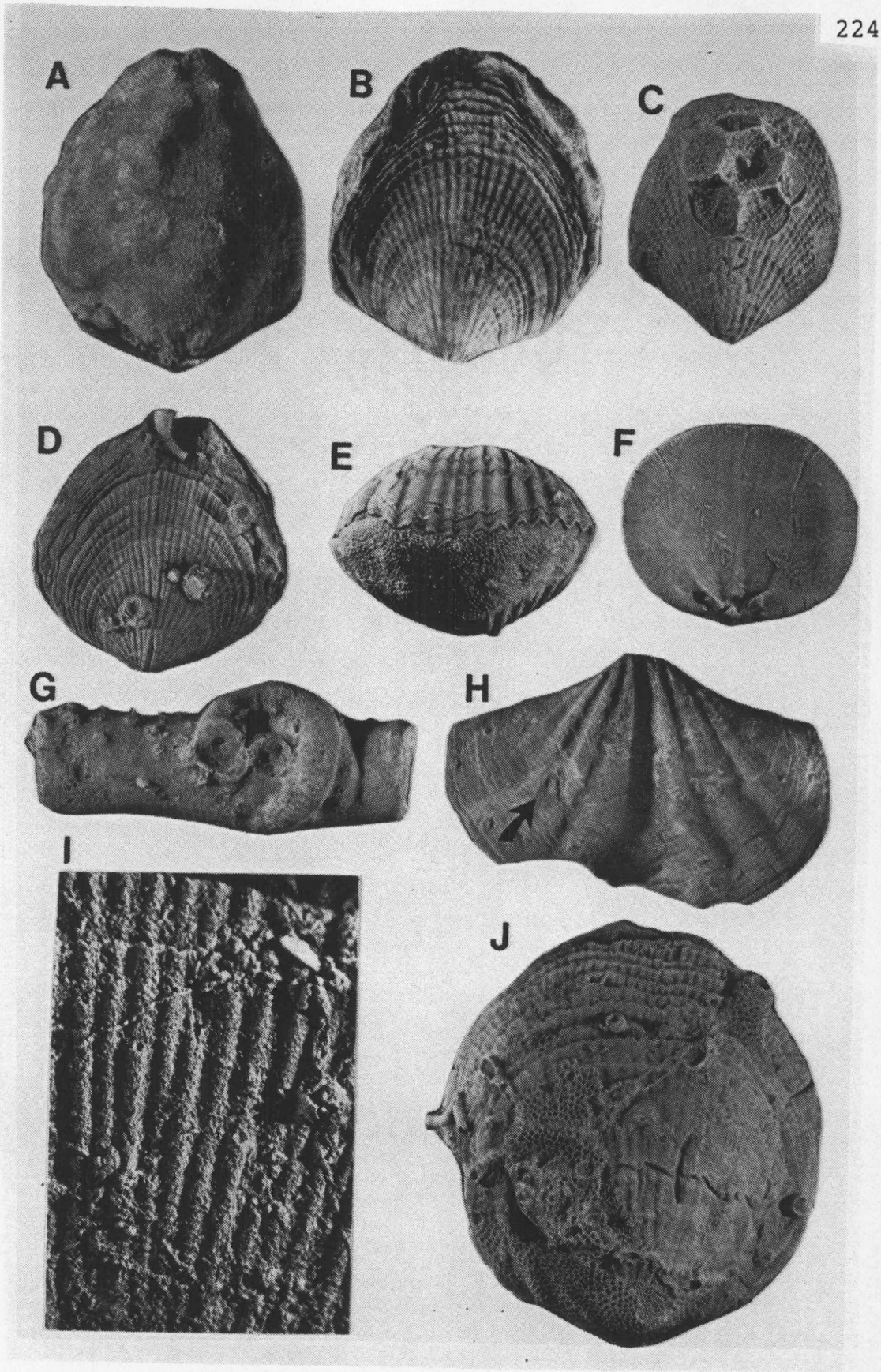
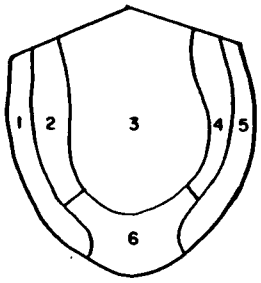
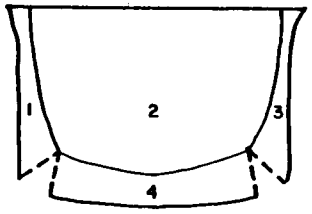

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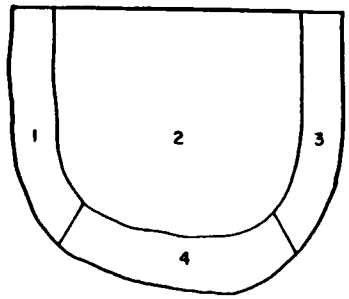
Fig. 56. Regions on hosts used in this study to plot epibiont distribution. Epibionts occurring in more than one region, or on the boundary between regions are designated with combinations of numbers (e.g. 123, 124, etc.). Specimens that lacked any reference points, such as species of Favosites, were not divided into regions.



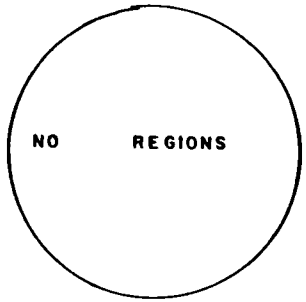
ATRYPA



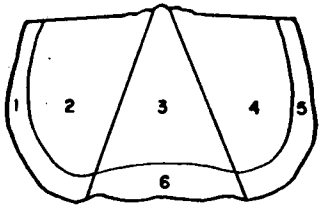
LEPTAENA



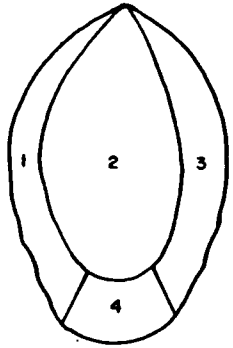
LEPTOSTROPHIA &
SCHELLWIENELLA



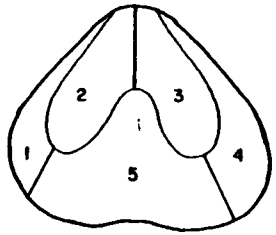
FAVOSITES



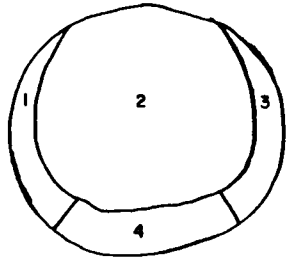
MACROPLEURA



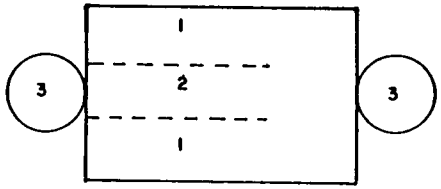
RENSSELAERINA



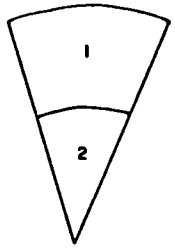
MERISTELLA



RHIPIDOMELLOIDES



CRINOID STEM



STREPTELASMA

Fig. 57. Distribution of three most common epibionts on all hosts. See figure 56 for definitions of regions used on various hosts for locating epibionts.

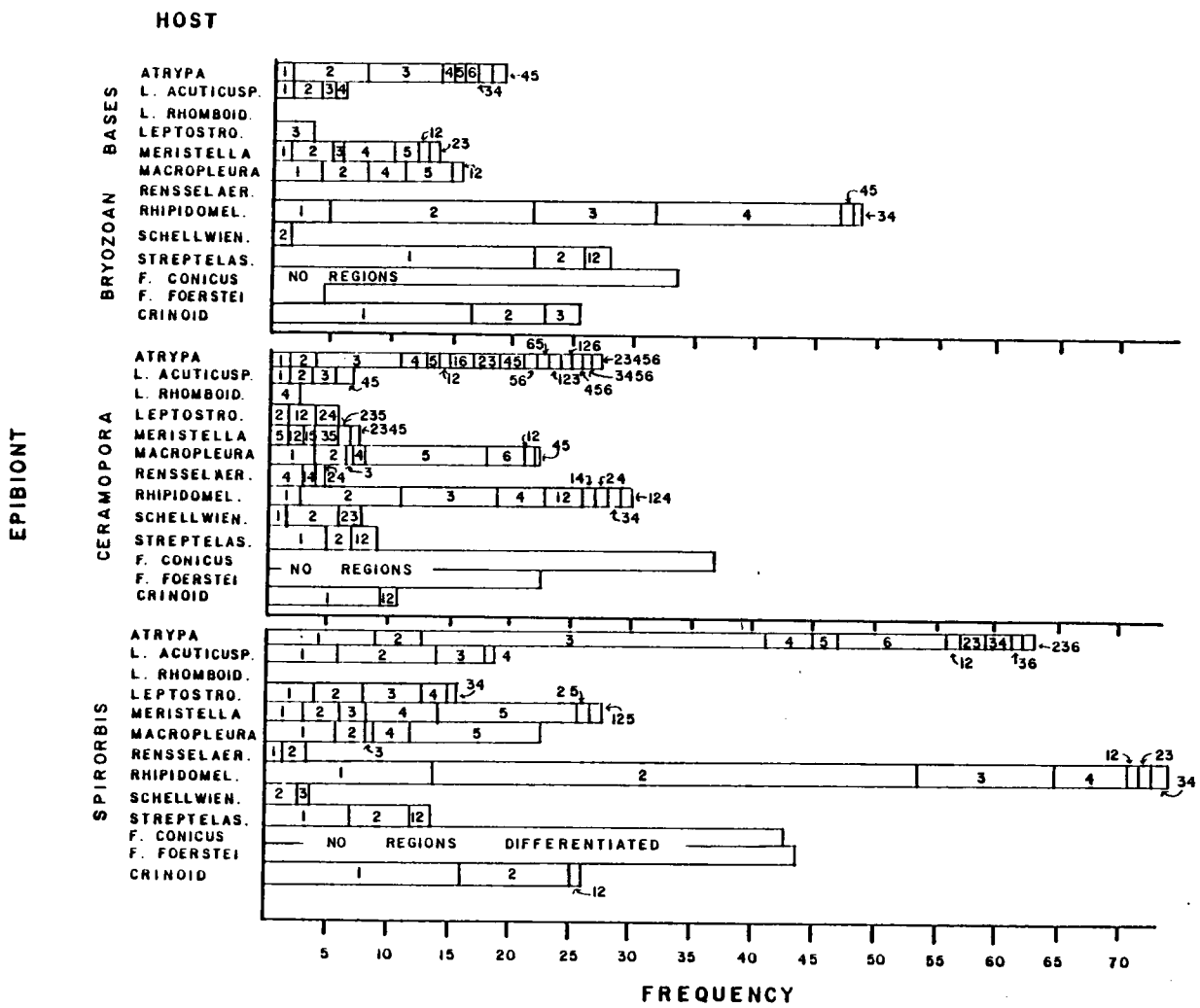
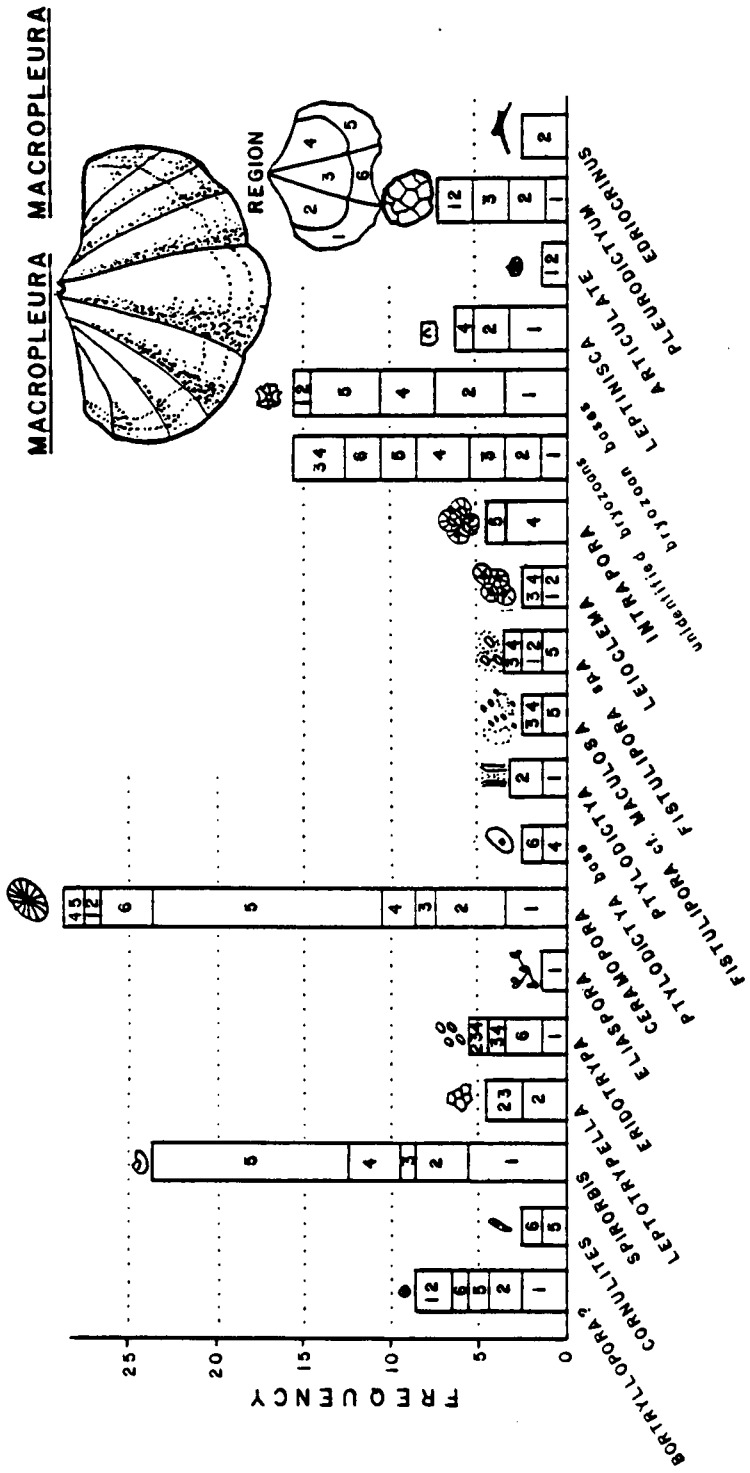

HOST
EPIBIONT
BRYOZOAN BASES
CERAMOPORA
SPIRORBIS
ATRYPA
L. ACUTICUSP.
L. RHOMBOID.
LEPTOSTRO.
MERISTELLA
MACROPLEURA
RENSSELAER.
RHIPIDOMEL.
SCHELLWIEN.
STREPTELAS.
F. CONICUS
F. FOERSTEI
CRINOID
NO REGIONS
NO REGIONS DIFFERENTIATED
5 10 15 20 25 30 35 40 45 50 55 60 65 70
FREQUENCY

Fig. 58. Distribution of epibionts on Macropleura macropleura by region. Spirorbis laxus and Ceramopora cf. parvicella exhibit a preference for the right side of host valves (regions 4 and 5) and avoidance for the fold and sulcus (region 3).


MACROPLEURA MACROPLEURA
REGION
FREQUENCY
0
5
10
15
20
25
BORRYLLOPORA ?
CORNULITES
SPIRORBIS
LEPTOTRYPELLA
ERIDOTRYPA
ELIASPORA
CERAMOPORA
PTYLODICTYA base
FISTULIPORA cf. MACULOSA
FISTULIPORA sp.
LEIOCLEMA
INTRAPORA
unidentified bryozoans
LEPTINISCA
ARTICULATE
PLEURODICTYUM
EDRIOCRINUS
EPIBIONT

reclined quasi-infaunally in the sediment. It is likely that the sulcus was oriented away from the substrate, allowing greater numbers of S. laxus to settle in that region. By settling in the sulcus, S. laxus was sheltered from currents passing over the shell. The shell may have created a lower velocity, turbulent eddy shadow in the sulcus region, similar to that described by Sparkes, et al. (1980) for Paraspirifer bownockeri, that facilitated feeding.

S. laxus, and many of the other epibionts, exhibit a stronger distributional relationship with M. macropleura (Fig. 57, 58). S. laxus shows a low preference for region three (fold and sulcus), is absent from region six (anterior margin of fold and sulcus), and shows a higher concentration in regions one and five (lateral margins). M. macropleura is a spiriferid with large, broadly rounded plicae, and well-developed finely striate fold and sulcus. The fold and sulcus is considered to be the excurrent region in spiriferids (Rudwick, 1970). S. laxus perhaps did not like the lower oxygen level and higher metabolic waste content of the brachiopod excurrent material, and was therefore, a facultative commensal on M. macropleura. S. laxus derived benefit from the currents generated near the inhalent lateral margins of the host and protection from scouring currents, but contributed nothing to the overall

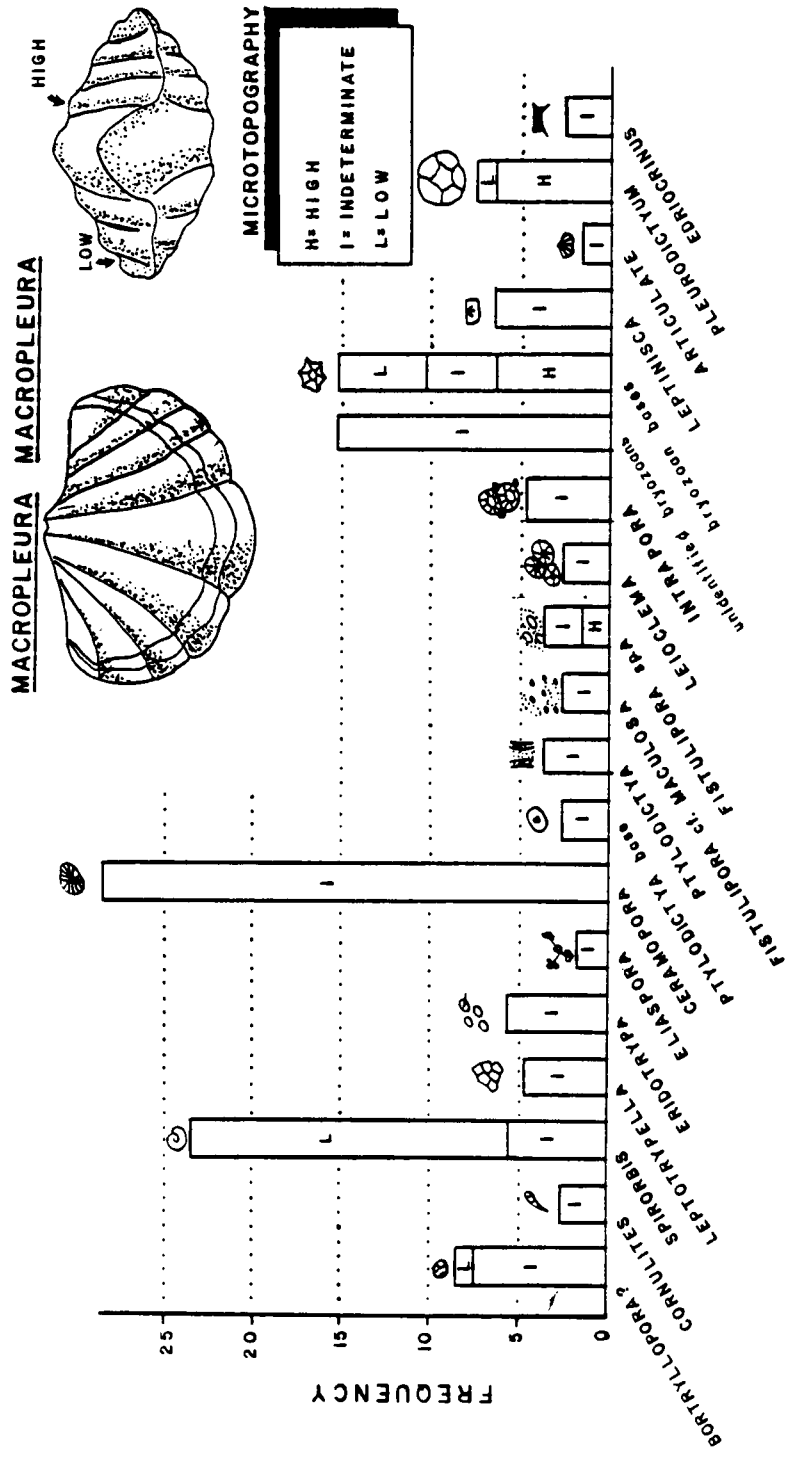
fitness of the epibiont's host.

The distribution of S. laxus, as well as other epibionts such as Ceramopora cf. parvicella, Fistulipora cf. maculosa, Intrapora puteolata, and Cornulites sp. (Fig. 58), is asymmetric with respect to right or left sides of the valves of M. macropleura. S. laxus exhibits a strong preference for the right side of the valve (regions 4 and 5). A similar asymmetry was noted on P. bownockeri by Sparks et al. (1980), only on the left side. This asymmetry probably resulted from a low velocity zone on the downcurrent side of the shell created by currents passing over the shell, which was oriented so that one side of the brachiopod faced up-current (Sparks et al., 1980).

S. laxus also shows a strong preference for microtopography on M. macropleura (Fig. 59) by settling in the low areas between the ribs. Once again, protection from currents or micropredators provides the best explanation for the prefered location. S. laxus shows no preference for microtopography of weakly ribbed hosts. This is probably due to the wider spacing of the plicae in M. macropleura.

Although many of the colonial epibionts show a preference for region (Fig. 59), they do not show one for topography. The adult colonies spread laterally and cross microtopography, thus are of "indeterminate" preference;

Fig. 59. Distribution of epibionts on Macropleura macropleura according to microtopography. Spirorbis laxus shows a preference for the troughs between plicae. Adult colonial organism show no preference; similarly, bryozoan bases show no preference suggesting that bryozoans are not site selective with respect to microtopography.


MACROPLEURA
MACROPLEURA
HIGH
LOW
MICROTOPOGRAPHY
H= HIGH
I = INDETERMINATE
L= LOW
FREQUENCY
0
5
10
15
20
25
EPIBIONT
BORRYLLOPORA ?
CORNULITES
SPIRORBIS
LEPTOTRYPELLA
ERIDOTRYPA
ELIASPORA
CERAMOPORA
PTYLODICTYA bose
FISTULIPORA cf. MACULOSA
FISTULIPORA spa
LEIOCLEMA
INTRAPORA
unidentified bryozoans
LEPTIMISCA bosse
ARTICULATE
PLEURODICTYUM
EORIOCRINUS

however, bryozoan bases (the ancestrula and a few initial zooids) are evenly distributed between high, low, intermediate (labeled as indeterminate) locations (Fig. 59). This suggests that bryozoans settled without preference, but could have grown in a preferential direction influenced by currents or gravity.

S. laxus and bryozoans, therefore, show different strategies toward epibiosis. The differing approaches are related to the settlement behavior and growth of the two groups of organisms. Spirorbis larvae have two mobile stages during settlement, one swimming and one crawling (Knight-Jones, 1951). The positive phototaxis phase and pelagic swimming phase result in maximum dispersal. Larvae can settle, explore and test the substrate, swim to new site, and resettle until a suitable location is found. Once settlement is accomplished, the larva crawls over the substrate, frequently changing directions, until an optimimum site is located (Knight-Jones, 1951). Knight-Jones et al. (1975) noted that most modern Spirorbis prefer sheltered areas, when available, and can crawl for a period of several days (Knight-Jones, 1951). In the Birdsong, settlement in the troughs of M. macropleura is probably an adaptation to avoiding more vigorous water movement or perhaps predation.

Bryozoan larvae also test substrata for suitability

(Soule and Soule, 1977) prior to final attachment. Ancestrula orientation and early colony budding is strongly phototropic or rheotropic (Ryland and Stebbing, 1971; Ryland, 1977). Once attached, the colony grows in preferred directions, depending upon the prevailing water and nutrient conditions (Soule and Soule, 1977; Ryland, 1977).

Once permanantly established, bryozoan colonies can grow and adjust toward favorable conditions or avoid unfavorable conditions throughout astogeny (Jackson, 1977, 1985; Coates and Jackson, 1985). Spirorbis can not adjust once cementation has been accomplished; therefore, it must cope with conditions as they are. It is therefore reasonable for solitary attached organisms, such as Spirorbis to be more selective about attachment sites and to show a greater tendency toward selectivity under optimum conditions.

Streptelasma strictum is a solitary rugosan coral which settled on hard substrates initially (such as bioclastic debris) and grew upright by sinking into the underlying sediment. It is therefore considered "liberosessile" (Neuman, 1988). In the Birdsong, S. strictum inhabited soft substrata. Only two regions were delineated on this host, both of which are equally encrusted by Spirorbis laxus. S. strictum is more heavily

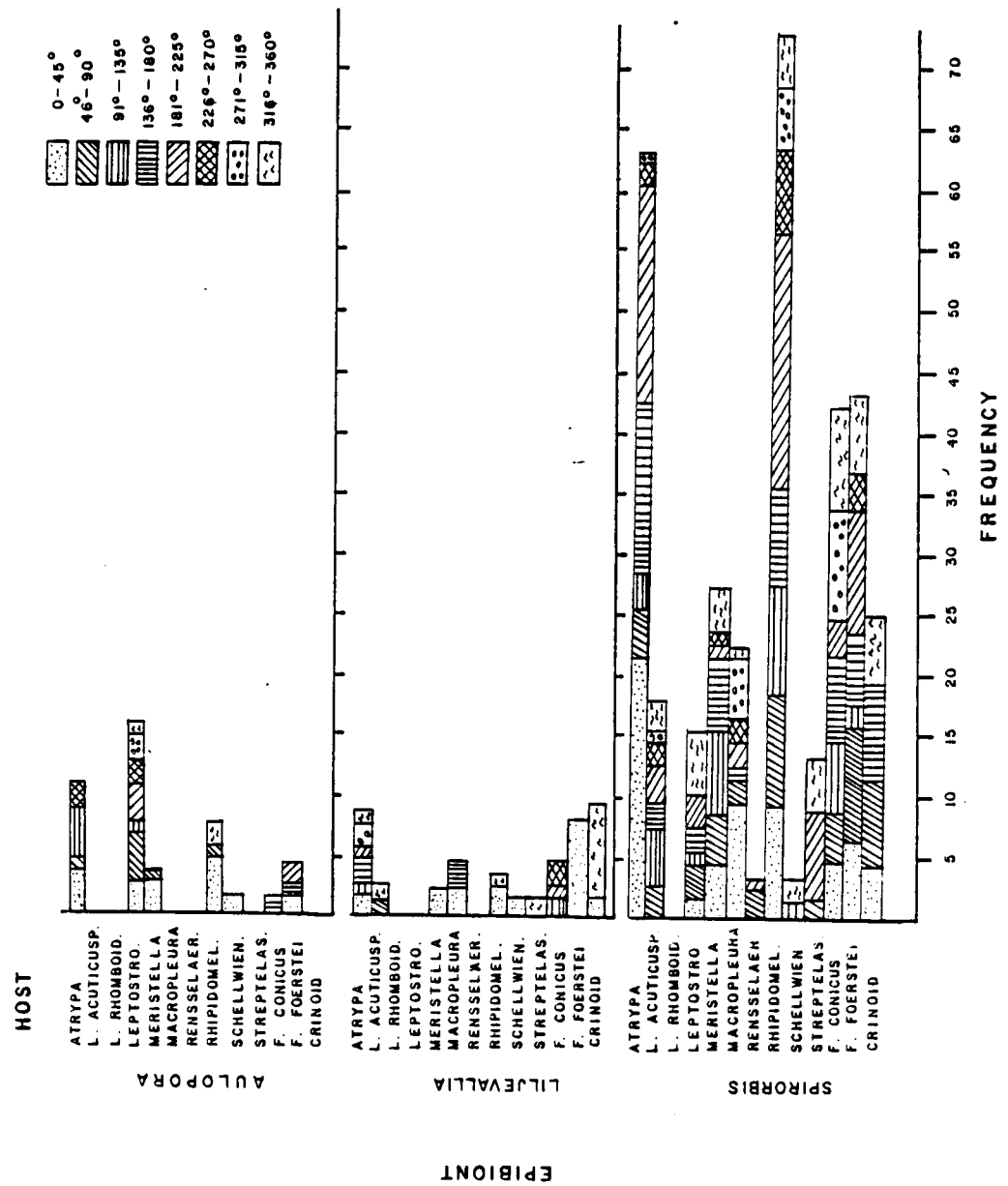
encrusted on the lower half by bryozoans, especially Ceramopora cf. parvicella (Fig. 57). Encrustations are randomly oriented, as they are for nearly all of the epibionts of the Birdsong (Fig. 60), suggesting that encrustation occurred post-mortem when the sides of the coral were exposed, or randomly around the exposed edges of coralla in living position. Coralla in living position were not observed in the Birdsong, however. This relationship represents an epitaphic association.

Epibiont-Epibiont Associations

No recurrent epibiont-epibiont associations were recognized from the digitized epibiont data for the Birdsong. Nearly all of the epibiont-epibiont interactions observed on specimens were clearly facultative in that they represented no apparent recurrent association. Two types of associations between epibionts were found, overlaps and successive settlment that resulted in an "epibiont stratigraphy".

Colonial organisms frequently partly overgrow other epibionts, including both solitary organism and other colonial organisms; however, none of these overgrowths show indications of epibiont competition for dominance. Indications of competitive overgrowth in modern and other fossil epizoans include: upturned margins at the junctions

Fig. 60. Frequency of occurrence of epibionts by orientation. Angular relationship expresses dominant direction of growth or orientation of epibiont from its initial larval attachment. The method for determining orientation is described in Appendix C.


0-45°
46°-90°
91°-135°
136°-180°
181°-225°
226°-270°
271°-315°
316°-360°
HOST
ATRYPA
L. ACUTICUSP.
L. RHOMBOID.
LEPTOSTRO.
MERISTELLA
MACROPLEURA
RENSSELAER.
RHIPIDOMEL.
SCHELLWIEN.
STREPTELAS.
F. CONICUS
F. FOERSTEI
CRINOID
AULOPORA
LILIJEVALLIA
SPIRORBIS
EPIBIONT
5 10 15 20 25 30 35 40 45 50 55 60 65 70
FREQUENCY

between colonies (Liddell and Brett, 1978; Jackson, 1979, 1983), budding around an obstacle (Jackson, 1979, 1983), multilamellar growth (Coates and Jackson, 1985), redirected and deflected growth (Coates and Jackson, 1985), and overgrowth. All five of these types of interactions are present in the Birdsong (Fig. 55), but occur only very rarely.

Overgrowths of colonies were common. No preference was shown for one byrozoan always overgrowing another. Solitary epibionts, especially Spirorbis laxus, were found frequently encrusting colonial epibionts. This suggests that these overlaps are epitaphic rather than competitive. Also, host shells that were repeatedly colonized represented substrates and not potential interacting associates. Either there was little or no substrate competition, or the Birdsong epibionts exhibited a successful defensive behavior (e.g., allelopathy) to discourage potential competitors from settling nearby that did not involve skeletal or colony form.

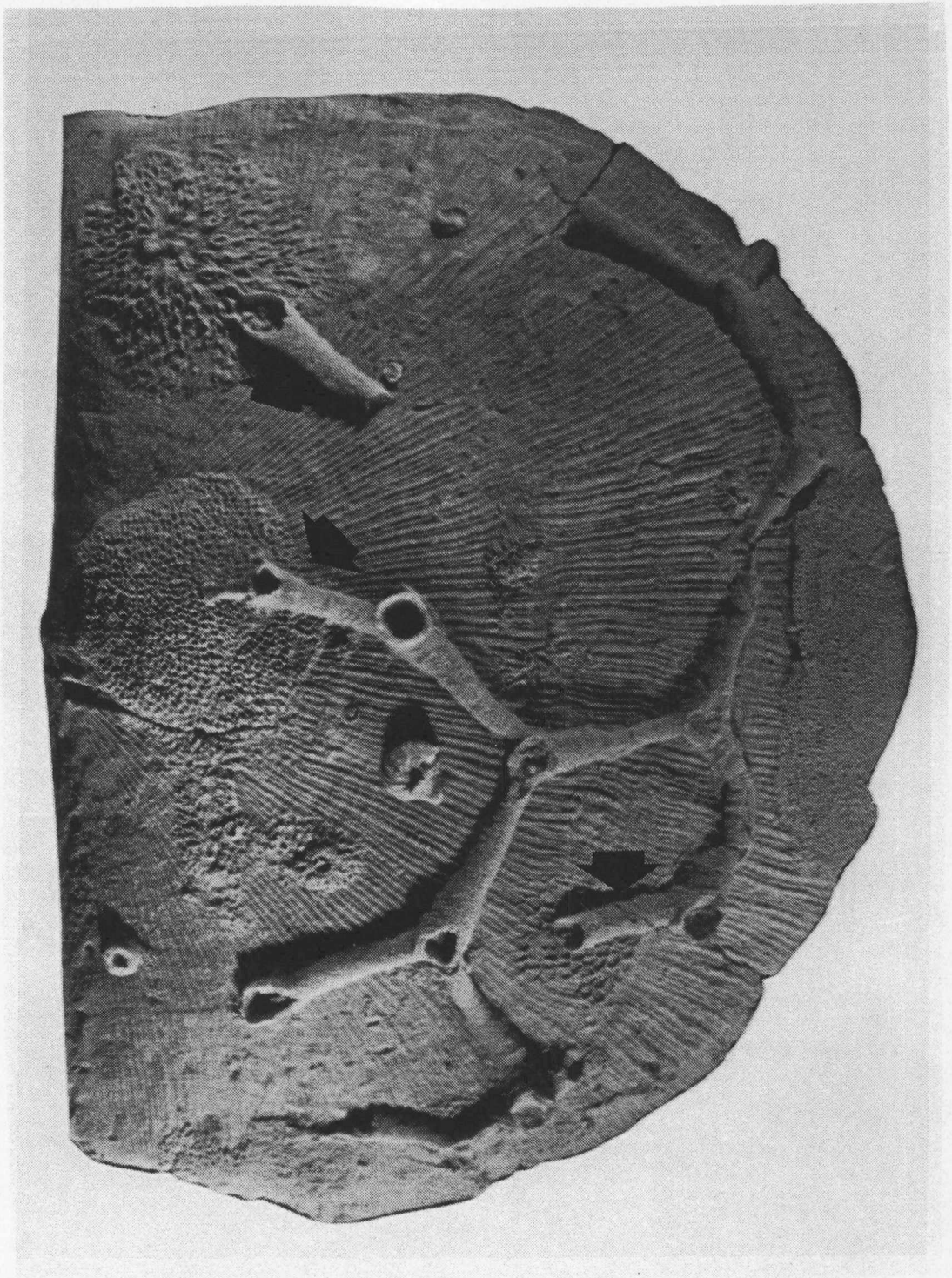
It is also likely, however, that the Birdsong bryzoans did become accustomed to sharing substrates with other epibionts. The bryozoans occur as regularly outlined, circular to slightly irregular patches that do not show embayments (such as might have developed around a soft bodied encruster not preserved). Most bryozoan colonies

and reptant auloporid corals also show fewer overlaps than would be expected if substrate was limiting and growth was not regulated. These relationships imply that the likely interaction was one of avoiding direct interactions, not by dominating the substrate, but by maintaining a small colony size or perhaps also by allelopathy. This would constitute amensalistic behavior, but can only be indirectly inferred by eliminating other possibilities.

An epibiont "paragenesis" or epibiont "stratigraphy" is abundantly evident, suggesting that most of the associations represent epitaphic occurrences. The relative timing of arrival or overgrowth can often be determined by examining the pattern of overlaps and overgrowths (Fig. 61).

Two recurrent associations between epibionts are recognized in the Birdsong - both involve auloporid corals and bryozoans. First, some auloporid corals inhabited the surface of fistuliporid bryozoan colonies, which in turn, covered the auloporid so that the apertures of the auloporid remained open to the surface. This relationship occurs in two forms, as coexisting massive encrustations of brachiopod shells (Fig. 55g, h, p. 224) and as thin bryozoan encrustions on auloporid corallite tubes, forming a delicate arborescent or reptant form (Fig. 55d, e, p. 224). Although brachiopod-auloporid associations are

Fig. 61. Specimen of ?Orthostrophia strophomenoides illustrating epibiont "paragenesis". Large arrows point to where the late arriving Aulopora schohariae encrusted earlier growths of various species of bryozoans. Growth of the coral away from the commissure, towards the highest point on the shell, suggests that the host brachiopod was not living, and that the association represents an epitaphic relationship. The large Spirorbis laxus that occurs between the branches of the coral may have settled prior to the growth of the coral causing the coral to change its pattern of branching to avoid the spirorbid. Alternatively, the spirorbid could have chosen this site, after the coral had branched, because of its position away from the corallites. Note the discrete, small, regular colony forms of the bryozoans and the apparent lack of direct competition for substrate.



common (Clarke, 1908; Yakovlev, 1926; Kesling, et al. 1980; Sparks, et al., 1980; Alvarez and Taylor, 1987), the auloporid-bryozoan association is less well known.

This relationship was probably mutualistic with the bryozoan generating currents for coral feeding while the coral provided the bryozoan with substrate, structural support above the sediment, and no need to develop maculae. The auloporid corallites were spaced apart at distances roughly equal to that of monticules and maculae on the bryozoans, possibly making the development of monticules and maculae unnecessary. Since both could survive independently, this interaction is probably facultative mutualism.

Discussion

The epibionts of the Birdsong differ from those mentioned in other studies of fossil and recent epibiosis in three ways. First, there were few truly interactive associations that can be positively documented in the Birdsong. Most associations were epitaphic and resulted simply from the larvae finding a large enough substrate to become established. Second, colony size may have remained small due to characteristics of the physical environment, for example, frequency of disturbance events. Alternatively, once the epibiont was established, substrate

competition remained minimal. The tendency seems to have been to maintain a small colony size or low numbers of gregarious individuals and avoid competition with any neighbors. This is different from what is generally seen in the recent marine environment. Most modern ecologists believe that substrate competition, along with predation, constitute the dominant types of interactions among most marine benthos (Jackson, 1977, 1983, 1985; Russ, 1982; Wulff, 1985; Keough, 1984; Coates and Jackson, 1985). The explanation for this difference is not clear; however, the frequency of disturbance events postulated for the Birdsong seafloor and the changes in sediment consistency described in the community development model suggest that there may not have been sufficient time between events to encourage substrate competiton. Also possible, but more difficult to prove, is that the organisms had not yet developed the highly efficient defense mechanisms that modern bryozoans and corals exhibit (e.g., avicularia, vibracula, nematocysts, etc.). The best adaptation to avoid competition in this case would be to remain small, overgrow or change growth direction, or use allelopathic chemicals. At the present time none of these hypotheses is testable.

CHAPTER 5

SUMMARY

1. Rocks of Late Silurian to Early Devonian age crop out along a north-south trending belt along the Tennessee River in western Tennessee. Recent studies of the stratigraphy and structure of the western Tennessee region, along with detailed bed-by-bed analysis of the Lower Devonian rocks using thin sections, grid counts, and a newly developed computer program for analyzing epibiont distributions, has allowed a hierarchical study of deposition and paleoecology of the Rockhouse and Birdsong members of the Ross Formation (Lower Devonian) within a regional paleogeographic setting.

2. The western Tennessee region consisted of a shallow carbonate platform, termed the Ross Shelf, bounded by the Illinois Basin, Reelfoot Rift, continental margin, and Nashville Dome, and located approximately 25° to 35° south latitude during the Early Devonian. The period of time represented by the deposition of the Rockhouse Limestone Member and Birdsong Shale Member of the Ross Formation was a time of increased terrigenous input onto the Ross Shelf. Prior to (Decatur Limestone) and

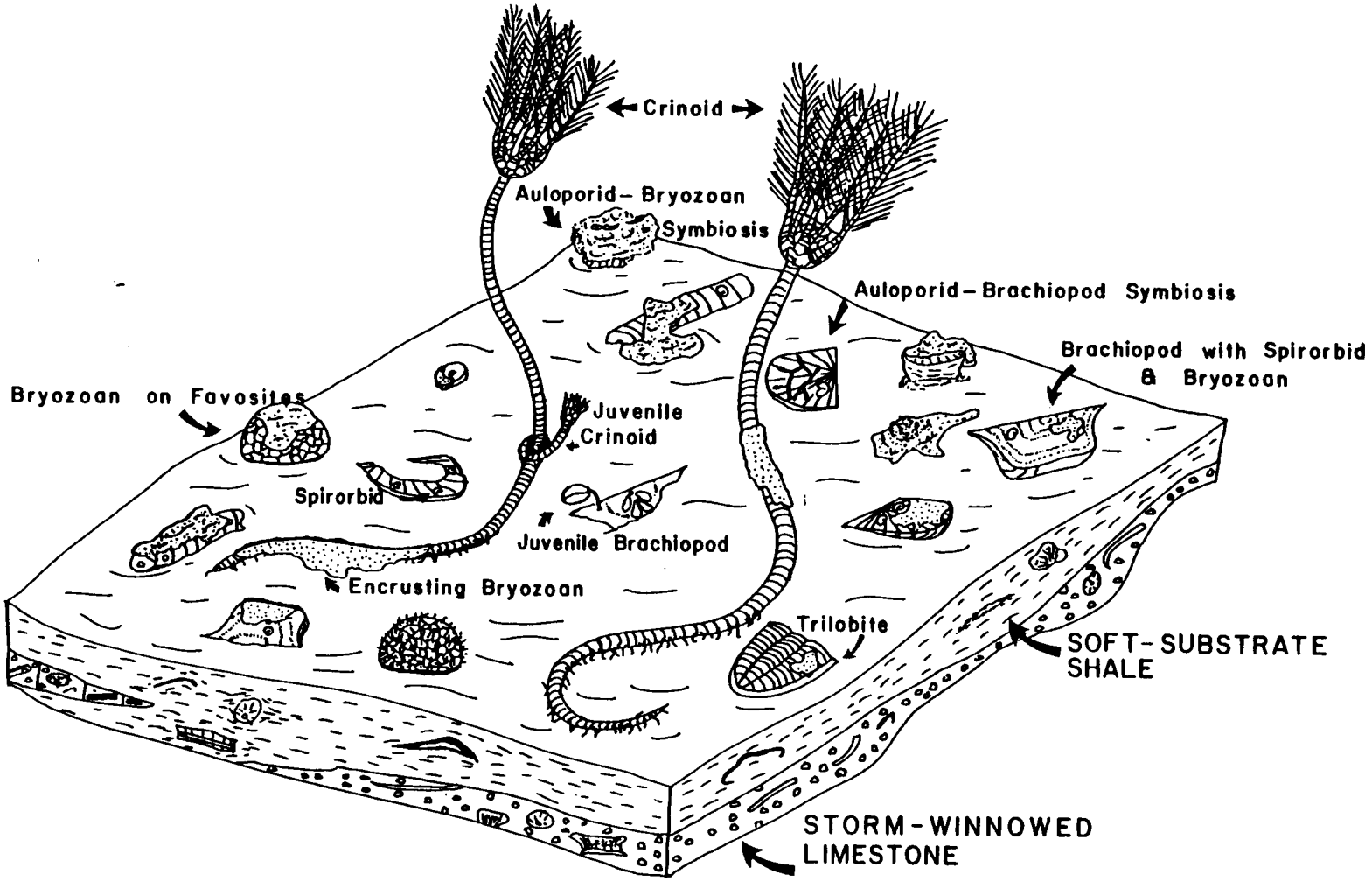
following (Camden Chert) the terrigenous-rich deposition of the Ross Formation, the western Tennessee region consisted of a carbonate shelf that developed between the Nashville Dome to the east and the Ozark Uplift and Reelfoot Rift to the west. The western Tennessee region was situated within a westerly storm track that was responsible for transporting the terrigenous material onto the Ross Shelf from the south as currents crossed the shelf into the Illinois Basin.

3. The Rockhouse Limestone Member is a mixed carbonate-terrigenous sequence that developed subtidally within the influence of storm wave activity. Locally, conditions were favorable for the formation of bryozoan-dominated mudmounds whose long dimensions were oriented northwestward toward the Illinois Basin in response to the currents moving basinward across the shelf at the time of formation. Drill core data indicate four vertical phases occurred in the development of the mudmounds. Phase I involved the introduction of an allochthonous fossiliferous terrigenous mud probably resulting from a storm event. Colonization and stabilization of patches of mud, less mobile than the surrounding sediment due to early lithification and algal binding, occurred in Phase II.

This early lithification, relative to the surrounding high energy regime was responsible for promoting the development of the mudmounds. Phase III consisted of an irregular surface with numerous open cavities in which encrusting Buskopora served a dual role as a coelobite and as the chief sediment binder and "framework" builder. This represents the first report of a coelobite as the dominant in a successional sequence. Phase IV represented the interruption of the dominance stage due to changing environmental conditions in the form of increased terrigenous input, with faunal diversity increasing and sediment influxes onto the mound altering the community structure.

4. The Birdsong Shale is a mixed carbonate-siliciclastic sequence that was dominated by muddy bottoms which were frequently scoured by storm activity (Fig. 62). The storms transported terrigenous mud onto the Ross Shelf from the south where subsequent events winnowed previously deposited sediment producing graded bioclastic limestone-shale couplets. Although the seafloor consisted of soft substrata much of the time, the substrate underwent synsedimentary substrate modification to form firmgrounds of fine-grained terrigenous clastics or coarse-grained bioclastic

Fig. 62. Schematic diagram depicting the Birdsong seafloor during muddy bottom conditions. During these phases of deposition, larval attachment sites were a major limiting factor promoting the development of specialized adult adaptations to cope with the substrate, the occurrence of symbiotic relationships, and epitaphic associations.


Crinoid
Auloporid – Bryozoan Symbiosis
Auloporid – Brachiopod Symbiosis
Brachiopod with Spirorbid & Bryozoan
Bryozoan on Favosites
Juvenile Crinoid
Spirorbid
Juvenile Brachiopod
Encrusting Bryozoan
Trilobite
SOFT-SUBSTRATE SHALE
STORM-WINNOWED LIMESTONE

debris. The consistency of the substrate was modified by compaction and dewatering of the muddy sediment, rather than by early marine cementation, as indicated by the lack of early marine cement in any of the rocks. The substrate could be modified from one form to another by compaction, could abruptly develop into a coare-grained substrate by winnowing during storm events, slowly develop into a coarse-grained substrate by the accumulation of skeletal debris, or abruptly develop into a soft substrate by mud incursion.

5. The biota that inhabited the Birdsong seafloor developed along one of several pathways depending upon the consistency and nature of the substrate and severity of storm activity. During periods of soft substrata, the fauna was characterized by adaptations that retarding sinking into the mud surface or by adaptations for avoiding the sediment altogether. Brachiopods were generally characterized by having large surface areas, having ambitopic life styles, or reduced pedicles and thickened umbo regions. Species of favosited corals exhibit structural modifications related to corallum geometry, interfacial material, and biotic associations that enabled them to survive in the terrigenous mud environment. Favosites conicus had a flat,

holotheca-covered base and a radial pattern of colony growth, but apparently had a short life spand and may not have survived beyond the first reproductive cycle. It was adapted for living between major sedimentation episodes of terrigenous influx. F. foerstei had a convex, pseudoholotheca-covered base and a modified axial pattern of colony growth. Its large size, in comparison to that of F. conicus suggests a longer lived colony, in which continued upward and outward growth enabled it to survive episodic sediment influx. Other elements of the Birdsong biota avoided the substrate altogether by becoming epibiotic on hosts that were adapted for living in soft substrata, resulting in the fauna being rich in epibionts.

6. Epizoans of the Birdsong, although abundant, do not show abundant obvious biotic interactions. Most associations with hosts were epitaphic and were responses to substrate conditions. Competitive biotic interactions are not well represented. Instead, the epibionts of the Birdsong are characterized by small discrete colonies suggesting that the epibionts avoided contact with other possible substrate competitors by remaining small. This is in constrast to modern epibionts, which show a

considerable range of competitive behaviors to dominate substrata.

Facultative associations occur with some hosts in the Birdsong. In particular, the spiriferid brachiopod Macropleura macropleura is commonly encrusted by the annelid worm Spirorbis laxus. S. laxus demonstrated a preference for living in the troughs between plications, where it was probably protected from currents and predation, and for avoiding the fold and sulcus region, which were probably low in nutrient content and high in waste products. This preference for location is not developed on hosts that lack the broad plicae that offered refuge to the worm.

Colonial organisms show little preference for location or orientation; however, preferred growth directions are exhibited by colonies, most likely in response to local substrate conditions at the time of encrustation. Two recurrent associations occur that involve auloporid byrozoans. The first occurs between Aulopora schohariae and fistuliporid byrozoans. Two forms are present; A. schohariae colonies occur with only their corallites exposed in either ramose symbiotic growth forms or as encrustations to form small masses. This relationship was probably mutualistic with the bryozoan benefiting from a substrate, structural support, and the reduced

need to develop monticules or maculae, while the coral benefited from structural support and currents generated by the bryozoan zoids. The other association, between auloporids and brachiopods, occurs either as an epitaphic encrustation or as a commensalistic association in which the auloporid grows to and along the commissure of the brachiopod to take advantage of the feeding currents generated by the brachiopod.

LIST OF REFERENCES

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Ache, B.W. 1974. Analysis of host location in symbiotic marine invertebrates. Bell Branch Library in Marine Sciences, 2:45-60.

Ager, D.V. 1961. The epifauna of a Devonian spiriferid. Quarterly Journal of the Geological Society of London, 117:1-10.

Ager, D.V. 1963. Principles of Paleoecology. McGraw Hill, N.Y., p. 245-266.

Aigner, T. 1982. Calcareous tempestites: storm-dominated stratification in Upper Muschelkalk limestones (Middle Trias, Southwest-Germany). In, G. Einsele and A. Seilacher, eds., Cyclic and Event Stratification. Springer-Verlag, Berlin, pp. 180-198.

Aigner, T. 1985. Storm Depositional Systems. Lecture Notes in Earth Sciences, 3:1-173.

Alberstadt, L.P., K.R. Walker, and R.P. Zurawski. 1974. Patch reefs in the Carters Limestone (Middle Ordovician) in Tennessee and vertical zonation in Ordovician reefs. Geological Society of America Bulletin, 85:1171-1187.

Aller, R.C. and R.E. Dodge. 1977. Animal-sediment relations in a tropical lagoon, Discovery Bay, Jamaica. Journal of Marine Research, 32:209-232.

Alvarez, R. and P.D. Taylor. 1987. Epizoan ecology and interactions in the Devonian of Spain. Palaeogeography, Palaeoclimatology, and Palaeoecology, 61:17-31.

Amsden, T.W. 1949. Stratigraphy and paleontology of the Brownsport Formation (Silurian) of western Tennessee. Peabody Museum of Natural History Bulletin, 5:1-138.

Amsden, T.W. 1951. Brachiopods of the Henryhouse Formation (Silurian) of Oklahoma. Journal of Paleontology, 25:69-96.

Amsden, T.W. 1958. Stratigraphy and paleontology of the Hunton Group in the Arbuckle Mountain region, Part V - Bois D'Arc articulate brachiopods. Oklahoma Geological Survey Bulletin, 82:1-110.

Amsden, T.W. and A.J. Boucot. 1958. Stratigraphy and paleontology of the Hunton Group in the Arbuckle Mountain region. Oklahoma Geological Survey Bulletin, 78:1-199.

Amsden, T.W. and W.P.S. Ventress. 1963. Early Devonian brachiopods of Oklahoma. Oklahoma Geological Survey Bulletin, 94:1-238.

Bambach, R.K. 1979. Historical development of paleogeography. In, Bambach, R.K. and Scotese, C.R., eds., Paleogeographic Reconstruction: The State of the Art. Southeastern Section, Geological Society of America, Virginia Polytechnical Insititute and State University Short Course Notes, p. 1-5.

Bambach, R.K. and C.R. Scotese. 1979. Paleogeographic reconstruction: the state of the art. Southeastern Section Geological Society of America, Virginia Polytechnical Institute and State University, Blacksburg, 31p. + figures.

Barrett, S.F. 1985. Early Devonian continental positions and climate: a framework for paleophytogeography, p. 93-127. In, B.H. Tiffney, ed., Geological Factors and the Evolution of Plants. Yale University Press, New Haven, 294p.

Bassler, R.S. 1953. Part G, Bryozoa, p, G1-G253. In, R.C. Moore, ed., Treatise On Invertebrate Paleontology, Geological Society of America and University of Kansas Press, Lawrence.

Bathurst, R.G.C. 1980. Stromatactis - origin related to submarine-cemented crusts in Paleozoic mud-mounds. Geology, 8:131-134.

Bathurst, R.G.C. 1982. Genesis of strmatactis cavities between submarine crusts in Paleozoic carbonate mud buildups. Journal of Geology, 139:165-181.

Biernat, G. 1961. Diorygma atrophophila n. gen., n. sp.: a parasitic organism on Atrypa zonata Schumann. Acta Palaeontologica Polanica, 6:17-28.

Boekschoten, G.J. 1966. Shell boring of sessile epibiontic organisms as paleoecological guides (with examples from the Dutch coast). Palaeogeography, Palaeoclimatology, and Palaeoecology, 2:333-279.

Boekschoten, G.J. 1970. On bryozoan borings from the Danian at Fakse, Denmark, p. 43-48. In, T.P. Crimes and J.C. Harper, eds., Trace Fossils. Geological Journal Special Issue, 3.

Born, K.E. 1944. The Devonian of west-central Tennessee. Illinois State Geological Survey Bulletin, 68:139-154.

Bottjer, D.J. 1982. Paleoecology of epizoans and borings on some Upper Cretaceous chalk oysters from the Gulf Coast. Lethaia, 15:75-84.

Boucot, A.J. 1958. Kozlowskiellina, new name for Kozlowskiella Boucot, 1957. Journal of Paleontology, 32:1031.

Boucot, A.J. 1963. The eospiriferidae. Palaeontology, 5:682-711.

Boucot, A.J. 1985a. The relevence of biogeography to palaeogeographical reconstructions. Philosophical Transactions Royal Society of London, B309:79-80.

Boucot, A.J. 1985b. Late Silurian-Early Devonian biogeography, provincialism, evolution, and extinction. Philosphical Transactions Royal Society of London, B309:323-339.

Boucot, A.J. and T.W. Amsden. 1958. New genera of brachiopods. Oklahoma Geolgical Survey Bulletin, 78:159-170.

Boucot, A.J. and J. Gray. 1983. A Paleozoic pangea. Science, 22:571-580.

Boucot, A.J., J.G. Johnson, and R.D. Stanton. 1964. On some atrypoid, retzoid, and athyridoid brachiopoda. Journal of Paleontology, 38:805-822.

Bourque, P.-A. and H. Gignac. 1983. Sponge-constructed stromatactis mud mounds, south of Gaspe, Quebec. Journal of Sedimentary Petrology, 53:521-532.

Braile, L.W., Hinze, W.J., Sexton, J.L., Keller, G.R., and Lidiak, E.G. 1984. Tectonic development of the New Madrid seismic zone. U.S. Geological Survey Open File Report, 84-770:204-233.

Bramlette, M.N. 1925. Paleozoic formations penetrated by wells in Thishomingo County northeastern Mississippi.

U.S. Geological Survey Bulletin, 781A:1-10.

Brande, S. 1982. Epibiont analysis of the fossil interaction among a benthic infaunal bivalve, a barnacle and a drilling gastropod. Journal of Paleontology, 56:1230-1234.

Branson, E.B. 1922. General account of Missouri Devonian. In, Branson, E.B., ed., Devonian of Missouri. Missouri Bureau of Geology and Mines, 2nd series, 17:1-129.

Brett, C.E. 1978. Host-specific pit-forming epizoans on Silurian crinoids. Lethaia, 11:217-232.

Brett, C.E. and G.L. Baird. 1985. Carbonate-shale cycles in the Middle Devonian of New York: an evaluation of model for the origin of limestone in terrigenous shelf sequences. Geology, 13:324-327.

Brett, C.E. and J.E. Cottrell. 1980. Substrate specificity in the Devonian tabulate coral Pleurodictyum. Lethaia, 15:247-262.

Broadhead, T.W. and R. McComb. 1982. Paedomorphosis in the Icriodontidae (Conodontophorida) and the evolution of Icriodus. Fossils and Strata, 15:149-154.

Broadhead, T.W. and H.R. Strimple. 1978. Systematics and distribution of the Callocystitidae (Echinodermata, Rhombifera). Journal of Paleontology, 52:164-179.

Broadhead, T.W., D.A. Capaccioli, N.E. Neff, and S.R. Reid. 1986. Sedimentary history and biostratigraphy of Late Silurian-Early Devonian of southern Appalachians and southeastern craton. American Association of Petroleum Geologists Bulletin, 70:569.

Broadhead, T.W., D.A. Capaccioli, R. McComb, S.R. Reid, and K.R. Walker. 1988. Early Devonian marine sedimentation near the southern margin of the North American craton. Canadian Society of Petroleum Geologists Bulletin, 14:in press.

Broadhead, T.W., N.E. Neff, S.R. Reid. 1983. Sedimentary history and biostratigraphy of Late Silurian-Early Devonian of the southern Appalachians and southeastern craton. Appalachian Basin Industrial Associates, 5:23-35.

Bromley, R.G. and F. Surlyk. 1973. Borings produced by

pedicles, fossil and recent. Lethaia, 6:349-365.

Burchette, T.P. 1981. European Devonian reefs: a review of current concepts and models. In, D.F. Toomey, ed., European Reef Models. Society of Economic Paleontologists and Mineralogists Special Publication, 30:85-142.

Burwell, H.B., C.W. Wilson, Jr., and E. Luther. in prep. Post-Carters Ordovician, Silurian, and Pre-Chattanooga Devonian stratrigraphy of central Tennessee: a synthesis of surface and subsurface. Tennessee Division of Geology Bulletin, 78.

Buschbach, T.C. 1985. New Madrid seismotectonic program, final report. U.S. Nuclear Regulatory Commission NUREG/CR, 4632:1-61p.

Butts, C. 1926. The Paleozoic Rocks. Alabama Geological Survey Special Report, 14:40-230.

Campbell, K.S.W. 1977. Trilobites of the Haragan, Boid D'Arc, and Frisco formations (Early Devonian) Arbuckle Mountains region, Oklahoma. Oklahoma Geological Survey Bulletin, 123:1-227.

Cameron, B. 1967. Fossilization of an ancient (Devonian) soft-bodied worm. Science, 155:1246-1248.

Cameron, B. 1969. Paleozoic shell-boring annelids and their trace fossils. American Zoologists, 9:689-703.

Capaccioli, D.A. 1987. Biostratigraphy, petrology, and paleodepositional environments of the Ross Formation, Upper Silurian-Lower Devonian, west-central Tennessee. Unpublished M.S. thesis, University of Tennessee, 125p.

Carriker, M.R. and E.H. Smith. 1969. Comparative calcibiocavitology: summary and conclusions. American Zoologist, 9:1011-1020.

Carriker, M.R. and E.L. Yochelson. 1968. Recent gastropod boreholes and Ordovician cylindrical borings. U.S. Geological Survey Professional Paper, 597B:1-26.

Chamberlain, T.C. 1882. Hypothetical map of currents of the Silurian interior seaway, p. 381. In, Geology of Wisconsin Survey of 1873-1879, vol. 4.

Chatterton, B.D.E. 1975. A commensial relationship between

a small filter feeding organism and Australian Devonian spiriferid brachiopods. Paleobiology, 1:371-378.

Cheng, T.C. 1970. Symbiosis: Organisms Living Together. University of South Carolina Press, Columbia, 276p.

Choi, D.R. 1985. Ecological succession of reef cavity-dwellers (coelobites) in coral rubble. Bulletin of Marine Science, 35:72-79.

Choi, D.R. and R.N. Ginsburg. 1983. Distribution of coelobites (cavity-dwellers) in coral rubble across the Florida reef tract. Coral Reefs, 2:165-172.

Choquette, P.W. and N.P. James. 1987. Diagenesis in limestones - 3. The deep burial environment. Geoscience Canada, 14:3-35.

Clarke, G.L. 1954. Elements of Ecology. Wiley and sons, New York, 534p.

Clarke, J.M. 1908. The beginnings of dependent life. New York State Museum Bulletin, 121:146-196.

Clarke, J.M. 1921. Organic dependence and disease. New York State Museum Bulletin, 221-222:113p.

Clarke, J.M. and C. Schuchert. 1899. The nomenclature of the New York series of geological formations. Science, 10:874-878.

Clement, C.R. in prep. Echinoderms of the Decatur and Ross Formations (Upper Silurian to Lower Devonian), western Tennessee. Unpub. Ph.D. dissertation, University of Tennessee, Knoxville.

Clement, C.R., M.A. Gibson, and T.W. Broadhead. 1987. Paleozoic recumbent crinoid stems as biogeopetal indicators. Palaios, 2:189-191.

Cloud, P.E., Jr. 1942. Terebratuloid brachiopoda of the Silurian and Devonian. Geological Society of America Special Paper, 38:1-187.

Cloud, P.E., Jr. 1948. Dicaelosia verses Bilobites. Journal of Paleontology, 22:373-374.

Coates, A.G. and J.B.C. Jackson. 1985. Morphological themes in the evolution of clonal and aclonal marine invertebrates, p. 67-106. In, J.B.C. Jackson, L.W.

Buss, and R.E. Cook, eds., Population Biology and Evolution of Clonal Organisms. Yale University Press, New Haven.

Collinson, C. 1967. Devonian of the north-central region, United States. In, Oswald, D.H., ed., Internation Symposium on the Devonian System, 1:933-971.

Collinson, C. and E. Atherton. 1975. Devonian System. In, Wilman, H.B., E. Atherton, T.C. Buschbach, C. Collinson, J.C. Frye, M.E. Hopkins, J.A. Lineback, and J.A. Simon, eds., Handbook of Illinois Stratigraphy. Illinois Geological Survey Bulletin, 95:104-113.

Connel, J.H. 1961. Effects of competition, predation by Thais lapillus and other factors on natural populations of the barnacle Balanus balanoides. Ecological Monographs, 31:61-102.

Cooper, G.A. 1944a. Remarks on correlation of Devonian formations in Illinois and adjacent states. Illinois Geological Survey Bulletin, 68:217-222.

Cooper, G.A. 1944b. Brachiopoda, p. 343. In, H.W. Shimer and R.R. Shrock, eds. Index Fossils of North America. The Technology Press, MIT.

Cooper, G.A. 1977. The Late Silurian brachiopod genus Atrypoidea. Geologiska Foreningen, Stockholm, Forhandlingar, 99:10-26.

Cooper, G.A., C. Butts, K.E. Caster, G.H. Chadwick, W. Goldring, E.M. Kindle, E. Kirk, C.W. Mirriam, F.M. Swartz, P.S. Warren, A.S. Warthin, and B. Willard. 1942. Correlation of the Devonian sedimentary formations of North America. Geological Society of America Bulletin, 53:1729-1794.

Copper, P. 1966. Ecological distribution of Devonian atrypid brachiopods. Palaeogeography, Palaeoclimatology, and Palaeoecology, 2:246-266.

Cooper, P. 1967. Adaptations and life habits of Devonian atrypid brachiopods. Palaeogeography, Palaeoclimatology, and Palaeoecology, 3:363-379.

Crowley, T.J., J.G. Mengel, and D.A. Short. 1987. Gondwanaland's seasonal cycle. Nature, 329:803-807.

Cuffey, R.J. 1977. Bryozoan contributions to reefs and

bioherms through geologic time. In, S.H. Frost, M.P. Weiss, and J.B. Saunders, eds., Reefs and Related Carbonates - Ecology and Sedimentology. American Association of Petroleum Geologists Studies in Geology, 4:181-194.

Cuffey, R.J., G.N. Abdo, and J.F. Taylor. 1986. Mid-Paleozoic bryozoan reef-rock-cystoporate lettucestone core within a latest Silurian patch reef in central Pennsylvania. Geological Society of America Abstracts with Program, 18:10-11.

Cuffey, R.J. and F.K. McKinney. 1979. Devonian bryozoa. Special Papers in Palaeontology, 23:307-311.

Curry, G.B. 1981. Variable pedicle morphology in a population of Recent brachiopod Terebratulina septentrionalis. Lethaia, 14:9-20.

Dayton, P.K. 1979. Ecology, a science and a religion, pp. 3-18. In, R.J. Livingston, ed., Ecological Processes in Coastal and Marine Systems. Plenum Press, New York.

De Bary, A. 1879. Die Erscheinong der sumbiose. Verlag Von Karl and Trubner, Strasburg.

De Laubenfels, M.W. 1955. Porifera, E21-E122. In, R.C. Moore, ed., Treatise on Invertebrate Palontology, Part E, Archeocyatha and Porifera. Geological Society of America and The University of Kansas Press, Lawrence.

de Verneuill, E.C. 1848. On the parallelism of the Paleozoic deposits of North America, with those of Europe; followed by a table of the species of fossils common to the two continents, with indication of the positions in which each occur, and terminated by a critical examination of each of these species (translated by and comments on by James Hall). American Journal of Science, 5:176-183, 359-370; 7:45-51, 218-231.

Delo, D.M. 1940. Phacopid trilobites of North America. Geological Society of America Special Paper, 29:1-135.

Dickson, J.A.D. 1965. A modified staining technique for carbonates in thin section. Nature, 205:587.

Dineley, D.L. 1984. Aspects of a Stratigraphic System: the Devonian. John Wiley and Sons, New York, 201p.

Dott, R.H. and L.J. Mayer. 1979. Orient.bas. Computer diskette.

Dunbar, C.O. 1917a. Stratigraphy and paleontology of the Devonian of western Tennessee. Unpublished Ph.D. dissertation, Yale University, New Haven, 257p.

Dunbar, C.O. 1917b. Devonian and black shale succession of western Tennessee. Geological Society of America Bulletin, 18:207.

Dunbar, C.O. 1917c. Rensselaerina, a new genus of Lower Devonian brachiopods. American Journal of Science, 43:466-470.

Dunbar, C.O. 1918. Stratigraphy and correlation of the Devonian of western Tennessee. American Journal of Science, 46:732-756.

Dunbar, C.O. 1919. Stratigraphy and correlation of the Devonian of western Tennessee. Tennessee Geological Survey Bulletin, 21:1-127.

Dunbar, C.O. 1920. New species of Devonian fossils from western Tennessee. Connecticut Academy of Arts and Sciences Transactions, 23:109-158.

Dunbar, C.O. 1928. On an ammonite shell investing commensal bryozoa. American Journal of Science, 16:164-165.

Duncan, H.M. 1939. Trepostomatous Bryozoa from the Traverse Group of Michigan. University of Michigan Museum of Paleontology Contributions, 5:171-270.

Duncan, P.M. 1879. On some lithistida, spongida from the Upper Silurian formations in New Brunswick. Annals and Magazine of Natural History, 5:84-91.

Dunham, R.J. 1962. Classification of carbonate rocks according to depositional texture. American Association of Petroleum Geologists Memoir, 1:108-121.

Duringer, P. 1985. Strategie adaptative de la croissance de Placunopsis ostracina Schlotheim, epizoaire du Muschelkalk superieur (Trias germanique, Est del la France). Neuse Jahrbuch fur Geologie und Palaontologie Monatshefte, 1:1-22.

Einsele, G. and A. Seilacher. 1982. Paleogeographic significance of tempestites and periodites, p. 531-536.

In, G. Einsele and A. Seilacher, eds., Cyclic and Event Stratification, Springer-Verlag, Berlin.

Eldridge, N. 1973. Systematics of Lower and lower Middle Devonian species of the trilobite Phacops Emmrich in North America. American Natural History Bulletin, 151:285-337.

Elias, R.J. 1986. Symbiotic relationships between worms and solitary rugose corals in the Late Ordovician. Paleobiology, 12:32-45.

Ervin, C.P. and L.D. McGinnis. 1975. Reelfoot Rift: reactivated precursor to the Mississippi Embayment. Geological Society of America Bulletin, 86:1287-1295.

Fagerstrom, J.A. 1987. The Evolution of Reef Communities. Wiley and Sons, New York, 600p.

Fahraeus, L.E. 1967. Possible Early Devonian conodontophorid provinces. Palaeogeography, Palaeoclimatology, and Palaeoecology, 19:201-213.

Feldman, H.R. 1980. Level-bottom brachiopod communities in the Middle Devonian of New York. Lethaia, 13:27-46.

Fenton, C.L. and M.A. Fenton. 1931. Some snail borings of Paleozoic age. American Midland Naturalist, 12:522-588.

Fenton, C.L. and M.A. Fenton. 1932a Boring sponges in the Devonian of Iowa. American Midland Naturalist, 13:42-62.

Fenton, C.L. and M.A. Fenton. 1932b Orientation and injury in the genus Atrypa. American Midland Naturalist, 13:63-74.

Fischer, D.W. 1981. History of Devonian geology in New York State-a synopsis. In, Oliver, Jr., W.A. and G. Klapper, eds., Devonian Biostratigraphy of New York, Part 1, Text. International Union of Geological Sciences Subcommission on Devonian Stratigraphy, p. 23-32.

Foerste, A.F. 1901. Silurian and Devonian limestones of Tennessee and Kentucky. Geological Society of America Bulletin, 12:395-444.

Foerste, A.F. 1903. Silurian and Devonian limestones of Tennessee. Journal of Geology, 11:554-583, 679-715.

Freeman, L.B. 1951. Regional aspects of Silurian and Devonian stratigraphy in Kentucky. Kentucky Geological Survey Bulletin, 6:1-40.

Gaines, S. and J. Roughgarden. 1987. Fish in offshore kelp forests affect recruitment to intertidal barnacle population. Science, 235:479-481.

Gibson, M.A., C.R. Clement, and T.W. Broadhead. 1986. Geometric configuration and paleogeographic significance of Devonian bryozoan mudmounds in a cratonic seaway. Geological Society of America Abstracts with Program, 18:613.

Gibson, M.A., C.R. Clement, and T.W. Broadhead. 1987. Bryozoan-dominated carbonate mudmounds in a cratonic setting from the basal Devonian of the southeastern United States. Second International Symposium on the Devonian System, Program with Abstracts, p. 93.

Ginsburg, R.N. and J.H. Schroeder. 1973. Growth and submarine fossilization of algal cup reefs, Bermuda. Sedimentology, 20:575-614.

Ginsburg, R.N. and N.P. James. 1974. Spectrum of Holocene reef-building communities in the western Atlantic. In, A.M. Ziegler, K.R. Walker, A.J. Anderson, E.G. Kaufman, R.N. Ginsburg, and N.P. James, eds., Principles of Benthic Community Analysis. Comparative Sedimentology Lab, Sedimenta IV:7.1-7.22.

Goff, L.J. 1982. Symbiosis and parasitism: another viewpoint. BioScience, 32:255-256.

Grant, R.E. 1981. Living habits of ancient brachiopods, p. 122-140. In, T.W. Broadhead, ed., Lophophorates: Notes for a Short Course. University of Tennessee Department of Geology Short Course Notes, 5.

Grause, R.R., J.R. Chamberlain Jr, and A.M. Boker. 1977. Structural modification of corals in relations to waves and currents, p. 135-153, In, S.H. Frost, M.P. Weiss, and J.B. Saunders, eds., Reefs and Related Carbonates-Ecology and Sedimentology. American Association of Petroleum Geologists Studies in Geology 4.

Grohskoph, J.G. 1955. Subsurface geology of the Mississippi Embayment of southeastern Missouri. Missouri Geological Survey Bulletin, 37:1-133.

Hall, J. 1857. Descriptions of Paleozoic fossils. New York State Cabinet of Natural History Annual Report, 10:41-186.

Hall, J. 1859. Palaeontology of New York. Volume III containing descriptions and figures of the organic remains of the Lower Helderberg Group and the Oriskany Sandstone, Part I, text. C. Van Benthuysen and Sons, Albany, 298p.

Hall, J. 1861. Palaeontology of New York. Volume III containing descriptions and figures of the organic remains of the Lower Helderberg Group and the Oriskany Sandstone, Part II, plates. C. Van Benthuysen and Sons, Albany, 120pl.

Hall, J. 1867. Descriptions and figures of fossil brachiopoda from the Upper Helderberg, Hamilton, Portage, and Chemung groups. Paleontology of New York, V. IV. Van Benthuysen and Sons, Albany, 428p.

Hall, J. 1874. Descriptions of bryozoa and corals of the Lower Helderberg Group. New York State Museum of Natural History Report, 26:93-115.

Hall, J. 1879. Corals and bryozoans of the Lower Helderberg Group. New York State Museum of Natural History Report, 32:141-176.

Hall, J. 1887. Palaeontology of New York. Volume VI. Corals and bryozoa: text and plates. C. Van Benthuysen and Sons, Albany, 198p. + plates.

Hall, J. and J.M. Clarke. 1888. Paleontology of New York. Volume VII. Text and plates containing descriptions of the trilobites and other crustacea of the Oriskany, Upper Helderberg, Portage, Chemung and Catskill groups. C. Van Benthuysen and Sons, Albany, 236p.

Hall, J. and J.M. Clarke. 1892. Palaeontology of New York. Volume VIII. An introduction to the study of the genera of Paleozoic brachiopoda, Part I. C. Van Benthuysen and Sons, Albany, 367p. + plates.

Hall, J. and J.M. Clarke. 1894. Palaeontology of New York. Volume VIII. An introduction to the study of the genera of Paleozoic brachiopoda, Part II. C. Van Benthuysen and Sons, Albany, 394p. + plates.

Heckel, P.H. 1974. Carbonate buildups in the geological record: a review. In, L.F. Laporte, ed., Reefs in Time and Space - Selected Examples from the Recent and Ancient. Society of Economic Paleontologists and Minteralogists Special Publication, 18:90-154.

Heckel, P.H. and B.J. Witzke. 1979. Devonian world palaeogeography determined from distribution of carbonate and related lithic palaeoclimatic indicators. Special Papers in Palaeontology, 23:99-123.

Hewitt, M.C. and R.J. Cuffey. 1985. Lichinaliid-fistuliporoid crust-mound (Silurian, New York-Ontario), typical Early Paleozoic bryozoan reefs. Proceedings Fifth International Coral Reef Congress, 6:599-604.

Hiedlauf, D.T., A.T. Hsui, and G. dev. Klein. 1986. Tectonic subsidence analysis of the Illinois Basin. Journal of Geology, 94:779-794.

Hill, D. 1981. Morphology, F6-F35. In, C. Teichert, ed., Treatise on Invertebrate Paleontology, Part F, Coelenterata. Geological Society of America and The University of Kansas Press.

Hinze, W.J., L.W. Braile, G.R. Keller, and E.G. Lidiak. 1977. A tectonic overview of the central midcontinent. U.S. Nuclear Regulatory Commission, NUREG-0382:1-106.

Hoare, R.D. and D.L. Steller. 1967. A Devonian spiriferid with epifauna. Ohio Journal of Science, 67:291-297.

Humphries, E.M. 1973. Seasonal settlement of bryozoans in Rehoboth Bay, Delaware, U.S.A., pp. 115-128. In, G.P. Larwood, ed., Living and Fossil Bryozoa. Proceedings of the International Bryozoology Association, Academic Press, London.

Hurst, J.M. 1974. Selective epizoan encrustations of some Silurian brachiopods form Gotland. Palaeontology, 17:423-429.

Illinois State Geological Survey. 1985. Illinois superdeep drillhole. Unpublished Illinois State Geological Survey Preliminary Proposal, 93p.

Jablonski, D. and D.J. Bottjer. 1983. Soft-bottom epifaunal suspension-feeding assemblages in Late Cretaceous: implications for the evolution of benthic

paleocommunities, pp. 747-812. In, M.J. Tevesz and P.L. McCall, eds., Biotic Interactions in Recent and Benthic Organisms. Plenum Press, New York.

Jackson, J.B.C. 1977. Competition on marine hard ssubstrata: the adaptive significance of solitary and colonial stratigies. American Naturalist, 3:743-767.

Jackson, J.B.C. 1979. Morphological stratagies of sessile animals, pp. 499-555. In, G. Larwood and B.R. Rosen, eds., Biology and Systematics of Colonial Organisms. Academic Press, London.

Jackson. J.B.C. 1983. Biological determinants of present and past sessile animal distribution, pp. 39-120. In, M.J. Tevesz and P.L. McCall, eds., Biotic Interactions in Recent and Fossil Benthic Organisms. Plenum Press, New York.

Jackson, J.B.C. 1985. Distribution and ecology of clonal and aclonal benthic invertebrates, pp. 297-355. In, J.B.C. Jackson, L.W. Buss, and R.E. Cook, eds., Population Biology and Evolution of Clonal Organisms. Yale University Press, New Haven.

James, N.P. 1983. Reef environment. In, P.A. Scholle, D.G. Bebout, and C.H. Moore, eds., Carbonate Depositional Environments. American Association of Petroleum Geologists Memoir, 33:346-440.

Jewell, J.W. 1969. An oil and gas evaluation of north Alabama. Alabama Geological Survey Bulletin, 93:1-53.

Jewell, W.B. 1931. Geology and mineral resources of Hardin County Tennessee. Tennessee Division of Geology Bulletin, 37:1-117.

Johnson, J.G., G. Klapper, and C.A. Sandberg. 1985. Devonian eustatic fluctuations in Euramerica. Geological Society of America Bulletin, 96:567-587.

Johnson, J.G. and M.A. Murphy. 1984. Time-rock model for Siluro-Devonian continental shelf; western U.S. Geological Society of America Bulletin, 95:1349-1359.

Johnson, M.E. 1987. North American Paleozoic oceanography: overview of progress toward a modern synthesis. Paleoceanography, 2:123-140.

Kauffman, E.G. and N.F. Sohl. 1974. Structure and evolution

of Antillean Cretaceous rudist frameworks. Verhandlungend der Naturforschenden Gesellishraft in Basel, 84:399-467.

Keller, G.R., E.G. Lidiak, W.J. Hinze, and L.W. Braile. 1983. The role of rifting in the tectonic development of the midcontinent, U.S.A. Tectonophysics, 94:391-412.

Kelling, G. and P.R. Mullin. 1975. Graded limestone and limestone-quartzite couplets: possible storm-deposits from the Moroccan Carboniferous. Sedimentary Geology, 13:161-190.

Keough, M.J. 1984. Dynamics of the epifauna of the bivalve Pinna bicolor: interactions amon recruitment, predation, and competition. Ecology, 65:677-688.

Kesling, R.V., R.D. Hoare, and D.K. Sparks. 1980. Epizoans of the Middle Devonian brachiopod Paraspirifer bownockeri: their relationships to one another and to their host. Journal of Paleontology, 54:1141-1154.

Klein, G. dev. 1987. Current aspects of basin analysis. Sedimentary Geology, 50:95-118.

Knight-Jones, E.W. 1951. Gregariousness and some other aspects of settling behavior of Spirorbis. Journal Biological Marine Association, 30:201-222.

Knight-Jones, P. Knight-Jones, and S.M. Al-Ogily. 1975. Ecological isolation in the spirorbidae. Proceedings Ninth European Marine Biology Symposium, p. 539-561.

Kobluk, D.R. and M.A. Lysenko. 1987. Impact of two sequential Pacific hurricanes on sub-rubble cryptic corals: the possible role of cryptic organisms in the maintenance of coral reef communities. Journal of Paleontology, 61:663-675.

Koch, II, G.F. 1981. Brachiopod community paleoecology, paleobiogeography, and depositional topography of the Devonian Onandaga Limestone and correlative strata of eastern North America. Lethaia, 14:83-103.

Koenig, J.W. 1967. The Ozark Uplift and midcontinent Silurian and Devonian stratigraphy. Tulsa Geological Society Digest, 35:119-147.

Krasnov, Y.V. and B.V. Preobrezhenskiy. 1972. O prirode i znachenii form taulyat i kolonial'nykh skleraktineiy

(The nature and significance of life forms in tabulates and colonial scleractinians). Paleontological Journal, 1972:2:264-268.

Krebs, W. 1974. Devonian carbonate complexes of central Europe. In, L.F. Laporte, ed., Reefs in Time and Space - Selected Examples from the Recent and Ancient. Society of Economic Paleontologists and Mineralogists Special Publication, 18:155-208.

Kreisa, J.D. 1981. Storm generated sedimentary structures in subtidal marine facies with examples from the Middle and Upper Ordovician of southwest Virginia. Journal of Sedimentary Petrology, 51:823-848.

Lawrence, D.R. 1969. The use of clionid sponges in paleoenvironmental analysis. Journal of Paleontology, 43:539-543.

Lees, W. 1974. Devonian carbonate complexes of central Europe. In, L.F. Laporte, ed., Reefs in Time and Space - Selected Examples from the Recent and Ancient. Society of Economic Paleontologists and Mineralogists Special Publication, 18:155-208.

Leleshus, V.L. 1985. K evolyutsiiyestestvennoy prodolzhitel'nosti zhizni korallovykh polopov v paleozoye Sredney Azii (Evolution of the natural life span of coral polyps during the Paleozoic of central Asia). Paleontological Journal, 1985:2:17-21.

Lewin, R.A. 1982. Symbiosis and Parasitism - definitions and evaluations. BioScience, 32:254, 256, 259.

Liddell, W.D. and C.E. Brett. 1982. Skeletal overgrowths among epizoans from the Silurian (Wenlockian) Waldron Shale. Paleobiology, 8:67-78.

Liljedahl, L. 1986. Endolithic micro-organisms and silicification of a bivalve fauna from the Silurian of Gotland. Lethaia, 19:267-278.

Longman, M.W. 1980. Carbonate diagenetic textures from nearsurface diagenetic environments. American Association of Petroleum Geologists Bulletin, 64:461-487.

Longman, M.W. 1981. A process approach to recognizing facies of reef complexes. In, D.F. Toomey, ed., European Reef Models. Society of Economic Paleontologists and Mineralogists Special Publication, 30:9-40.

Lundin, R.F. and G.D. Newton. 1970. Ostracoda and the Silurian stratigraphy of northwestern Alabama. Alabama Geological Survey Bulletin, 95:1-51.

Lundin, R.F. and L.E. Petersen. 1974. Ostracoda from the Rockhouse Formation (Devonian) of western Tennessee. Journal of Paleontology, 48:236-255.

Makurath, J.H. 1977. Marine faunal assemblages in the Silurian-Devonian Keyser Limestone of the central Appalachians. Lethaia, 10:235-256.

Marcher, M.V. and R.G. Stearns. 1962. Tuscaloosa Formation in Tennessee. Geological Society of America Bulletin, 73:1365-1386.

Markello, J.R. and J.F. Read. 1981. Carbonate-to-deeper shale shelf transitions of an Upper Cambrian intrashelf basin: Nolichucky Formation, southwestern Virgina. Sedimentology, 28:573-597.

McCall, P.L. and M.J.S. Tevesz. 1983. Soft-bottom succession and the fossil record, p. 157-194. In, Tevesz, M.J.S. and McCall, P.L., eds., Biotic Interactions In Recent and Fossil Benthic Organisms. Plenum Press, New York.

McComb, R. 1987. Petrology, paleodepositional environments, biostratigraphy, and paleoecology of the Decatur and Rockhouse limestones (Upper Silurian-Lower Devonian), west-central Tennessee: Unpublished M.S. thesis, University of Tennessee, 309p.

McComb, R. and T.W. Broadhead. 1980. Silurian-Devonian correlation in eastern United States. Geological Society of America Abstracts with Program, 12:479.

McNamera, K.J. 1978. Symbiosis between gastropods and bryozoans in the Late Ordovician of Cumbria, England. Lethaia, 11:25-40.

Menge, B.A. and J.P. Sutherland. 1976. Some diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. American Naturalist, 110:351-369.

Meyer, D.L. and W.I. Ausich. 1983. Biotic interactions among recent and fossil crinoids, p. 377-427. In, M.J.S. Tevesz and P.L. McCall, eds., Biotic Interactions in Recent and Fossil

Benthic Organisms. Plenum Press, New York.

Miller, W. and L.M. Alvis. 1986. Temporal change as an aspect of biogenic shell utilization and damage, Pliestocene of North Carolina. Palaeogeography, Palaeoclimatology, and Palaeoecology, 56:197-215.

Morris, R.W. and H.B. Rollins. 1971. The distribution and paleoecological interpretation of Cornulites in the Waynesville Formation (Upper Ordovician) of southwest Ohio. Ohio Journal of Science, 71:159-174.

Morse, W.C. 1930. Paleozoic rocks. Mississippi State Geological Survey Bulletin, 23:1-212.

Mount, J.F. 1984. Mixing of siliciclastic and carbonate sediments in shallow shelf environments. Geology, 12:432-435.

Muscatine, L. and J.W. Porter. 1977. Reef symbiosis: mutualistic symbiosis adapted to nutrient-poor environments. Bioscience, 27:454-460.

Newman, W.A. and H.S. Ladd. 1974. Origin of coral-inhabiting balanids (Cirripedia: Thoracica). Verhandlungen der Naturforschenden Gesellschaft in Basel, 84:381-397.

Newall, G. 1970. A symbiotic relationship between Lingula and the coral Heliolites in the Silurian, p. 335-344. In, T.P. Crimes and J.C. Harper, eds., Trace Fossils. Geological Journal Special Issue 3.

Nield, E.W. 1986. Liljevallia gottlandica: encrustation patterns in the earliest cemented articulate brachiopod and their implications for its larval behavior. Paleoclimatology, Paleogeography, Paleoecology, 56:277-290.

Ohern, D.W. and T.P. Maynard. 1913. Gastropoda. In, Lower Devonian of Maryland. Maryland Geological Survey, 5:465-486.

Ohern, D.W. and T.P. Maynard. 1913. Pelecypoda. In, Lower Devonian of Maryland. Maryland Geological Survey, 5:450-464.

Ohern, D.W. and T.P. Maynard. 1913. Trilobita. In, Lower Devonian of Maryland. Maryland Geological Survey, 5:489-512.

Oliver, W.A. 1968. Some aspects of colony development in corals, pp. 16-34. In , B.D. Macurda Jr., ed., Paleobiological Aspects of Growth and Development, A Symposium. Paleontological Society Memoir 2.

Oliver, W.A. 1976. Biogeography of Devonian rugose corals. Journal of Paleontology, 50:365-373.

Oliver, W.A. 1983. Symbiosis of Devonian rugose corals. Memoir Association of Australas Paleontols, 1:261-274.

Osman, R.W. 1977. The establishment and development of a marine epifaunal community. Ecological Monographs, 47:37-63.

Osman, R.W. and J.A. Haugsness. 1981. Mutualism among sessile invertebrates: a mediator of competition and predation. Science, 211:846-848.

Paine, R.T. 1966. Food web complexity and species diversity. American Naturalist, 100:65-76

Pandolfi, J.M. 1984. Environmental influence of growth form in some massive tabulate corals from the Hamilton Group (Middle Devonian) of New York State. Palaeontographica Americana, 54:538-542.

Pestana, H. 1985. Carbonate sediment production by Sargassum epibionts. Journal of Sedimentary Petrology, 55:184-186.

Petersen, L.E. 1972. Ostracodes and stratigraphy of the Birdsong Formation (Devonian) of western Tennessee. Unpublished M.S. thesis, Arizona State University, 180p.

Petersen, R.M. and R.D. Hoare. 1973. Epizoan rugose coelenterates from the Ames Limestone (Conemaugh) of Ohio. Compass, 50:22-24.

Philcox, M.E. 1971. Growth forms and role of colonial coelenterates in reefs of the Gower Formation (Silurian), Iowa. Journal of Paleontology, 45:338-346.

Pickerill, R.K. and T.L. Harland. 1984. Middle Ordovician microborings of probable sponge origin from eastern Canada and southern Norway. Journal of Paleontology, 58:885-891.

Pickett, S.T.A. and P.S. White. 1985. Patch dynamics: a synthesis, pp. 371-384. In, P.S. White and S.T.A. Pickett, eds., The Ecology of Natural Disturbances and

Patch Dynamics. Academic Press, New York.

Pitrat, C.W. and F.S. Rogers. 1978. Spinocyrtia and its epibionts in the Traverse Group (Devonian) of Michigan. Journal of Paleontology, 52:1315-1324.

Pohl, E.R. 1930. Devonian formations of the Mississippi Basin. Journal Tennessee Academy of Science, 5:54-63.

Probert, P.K. 1984. Disturbance, sediment stability and trophic structure of soft bottom communities. Journal of Marine Research, 42:893-921.

Raymond, A. 1987. Paleogeographic distribution of Early Devonian plant traits. Palaios, 2:113-132.

Read, J.F. 1982. Carbonate platforms of passive (extensional) continental margins: types, characteristics, and evolution. Tectonophysics, 8:195-212.

Reid, S.R. 1983. Petrology, paleodepositional environment, and paleoecology of the Lower Devonian Ross Formation, West-Central Tennessee: unpublished M.S. thesis, University of Tennessee, 143p.

Reid, S.R. and T.W. Broadhead. 1983. Epibiont encrustations as indicators of life, and hydrodynamic orientation of Leptaena (Brachiopoda, Strophomenida). Geological Society of America Abstracts with Program, 15:669.

Rhoads, D.C. 1970. Mass properties, stability, and ecology of marine muds related to burrowing activity. Geological Journal Special Issue, 3:391-406.

Richards, R.P. 1974. Ecology of the cornulitidae. Journal of Paleontology, 48:514-523.

Richardson, J.R. 1986. Brachiopods. Scientific American, 255:100-106.

Rodriguez, J. and R.C. Gutschick. 1975. Epibiontic relationships on a Lower Devonan algal bank. Journal of Paleontolgy, 49:1112-1120.

Roemer, F. 1861. Die Silurische fauna des westlichen Tennessee. American Journal of Science, 31:127-128.

Rohr, D.M. 1976. Silurian predatory borings in the brachiopod Dicaelosia from the Canadian arctic. Journal of Paleontology, 50:1175-1179.

Ross, R.M. 1942. Reverse faulting in the Paleozoic strata near Camden, Tennessee. Journal Tennessee Academy of Science, XX:201-204.

Rudwick, J.M.S. 1970. Living and Fossil Brachiopods. Hutchinson and Company, London, 199p.

Russ, G.R. 1980. Effects of predation by fish, composition and structural complexity of the substratum on the establishment of a marine epifaunal community. Journal of Experimental Marine Biology and Ecology, 42:55-69.

Russ, G.R. 1982. Overgrowth of marine epifaunal community: competitive hierarchies and competitive networks. Oecologia, 53:12-19.

Ryland, J.S. 1977. Taxes and tropisms of bryozoans, pp. 411-436. In, R.M. Woolacott and R.L. Zimmer, eds., Biology of the Bryozoa. Academic Press, New York.

Ryland, J.S. and A.R. Stebbins. 1971. Settlement and oriented growth in epiphytic and epizoic bryozoans, pp. 105-123. In, D.J. Crisp, ed., Fourth European Marine Biology Symposium, Cambridge Press, London.

Safford, J.M. 1851. The Silurian basin of western Tennessee, with notices of the strata surrounding it. American Journal of Science, 12:352-361.

Safford, J.M. 1856. A geological reconnaissance of the state of Tennessee. First Bienial Report to the General Assembly of Tennessee.

Safford, J.M. 1861. The Upper Silurian beds of western Tennessee; and Dr. F. Roemer's monograph. American Journal of Science, 31:205-209.

Safford, J.M. 1869. Geology of Tennessee. Nashville, 550p.

Safford, J.M. and J.D. Killebrew. 1876. An Elementary Geology of Tennessee. Nashville, TN, 264 p.

Safford, J.M. and C. Schuchert. 1899. The Camden Chert of Tennessee and its Lower Oriskany fauna. American Journal of Science, 7:429-432.

Sando, M.J. 1984. Significance of epibionts on horn corals from the Chainman Shale (Upper Mississippian) of Utah. Journal of Paleontology, 58:185-196.

Sarle, C.J. 1901. Reef structures in Clinton and Niagara strata of western New York. American Geologist, 28:282-299.

Savage. T.E. 1931. The Devonian fauna of Kentucky. In, W.R. Jillson, ed., The Paleontology of Kentucky. Kentucky Geological Survey, series 6, 36:215-247.

Scanland, T.B. 1979. The epibiota of Arca zebra and Arca imbricata: a community analysis. Veliger, 21:475-485.

Schumann, D. 1967. Die liebenswiese von Mucrospirifer Grabeau, 1831 (brachiopoda). Paleogeography, Paleoclimatology, Paleoecology, 3:381-392.

Schuchert, C. 1910. Paleogeography of North America. Geological Society of America Bulletin, 20:427-606.

Schuchert C. and C.M. LeVene. 1929. Brachiopoda. Fossilium Catalogus 1. Animalia. Pompeckj, Berlin, 140p.

Schuchert, C. and T.P. Maynard. 1913. Brachiopoda. In, Lower Devonian of Maryland. Maryland Geological Survey, 5:290-449.

Schwalb, H.R. 1983. Paleozoic geology of the New Madrid area. U.S. Nuclear Regulatory Commission, NUREG/CR-3173:42-68.

Scotese, C.R. and S.F. Barrett. 1987. Devonian paleogeographic reconstructions. Second International Symposium on the Devonian System Program and Abstracts, p. 205.

Scotese, C.R., R.K. Bambach, C. Barton, R. Van der Voo, and A.M. Ziegler. 1979. Paleozoic base maps. Journal of Geology, 87:217-277.

Scotese, C.R., R. Van der Voo, S.F. Barret. 1985. Silurian and Devonian base maps. Philosophical Transactions Royal Society of London, B309:57-77.

Seilacher, A. 1960. Epizoans as a key to ammonoid ecology. Journal of Paleontology, 34:189-193.

Seilacher, A. 1969. Swimming habits of belemnites-recorded by boring barnicles. Paleogeography, paleoclimatology, Paleoecology, 4:279-285.

Shou-Hsin, C. 1959. Note on the paleoecological relation between Aulopora and Mucrospirifer. Acta

Palaeontologica Sinica, 7:502-504.

Smith, A.E., A.M. Hurley, and J.C. Briden. 1981. Phanerozoic paleocontinental world maps. Cambridge University Press, London.

Sohl, N.F. 1969. The fossil record of shell boring by snails. American Zoologist, 9:725-734.

Sousa, W.P. 1977. Fouling adn bioadhesion life strategies in bryozoans, pp. 437-457. In, R.M. Woollacott, and R.L. Zimmer, eds., Biology of the Bryozoa. Academic Press, New York.

Sousa, W.P. 1979. Disturbance in marine intertidal boulder fields: the non equilibrium maintenance of species diversity. Ecology, 60:1225-1239.

Sousa, W.P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics, 15:353-391.

Sousa, W.P. 1985. Disturbance and patch dynamics on rocky intertidal shores, pp. 101-124. In, P.S. White and S.T.A. Pickett, eds., The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Sparks, D.K., R.D. Hoare, and R.V. Kesling. 1980. Epizoans on the brachiopod Paraspirifer bownockeri (Stuart) from the Middle Devonian of Ohio. University of Michigan Museum Papers on Paleontology, 23:1-105.

Specht, R.W. and R.L. Brenner. 1979. Storm-wave genesis of bioclastic carbonates in Upper Jurassic epicontinental mudstones, east-central Wyoming. Journal of Sedimentary Petrology, 49:1307-1322.

Spjednaes, N. 1984. Epifauna as a tool in autecological analysis of Silurian brachiopods. Special Papers in Paleontology, 32:225-235.

Springer, F. 1917. On the crinoid genus Scyphocrinus and its bulbous root Camarocrinus. Smithsonian Institute Publicatio, 2440:1-74.

Springer, F. 1920a. The crinoidea flexibilia - text. Smithsonian Institute Publication, 2501:1-486.

Springer, F. 1920b. The crinoidea flexibilia - plates. Smithsonian Institute Publication, 2501: 1-158.

Springer, F. 1926. American Silurian crinoids. Smithsonian Institute Publication, 2871:1-239.

Starr, M.D. 1975. A generalized scheme for classifying organismic associations. Bulletin of Experimental Biology, 24:1-20.

Stearns, R.G. and M.V. Marcher. 1962. Late Cretaceous and subsequent structural development of the northern Mississippi Embayment area. Geological Society of America Bulletin, 73:1387-1394.

Stearns, R.G. and A.L. Reesman. 1986. Cambrian to Holocene structural and burial history of Nashville Dome. American Association of Petroleum Geologists Bulletin, 70:143-154.

Steller, D.L. 1965. The epifaunal elements on the brachiopods of the Silica Shale Formation. Unpublished Master of Science Thesis, Bowling Green State University, Bowling Green, 79p.

Stewart, G.A. 1922. The fauna of the Little Saline Limestone in Ste. Genevieve County. In, E.B. Branson, ed., The Devonian of Missouri. Missouri Bureau of Geology and Mines, 2nd series, 17:166-212 + plates.

Strimple, H.L. 1963. Crinoids of the Hunton Group (Devonian - Silutrian) of Oklahoma. Oklahoma Geological Survey Bulletin, 100:1-169.

Strimple, H.L. 1975. The rare inadunate crinoid genus Thalamocrinus. Southeastern Geology, 16:249-253.

Strimple, H.L. 1981. Thalamocrinus cf. elongatus Springer from the Henryhouse Formation (Silurian) of Oklahoma. Oklahoma Geology Notes, 41:116-119.

Sutherland, J.P. and R.H. Karlson. 1977. Development and stability of a fouling community at Beaufort, N.C. Ecological Monographs, 47:425-446.

Sutherland, P.K. 1965. Henryhouse rugose corals. Oklahoma Geological Survey Bulletin, 109:1-92.

Swartz, C.K. 1913. Coelenterata. In, Lower Devonian of Maryland. Maryland Geological Survey, 5:195-226.

Tansey, V.O. 1922. The fauna and the correlation of the Baily Limestone in the Little Saline Creek area of Ste. Genevieve County, Missouri. In, E.B. Branson, ed., The

Devonian of Missouri. Missouri Bureau of Geology and Mines, 2nd series, 17:166-212 + plates.

Taylor, P.D. 1979. Palaeoecology of the encrusting epifauna of some British Jurassic bivalves. Palaeogeography, Palaeoclimatology, Palaeoecology, 28:241-262.

Taylor, P.D. 1982. Probable predatory borings in Late Cretaceous bryozoans. Lethaia, 15:67-74.

Taylor, P.D. 1984. Adaptations for spatial competition and utilization in Silurian encrusting bryozoans. Special Papers in Palaeontology, 32:197-210.

Teichert, C. 1945. Parasitic worms in Permian brachiopod and pelecypod shells in western Australia. American Journal of Science, 233:197-209.

Tevesz, M.J.S and P.L. McCall. 1983. Biotic Interactions In Recent and Fossil Benthic Organisms. Plenum Press, New York.

Textoris, D.A. and A.V. Carozzi. 1964. Petrography and evolution of Niagaran (Silurian) reefs, Indiana. American Association of Petroleum Geologists Bulletin, 48:397-426.

Thayer, C.W. 1974. Substrate specificity of Devonian epizoa. Journal of Paleontology, 48:881-894.

Thayer, C.W. 1975. Morphological adaptations of benthic invertebrates to soft substrates. Journal of Marine Research, 33:177-189.

Thayer, C.W. 1985. Brachiopods versus mussels: competition, predation, and palatability. Science, 228:1727-1528.

Thomas, W.A. 1972. Regional Paleozoic stratigraphy in Mississippi between Ouachita and Appalachian mountains. American Association of Petroleum Geologists Bulletin, 56:81-106.

Thomsen, E. 1977. Relations between encrusting bryozoans and substrate: an example from the Danian of Denmark. Bulletin of the Geological Society of Denmark, 26:133-145.

Trueman, A.E. 1942. Supposed commensalism of Carboniferous Spirorbis and certain non-marine lamellibranchs. Geological Magazine, 79:312-320.

Tsien, H.H. 1985a. Algal-bacterial origin for micrites in mud mounds, pp. 290-296. In, D.F. Toomey and M.H. Nitecki, eds., Paleoalgology: Contemporary Research and Applications. Springer-Verlag, Berlin.

Tsien, H.H. 1985b. Origin of stromatactis - a replacement of colonial microbial accretions, pp. 274-289. In, D.F. Toomey and M.H. Nitecki, eds., Paleoalgology: Contemporary Research and Applications. Springer-Verlag, Berlin.

Ulrich, E.O. and R.S. Bassler. 1913. Bryozoa. In, Lower Devonian of Maryland. Maryland Geological Survey, 5:259-289.

Van der Voo, R. 1988. Paleozoic paleogeography of North America, Gondwanaland, and intervening displaced terranes: comparisons of paleomagnetism with paleoclimatology and biogeographical patterns. Geological Society of America Bulletin, 100:311-324.

Vance, R.R. 1978. A mutualistic interaction between a sessile marine clam and its epibionts. Ecology, 59:679-685.

Vogel, K., S. Golubic, and C.E. Brett. 1987. Endolith associations and their relation to facies distribution in the Middle Devonian of New York State. Lethaia, 20:243-255.

Voynovkiy-Kriger, K.G. 1970. O "konechnykh chashkakh" tabulyat i nekotorykh problemakah "opredelennogo rosta" u iskopayemykh korallov ("Terminal calices" of tabulate corals and problems of "determinate growth" in fossil corals). Paleontological Journal, 1970:2:248-250.

Wade, B. 1914. The geology of Perry County and vicinity, Resouces of Tennessee, 4:150-181.

Walker, K.R. 1974. Mud substrates, In, A.M. Ziegler, K.R. Walker, A.J. Anderson, E.G. Kaufman, R.N. Ginsburg, and N.P. James, eds., Principles of Benthic Community Analysis, Comparative Sedimentology Lab, Sedimenta IV:5.1-5.11.

Walker, K.R. 1988. The Fabric of Cements in Paleozoic Carbonate Rocks: A Workshop. Appalachian Basin Industrial Associates. Knoxville, 177p.

Walker, K.R. and L.P. Alberstadt. 1975. Ecological succession as an aspect of structure in fossil

communities. Paleobiology, 1:238-257.

Walker, K.R. and K.F. Ferrigno. 1973. Major Ordovician reef tract in east Tennessee. American Journal of Science, 273A:294-325.

Walker, K.R. and W.W. Diehl. 1985. The role of marine cementation in the preservation of Lower Paleozoic assemblages. Philosphical Transactions Royal Society of London, B311:143-153.

Walker, K.R. and W.W. Diehl. 1986. The effect of synsedimentary substrate modification on the composition of paleocommunities: paleoecological succession revisited. Palaios, 1:50-74.

Walker, K.R. and W.C. Parker. 1976. Population structure of a pioneer and a later stage species in an Ordovician ecological succession. Paleobiology, 2:191-201.

Walker, K.R., G. Shanmugam, and S.C. Ruppel. 1983. A model for carbonate to terrigenous clastic sequences. Geological Society of America Bulletin, 94:700-712.

Walker, L.G. and G.N. Pruitt. 1975. Devonian and Silurian at the Vulcan Materials Company Parsons Quarry. Tennessee Division of Geology Reports of Investigations, 36:8-13.

Walker, R.G. 1985. Geologic evidence for storm transportation and deposition on ancient shelves, pp. 243-302. In, R.W. Tillman, D.J.P. Swift, and R.G. Walker, eds., Shelf Sands and Sandstone Reservoirs. Society of Economic Paleontologists and Mineralogists Short Course Notes, 13.

Wallace, M.W. 1987. The role of internal erosion and sedimentation in the formation of stromatactis mudstones and associated lithologies. Journal of Sedimentary Petrology, 57:695-700.

Wanless, H.R. 1979. Limestone response to stress: pressure solution and dolomitization. Journal of Sedimentary Petrology, 49:437-462.

Warn, J.M. 1974. Presumed myzostomid infestation of an Ordovician crinoid. Journal of Paleontology, 48:506-507.

Watkins, R. 1981. Epizoan ecology in the type Ludlow Series (Upper Silurian), England. Journal of Paleontology, 55:29-32.

Watzin, M.C. 1986. Larval settlement into marine soft-sediment systems: interactions with the meiofauna. Journal of Experimental Marine Biology and Ecology, 98:65-113.

Weidman, L.A. 1985. Community paleoecological study of the Silica Shale equivalents in northeastern Indiana. Journal of Paleontology, 59:160-182.

Welch, J.R. 1976. Phosphannalus on Paleozoic crinoid stems. Journal of Paleontology, 50:218-225.

Weidner, W.E. and R.M. Feldman. 1985. Paleoecological interpretation of echinocariid arthropod assemblages in the Late Devonian (Famenian), Chagrin Shale, northeastern Ohio. Journal of Paleontology, 59:86-1004.

Weller, J.M. 1944. Devonian correlations in Illinois and surrounding states: a summary. Illinois State Geological Survey Bulletin, 68:205-216.

Weller, S. 1903. The Paleozoic faunas. New Jersey Geological Survey. Report on Paleontology, 31-462.

Werle, N.G., T.J. Frest, and R.H. Mapes. 1984. The epizoan Phosphanulus on a Pennsylvanian crinoid stem from Texas. Journal of Paleontology, 58:1163-1166.

White, P.S. and S.T.A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction, pp. 3-13. In, P.S. White and S.T.A. Pickett, eds., The Ecology of Natural Disturbances and Patch Dynamics. Academic Press, New York.

Williams, H.S. 1897. On the southern Devonian formations. American Journal of Science, 8:393-403.

Willis, B. 1909. Paleogeographic maps of North America. Journal of Geology, 17:253-256, 286-288.

Wilson, Jr., C.W. 1935. The ostracode fauna of the Birdsong Shale, Helderberg, of western Tennessee. Journal of Paleontology, 9:629-646.

Wilson, Jr., C.W. 1939. Probable connection of the Nashville and Ozark domes by a complimentary arch. Journal of Geology, 47:583-597.

Wilson, Jr., C.W. 1949. Pre-Chattanooga stratigraphy of central Tennessee. Tennessee Geological Survey Bulletin, 56:1-169.

Wilson, Jr., C.W. 1963. Quantitative analysis of Ordovician and younger structural development of Nashville Dome, Tennessee. American Association of Petroleum Geologists Bulletin, 47:823-832.

Wilson, J.L. 1975. Carbonate Facies in Geologic History. Springer-Verlag, New York, 471p.

Witzke, B.J. and P.H. Heckel. 1987. Paleoclimatic indicators and inferred Devonian paleolatitudes of Euramerica. Second International Symposium on the Devonian System Program and Abstracts, p. 250.

Woodin, S.A. 1976. Adult larval interactions in dense infaunal assemblages: patterns of abundance. Journal of Marine Research, 34:25-41.

Woodin, S.A. 1978. Refuges, disturbance, and community structure: a marine soft bottom example. Ecology, 59:274-284.

Woodin, S.A. 1983. Biotic interactions in Recent marine sedimentary environments, p. 3-38. In, M.J.S. Tevesz and P.L. McCall, eds., Biotic Interactions in Recent and Fossil Benthic Organisms. Plenum Press, New York.

Woodin, S.A. and J.B.C. Jackson. 1979. Interphyletic competition among marine benthos. American Zoologist, 19:1029-1043.

Wulff, J.L. 1985. Clonal organisms and the evolution of mutualism, p. 437-466. In, L.W. Buss and R.J. Cook, eds., Population Biology and Ecology of Clonal Organisms. Yale University Press, New Hampshire.

Yakovlev, N.N. 1926. The phenomena of the parasitism, commensalism, and symbiosis in the Paleozoic invertebrata. Vserossiiskoe Paleontolgicheskoe Obschchestvo, Lenningrad Annaire, 4:113-124.

Ziegler, A.M., C.R. Scotese, W.S. McKerrow, M.E. Johnson, and R.K. Bambach. 1979. Paleozoic paleogeography. Annual Reviews Earth and Planetary Science, 7:473-502.

Zumwalt, G.S. and T.E. Delca. 1983. Utilization of brachiopod feeding currents by epizoic foraminifera. Journal of Paleontology, 54:477-484.

APPENDICES

APPENDIX A

DESCRIPTIONS OF MEASURED SECTIONS

Three measured sections of the Rockhouse and Birdsong members of the Ross Formation were used in this study. Each section is described below beginning with the oldest unit at the bottom of the sequence and ending with the youngest unit at the top of each sequence. The secton at McClannahan Quarry consists of the Birdsong Shale only and the descriptions are based on bed-by-bed measurements, thin section analysis, and field observations. The Parsons Quarry consists of the lower Rockhouse Limestone only and is based on three continuous cores from which thin sections were prepared. The Elkin's Quarry section consists of a measured section of Birdsong Shale and Rockhouse Limestone with lithologic descriptions made in the field using spoil blocks.

The lithologic classification used is that of Dunham (1962). Bedding thickness conventions used (Table 4) are that of McKee and Weir (1953) as modified by Ingram (1954). All measurements are given in meters.

Table 4. Bedding thickness classification used in this study.

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

Parsons Quarry

Unit	Thickness m	Cummulative Thickness m	Description
PQC2: Core Through Mound Center			
unnamed	0.50	0.50	Decatur Limestone. Pink, medium-bedded, sparsely glauconitic, graded and cross stratified echinodermal packstone to grainstone. Thin sections: PQC-2J.
Phase I	0.08	0.58	Rockhouse Limestone. Greenish gray echinoderm-rich, terrigenous mudstone; fines upward; echinoderm grains fractured, angular to subrounded, bored; cryptostome bryozoans and articulate brachiopods common; compaction breakage and pressure solution common; contact with underlying Decatur Limestone sharp. Thin sections: PQC2-I
Phase II	0.60	1.18	Gray echinodermal-bryozoan packstone that fines upward; shale drapes cap each fining-upward sequence; allochems broken, fragmented, dominated by cryptostome bryozoans with lesser amounts of cystoporate and bifoliate bryozoans; cystoporates commonly encrusting mud lithoclasts; umbrella voids common; vertical and lateral contacts gradational. Thin sections: PQC2-H, PQC2-G
Phase III	1.70	2.88	Non-laminated, massive,

			greenish-gray, lime mudstone to bryozoan boundstone dominated by Buskopora sp.; colony forms platy to contorted; upper part of phase contains spar-filled, Buskopora-lined, cavities; contact with underlying and overlying phases gradational, laterally gradational into bedded intermound lithofacies. Thin sections: PQC2-F, PQC2-E, PQC2-D, PQC2-C
Phase IV	.70	3.58	Gray, poorly laminated, echinoderm-bryozoan lime mudstone to wackestone with lenses of packstone to grainstone; void-filling spar common, epecially as umbrella voids. Thin sections: PQC2-B, PQC2-A
PQC3: Transition between mound and intermound.			
unnamed	0.60	0.60	Decatur Limestone. Pink to gray, medium-bedded, sparsely glauconitic, echinodermal packstone to grainstone exhibiting graded bedding and cross stratification. Thin sections: PQC3-H
Phase II	0.20	0.80	Rockhouse Limestone. Gray, echinoderm-bryozoan packstone, fines upward with thin shale drapes capping sequences, cryptostome bryozoans dominate. Thin sections: none
Phase III	1.50	2.30	Non-laminated, massive, greenish-gray, lime mudstone to bryozoan boundstone dominated by cystoporate

			bryozoans; contact with overlying and underlying phases gradational; grades upward into bryozoan-echinoderm packstone to grainstone with shale drapes. Thin sections: PQC3-G, PQC3-F, PQC3-E, PQC3-D,
PQC1: Core Through Intermound			
intermound	0.30	2.30	Gray, skeletal packstone and grainstone with minor ammounts of glauconite; dominated by echinoderms and cystoporate bryozoans; fining upward graded bedding common. Thin sections: PQC3-B
Phase IV	0.20	2.50	Gray, poorly laminated, echinoderm-bryozoan, lime mudstone to wackestone with packstone grainstone lenses. Thin sections: none
intermound	0.30	2.80	Gray, skeletal packstone and grainstone with minor amounts of glauconite; dominated by echinoderms and cystoporate bryozoans; fining upward graded bedding. Thin sections: PQC3-A

Elkins Quarry

The section at Elkins Quarry (EQ) is in an abandoned limestone quarry located off State Route 20 miles (33 km) east of the Tennessee River. Direct sampling of the highwall was not possible; therefore, measurements were obtained by hanging a tape measure over the highwall to

obtain measure beddding thickness, and lithology was described using spoil and slump blocks along the floor of the quarry. No thin sections were prepared. Biotic abundances were obtained using a 0.5 m^2 quadrate, counting 100 points. Only the Birdsong was studied in detail.

UNIT	THICKNESS m	CUMMULATIVE THICKNESS m	DESCRIPTION
EQ0	4.4 m	4.4 m	Rockhouse Limestone. Tan weathering, medium bedded, skeletal limestone overlying vuggy bioclastic-rich, locally cross stratified limestone. Grid Counts: none
EQ1	0.7	5.1	Birdsong Shale. Gray, medium-bedded, skeletal limestone interbedded with thin, unfossiliferous to fossiliferous, burrowed, glauconitic shale dominated by brachiopods. Grid Counts: none
EQ2	2.4	7.5	Tan-, olive-, to red-weathering, medium-bedded, shaly limestone that fines upward; interbedded with gray, medium-bedded, unfossiliferous to fossiliferous, bioturbated shale; fossils highly fragmented, locally accumulated in thin (4 cm thick) shell beds, minor nodular carbonate beds; brachiopod-dominated. Grid Counts: EQG-1, 3
EQ3	1.1	8.6	Dark gray, thick-bedded,

			bioturbated, unfossiliferous to fossiliferous shale with thin nodular fossiliferous calcareous mudstone beds near middle of unit; skeletal lenses throughout; brachiopod-dominated; fossil abundance increases near the top of the unit; allochems fragmented, abraided, rounded. Grid Counts: EQG-2, 5
EQ4	0.3	8.9	Dark gray, thin-bedded, sparsely fossiliferous, trace fossil rich, shaly mudstone, trace fossils dominately horizontal, straight to slightly sinuous with coarse clastic infill, pyrite surface coatings on bedding planes; grades vertically into 4 - 5 cm thick fissile shale with minor amounts of bryozoans and brachiopods. Grid Counts: EQG-4
EQ5	0.9	9.8	Dark gray to olive-weathering, medium-bedded, interbedded sparsely fossiliferous shaly limestone and shale. Ramose bryozoans dominate. Grid Counts: none
EQ6	1.2	10.0	Dark gray to tan-weathering, bryozoan-echinoderm packstone to grainstone with thin shaly partings. Grid Counts: none
unnamed	1.6	11.6	Camden Chert. White, blocky, bedded chert interbedded with white clay; mostly covered by vegetation. No samples.

McClahanan's Quarry

The section at McClanahan's Quarry exposes the entire sequence of Rockhouse Limestone and Birdsong Shale; however, only the Birdsong Shale and uppermost few beds of the Rockhouse were able to be sampled because the level of overburden removal coincides with the base of the Birdsong.

UNIT	THICKNESS m	CUMMULATIVE THICKNESS m	DESCRIPTION
UNNAMED	0.2	0.2	Rockhouse Limestone. Medium-bedded, crinoidal packstone at base to crinoidal grainstone at top. Dominated by crinoid plates with clear syntaxial overgrowths, impunctate and punctate brachiopods, and ramose bryozoans. Samples: MQ1
MQ1	1.2	1.4	Birdsong Shale. Medium gray, thin-bedded, glauconitic, crinoidal wackestone to packstone to grainstone interbedded with dark gray, fossiliferous shale. Limestones show repeated fining-upward sequences (1-4 cm thick) of grainstone with shale caps. Burrows common. Samples: MQ2-10.
MQ2	11.8	13.2	Very thin- to thick-bedded, fossiliferous gray shale and very thin- to medium-bedded fossiliferous mudstone interbedded with very thin- to

			medium-bedded brachiopod, echinoderm wackestone to packstone. Uppermost bed a thick-bedded, fossiliferous, calcareous mudstone that grades upwards to echinodermal packstone and grainstone. Samples: MQ11-23, MQ1A-7A, MQ24-44.
MQ3	1.9	15.1	Thick-bedded sequence of fossiliferous gray mudstone to fossiliferous shale with abundant brachiopods and echinoderms, and lesser amounts of bryozoans. Nodular calcareous mudstone to wackestone development near the center of individual mudstone beds. Samples: MQ45-48T
MQ4	0.3	15.4	Poorly fossilifeous but trace fossil rich, dark gray, calcareous mudstone to wackestone with minor shale. Exhibits a notable change in body fossil composition upsection. Lower part brachiopod-rich with lesser amounts of echinoderms and bryozoans. Central part body-fossil poor, Planolites and other horizontal traces abundant. Upper part bryozoan-rich, echinoderm- and brachiopod-poor. Samples: MQ49-52
MQ5	3.0	18.4	Thick sequence of thin- to medium-bedded, fossiliferous, calcareous mudstone, wackestone, and packstone interbedded with thin-bedded, discontinuous lenticular packstone to grainstone. Cryptostome bryozoans (ramose

			and circumrotary) and echinoderms abundant. Samples: MQ53-1, -2, -3.
MQ6	1.1	19.5	Very thin- to thin-bedded, bryozoan packestone, with abundant stoloniferous crinoid stems, interbedded with thin-bedded, sparsely fossiliferous shale and thin shale drapes. Samples: MQ53-3, -4, 54-61.

APPENDIX B

POINT COUNT DATA

Point count data from McClanahan Quarry. All counts are given as percentages, + = present but not counted in thin section, - = not present.

ALLOCHEMS THIN SECTION

	M1	M3	M5	M7	M8
NON-FOSSIL ALLOCHEMS:					
Terrigenous Mud	20.0	56.1	56.0	70.3	78.0
Micrite	0.7	1.3	0.6	2.2	-
Sparry Calcite	2.6	1.6	0.6	0.3	-
Silica	+	+	-	+	1.3
Syntaxial Overgrowth	11.3	-	-	-	1.3
FOSSIL ALLOCHEMS:					
Echinoderm:	53.3	31.0	35.0	11.6	15.3
Bryozoan:					
Trepostome	-	-	-	+	-
Cryptostome	2.0	+	+	+	+
Fenestrate	-	-	-	-	-
Cystoporate	-	-	-	-	-
Brachiopod:					
Punctate	0.6	-	-	1.3	0.3
Impunctate	5.3	3.6	2.0	14.0	3.8
Pseudopuncatate	-	+	+	+	-
Arthropods:					
Ostracode	-	-	-	-	-
Trilobite	1.3	1.3	-	-	-
Corals:					
Rugose	-	-	-	-	-
Tabulate	-	-	-	-	-
Molluscs:					
Gastropod	-	-	-	-	-
Other:					
Spirorbid	-	-	-	-	-
Foram	-	-	-	-	-
Sponge	-	-	-	-	-
Burrows	2.3	4.6	4.3	+	+
Unidentified	0.6	0.5	1.5	0.3	-
TOTAL (%)	100	100	100	100	100

ALLOCHEMS	THIN SECTION				
	M9	M10	M11	M13	M14
NON-FOSSIL ALLOCHEMS:					
Terrigenous Mud	58.3	-	40.6	7.3	51.6
Micrite	13.0	62.6	0.6	8.6	0.6
Sparry Calcite	-	15.3	6.6	11.3	-
Silica	+	+	+	+	-
Syntaxial Overgrowth	-	-	1.3	15.0	-
FOSSIL ALLOCHEMS:					
Echinoderm:	20.0	5.0	31.3	41.0	15.0
Bryozoan:					
Trepostome	-	0.6	+	-	-
Cryptostome	-	2.0	0.6	-	2.6
Fenestrate	-	-	-	-	-
Cystoporate	-	-	-	-	-
Brachiopod:					
Punctate	0.3	-	0.6	0.3	0.3
Impunctate	7.3	5.6	15.0	14.6	23.3
Pseudopuncatate	0.3	1.0	+	1.0	+
Arthropods:					
Ostracode	-	-	1.0	0.6	-
Trilobite	-	0.3	0.6	0.3	0.3
Corals:					
Rugose	-	-	-	-	-
Tabulate	-	-	-	-	-
Molluscs:					
Gastropod	-	-	-	-	-
Other:					
Spirorbid	-	-	-	-	-
Foram	-	-	-	-	-
Sponge	-	-	-	-	-
Burrows	+	7.3	+	+	8.6
Unidentified	0.8	0.3	1.8	-	-
TOTAL (%)	100	100	100	100	100

ALLOCHEMS	THIN SECTION				
	M15	M17	M18	M19	M20
NON-FOSSIL ALLOCHEMS:					
Terrigenous Mud	41.0	56.0	-	6.0	62.0
Micrite	10.0	-	39.6	+	-
Sparry Calcite	0.3	1.3	+	8.3	-
Silica	+	+	+	+	+
Syntaxial Overgrowth	-	-	-	24.0	-
FOSSIL ALLOCHEMS:					
Echinoderm:	33.6	30.0	10.6	49.3	29.3
Bryozoan:					
Trepostome	-	-	-	-	-
Cryptostome	0.6	-	4.6	1.6	0.3
Fenestrate	-	-	-	-	-
Cystoporate	-	-	-	-	-
Brachiopod:					
Punctate	0.3	1.0	2.3	-	-
Impunctate	12.6	11.6	22.3	9.3	8.3
Pseudopuncatate	-	-	-	0.3	-
Arthropods:					
Ostracode	-	-	-	0.6	-
Trilobite	0.3	-	0.3	0.3	+
Corals:					
Rugose	-	-	-	-	-
Tabulate	-	14.3	14.3	-	-
Molluscs:					
Gastropod	-	-	-	-	-
Other:					
Spirorbid	-	-	-	-	-
Foram	-	-	-	-	-
Sponge	-	-	-	-	-
Burrows	+	+	5.3	+	-
Unidentified	1.3	0.3	0.6	3.0	0.1
TOTAL (%)	100	100	100	100	100

ALLOCHEMS	THIN SECTION				
	M22	M23	M24	M6A	M6B
NON-FOSSIL ALLOCHEMS:					
Terrigenous Mud	75.3	78.3	20.6	50.6	50.6
Micrite	-	0.6	36.0	-	17.6
Sparry Calcite	-	1.0	8.0	+	0.6
Silica	+	+	+	-	-
Syntaxial Overgrowth	-	1.0	4.0	-	0.3
FOSSIL ALLOCHEMS:					
Echinoderm:	14.3	12.6	13.0	25.3	20.0
Bryozoan:					
Trepostome	-	-	+	-	-
Cryptostome	0.3	-	4.6	0.6	1.3
Fenestrate	-	-	+	-	+
Cystoporate	-	-	-	-	-
Brachiopod:					
Punctate	-	1.0	-	-	0.3
Impunctate	7.6	5.0	12.0	23.2	8.6
Pseudopuncatate	-	0.3	-	-	-
Arthropods:					
Ostracode	-	-	-	-	-
Trilobite	-	-	0.3	-	-
Corals:					
Rugose	-	-	-	-	-
Tabulate	-	-	-	-	-
Molluscs:					
Gastropod	-	-	-	-	-
Other:					
Spirorbid	-	-	-	-	-
Foram	-	-	-	-	-
Sponge	-	-	+	-	-
Burrows	2.3	+	-	+	+
Unidentified	0.2	0.2	1.5	0.3	0.7
TOTAL (%)	100	100	100	100	100

ALLOCHEMS	THIN SECTION				
	M26	M27	M28	M30	M31
NON-FOSSIL ALLOCHEMS:					
Terrigenous Mud	73.0	65.0	52.0	7.0	59.6
Micrite	-	-	6.0	16.3	5.3
Sparry Calcite	-	+	2.7	15.0	-
Silica	0.6	+	2.0	+	+
Syntaxial Overgrowth	-	-	3.6	8.6	-
FOSSIL ALLOCHEMS:					
Echinoderm:	8.6	19.3	13.6	41.3	24.0
Bryozoan:					
Trepostome	-	-	-	-	-
Cryptostome	3.3	3.0	4.3	0.6	1.6
Fenestrate	-	-	-	-	-
Cystoporate	-	-	-	-	-
Brachiopod:					
Punctate	-	+	0.3	-	-
Impunctate	13.0	11.6	10.3	10.0	8.6
Pseudopuncatate	-	0.3	-	-	-
Arthropods:					
Ostracode	+	-	-	-	0.3
Trilobite	-	0.3	0.6	1.0	0.3
Corals:					
Rugose	0.6	-	-	-	-
Tabulate	-	-	-	-	-
Molluscs:					
Gastropod	-	-	-	-	-
Other:					
Spirorbid	-	-	-	-	-
Foram	-	-	-	-	-
Sponge	-	-	-	-	-
Burrows	+	+	-	-	+
Unidentified	0.9	0.5	-	0.2	0.3
TOTAL (%)	100	100	100	100	100

ALLOCHEMS	THIN SECTION				
	M32	M33B	M33T	M35	M36
NON-FOSSIL ALLOCHEMS:					
Terrigenous Mud	68.6	77.0	67.0	72.0	75.6
Micrite	-	-	-	-	-
Sparry Calcite	0.6	-	+	-	+
Silica	+	+	+	+	-
Syntaxial Overgrowth	-	-	-	-	-
FOSSIL ALLOCHEMS:					
Echinoderm:	17.6	8.0	9.6	13.0	15.6
Bryozoan:					
Trepostome	-	-	-	-	-
Cryptostome	+	-	+	0.6	1.3
Fenestrate	+	2.6	6.6	-	-
Cystoporate	2.3	-	-	0.3	+
Brachiopod:					
Punctate	+	2.6	+	-	+
Impunctate	8.0	6.3	10.3	11.6	6.6
Pseudopuncatate	+	-	-	-	-
Arthropods:					
Ostracode	+	0.3	+	0.3	+
Trilobite	0.3	1.3	0.3	1.0	-
Corals:					
Rugose	-	-	0.6	-	-
Tabulate	-	0.3	-	-	-
Molluscs:					
Gastropod	-	-	-	-	-
Other:					
Spirorbid	-	-	-	-	-
Foram	-	-	-	-	-
Sponge	-	-	-	-	-
Burrows	2.3	+	3.3	1.0	+
Unidentified	0.3	1.6	2.3	0.2	0.9
TOTAL (%)	100	100	100	100	100

ALLOCHEMS	THIN SECTION				
	M37	M38	M44	M45	M46
NON-FOSSIL ALLOCHEMS:					
Terrigenous Mud	82.0	+	+	84.0	79.3
Micrite	-	61.6	87.6	-	-
Sparry Calcite	-	3.0	+	-	-
Silica	-	+	+	+	+
Syntaxial Overgrowth	-	0.3	-	-	-
FOSSIL ALLOCHEMS:					
Echinoderm:	10.6	8.0	20.0	7.0	10.5
Bryozoan:					
Trepostome	-	1.0	-	-	-
Cryptostome	+	13.3	+	2.6	1.0
Fenestrate	-	-	-	-	-
Cystoporate	+	+	+	0.3	-
Brachiopod:					
Punctate	-	-	-	-	0.6
Impunctate	5.6	10.3	9.0	5.5	7.6
Pseudopuncatate	-	+	1.3	+	-
Arthropods:					
Ostracode	1.0	+	-	+	-
Trilobite	0.3	1.6	-	0.6	-
Corals:					
Rugose	-	0.3	-	-	-
Tabulate	-	-	-	-	-
Molluscs:					
Gastropod	-	-	-	-	-
Other:					
Spirorbid	-	-	-	-	-
Foram	-	-	-	-	-
Sponge	-	-	-	+	-
Burrows	+	+	+	+	+
Unidentified	0.5	0.6	0.1	-	1.0
TOTAL (%)	100	100	100	100	100

ALLOCHEMS	THIN SECTION				
	M47	M48B	M48M	M48T	M49
NON-FOSSIL ALLOCHEMS:					
Terrigenous Mud	77.3	28.3	49.6	60.6	-
Micrite	-	2.3	-	-	73.0
Sparry Calcite	-	-	-	4.0	0.3
Silica	+	+	+	+	+
Syntaxial Overgrowth	-	0.3	-	-	-
FOSSIL ALLOCHEMS:					
Echinoderm:	7.6	53.3	21.0	3.3	10.0
Bryozoan:					
Trepostome	-	-	0.6	-	1.0
Cryptostome	5.6	3.3	4.6	7.6	1.3
Fenestrate	-	2.6	-	-	-
Cystoporate	-	2.0	3.0	-	-
Brachiopod:					
Punctate	0.6	0.3	0.3	2.3	1.3
Impunctate	7.0	7.0	16.3	19.3	10.0
Pseudopuncatate	-	-	+	-	-
Arthropods:					
Ostracode	+	-	-	-	+
Trilobite	1.3	0.3	0.3	0.3	0.3
Corals:					
Rugose	-	0.3	2.6	2.0	-
Tabulate	-	-	-	-	-
Molluscs:					
Gastropod	-	-	-	-	-
Other:					
Spirorbid	-	-	-	-	-
Foram	-	-	-	-	-
Sponge	-	-	-	-	-
Burrows	+	-	-	+	+
Unidentified	0.6	-	1.7	0.6	2.8
TOTAL (%)	100	100	100	100	100

ALLOCHEMS	THIN SECTION				
	M50	M51	M52	M53-1	M53-2
NON-FOSSIL ALLOCHEMS:					
Terrigenous Mud	5.6	45.3	68.6	5.0	-
Micrite	65.0	5.3	-	21.6	8.6
Sparry Calcite	-	-	-	+	+
Silica	-	-	-	-	-
Syntaxial Overgrowth	-	-	-	3.0	8.6
FOSSIL ALLOCHEMS:					
Echinoderm:	9.6	24.3	14.6	32.6	36.0
Bryozoan:					
Trepostome	-	0.3	0.6	3.0	5.3
Cryptostome	8.6	8.0	8.6	28.0	22.3
Fenestrate	-	-	-	0.3	0.6
Cystoporate	0.6	4.6	0.3	1.6	7.3
Brachiopod:					
Punctate	1.3	0.3	+	0.3	-
Impunctate	8.6	11.6	6.6	3.3	9.3
Pseudopuncatate	-	-	-	-	-
Arthropods:					
Ostracode	-	-	0.3	-	-
Trilobite	0.3	+	-	-	-
Corals:					
Rugose	-	-	-	0.6	0.3
Tabulate	-	-	-	-	-
Molluscs:					
Gastropod	-	-	-	-	-
Other:					
Spirorbid	-	-	-	-	-
Foram	-	-	-	-	-
Sponge	-	-	-	-	-
Burrows	-	+	-	-	-
Unidentified	0.4	0.3	0.4	0.7	0.7
TOTAL (%)	100	100	100	100	100

ALLOCHEMS	THIN SECTION				
	M53-3	M53-4	M56	M58	M59
NON-FOSSIL ALLOCHEMS:					
Terrigenous Mud	31.0	+	9.3	2.6	-
Micrite	15.3	29.3	16.2	-	+
Sparry Calcite	-	-	8.3	0.3	20.3
Silica	-	-	-	-	-
Syntaxial Overgrowth	-	-	0.3	25.0	-
FOSSIL ALLOCHEMS:					
Echinoderm:	20.3	23.0	18.0	25.6	10.3
Bryozoan:					
Trepostome	2.3	0.3	3.3	1.3	-
Cryptostome	14.3	17.3	27.7	38.6	30.1
Fenestrate	0.3	-	0.3	-	-
Cystoporate	11.6	28.6	15.6	5.0	38.3
Brachiopod:					
Punctate	-	-	-	-	-
Impunctate	3.6	1.3	1.0	0.3	0.3
Pseudopuncatate	-	-	-	-	0.1
Arthropods:					
Ostracode	-	-	+	-	-
Trilobite	0.3	-	-	-	-
Corals:					
Rugose	-	-	-	-	-
Tabulate	-	-	-	0.3	-
Molluscs:					
Gastropod	-	-	-	-	-
Other:					
Spirorbid	-	-	-	-	-
Foram	-	-	-	-	0.6
Sponge	0.6	-	-	-	-
Burrows	+	+	+	-	-
Unidentified	0.4	0.2	-	1.0	-
TOTAL (%)	100	100	100	100	100

ALLOCHEMS	THIN SECTION	
	M60	M61
NON-FOSSIL ALLOCHEMS:		
Terrigenous Mud	+	+
Micrite	-	76.6
Sparry Calcite	18.3	+
Silica	-	-
Syntaxial Overgrowth	9.6	+
FOSSIL ALLOCHEMS:		
Echinoderm:	11.0	21.3
Bryozoan:		
Trepostome	-	-
Cryptostome	29.6	-
Fenestrate	-	-
Cystoporate	31.3	-
Brachiopod:		
Punctate	-	-
Impunctate	-	2.1
Pseudopuncatate	-	-
Arthropods:		
Ostracode	-	-
Trilobite	-	-
Corals:		
Rugose	-	+
Tabulate	+	-
Molluscs:		
Gastropod	-	-
Other:		
Spirorbid	-	-
Foram	-	-
Sponge	-	-
Burrows	-	+
Unidentified	0.2	-
TOTAL (%)	100	100

APPENDIX C

DIGITIZING PROGRAM

Pre-digitizing Preparations

Sample Preparation

Specimens were cleaned of matrix by boiling in water and Miramine OC-ES. Each specimen was numbered sequentially. Broken specimens were discarded unless the number of specimens in the collection were low.

Preparation of Overlays

Two methods of making overlays were utilized. In the first method, 8 x 10 glossy photographs of the fossils to be digitized were made. Combinations of one, two, or three specimens per photograph were tried. The best results were achieved using one or two specimens per print. The advantages of this approach are that it provides a permenant record of the specimen and allows the observer to view the entire surface of the specimen during digitizing. This approach, however, proved to be unsatifactory for several reasons. First, the proceedure for making good quality prints is too expensive for large quantities of fossils. Second, photographs of fossil surfaces usually

contain other feature related to weathering and abrasion that obscure the distribution of epibionts. Third, photographing large numbers of specimens is time consuming. Fourth, specimens with high relief could not be photographed with the entire specimen in focus, because of the short focal length relative to the depth of field, which caused distortion in the photographs.

The second method tried was more successful and was the approach used in this study. Specimens were placed in a Vu-Lyte III Opaque Projector and the image projected onto a wall. To ensure that the specimen was not being distorted, a box was drawn on the projecting surface and the specimen placed within the box. Any distortion of the box meant that the opaque projector was not situated perpendicular to the wall. A graphic scale was placed beside each specimen. Images of specimens with high relief were compensated by focusing through the specimen as sketching was done.

An overlay was made by placing an 8 x 11 sheet of smooth-surfaced tracing paper over the projected image on the wall. The outlines of the host and its epibionts were drawn, reference points for orienting the specimens (e.g., beaks of brachiopods, etc.) labeled, and the scale (in:mm) drawn. Identification, orientation, growth direction, etc. of each epibiont was made directly on the overlay. A

Bausch and Lomb Stereozoom-4 binocular microscope with doubling lens was set up next to the projecting apparatus to help in identifying epibionts too small to be identified from the projected image.

Specimens with high relief or with morphologies that could not be projected as a flat surface (e.g., crinoid stems, gastropods, geniculate brachiopods, rugose corals, etc.) were not projected directly. Molds were made by rolling the specimen across flattened modeling clay. Each specimen had a marked reference point to signal the beginning and end of the 'unrolled' surface to be digitized. Ends or cross sections were also molded and digitized.

Digitizing Proceedure

Introduction

The Epibiont Digitizing Program (EDP) is written in Basic for use with a PC interfaced with an electronic digitizer, which allows the operator to directly interact with the digitizing proceedure. In this study, a Numonics Model 1224 Electronic Digitizer, with digitizing and area/length capabilities, and an IBM PC with 512K memory was used (Fig. 63). It was necessary to configure the PC with the proper communication parameters for the digitizer.

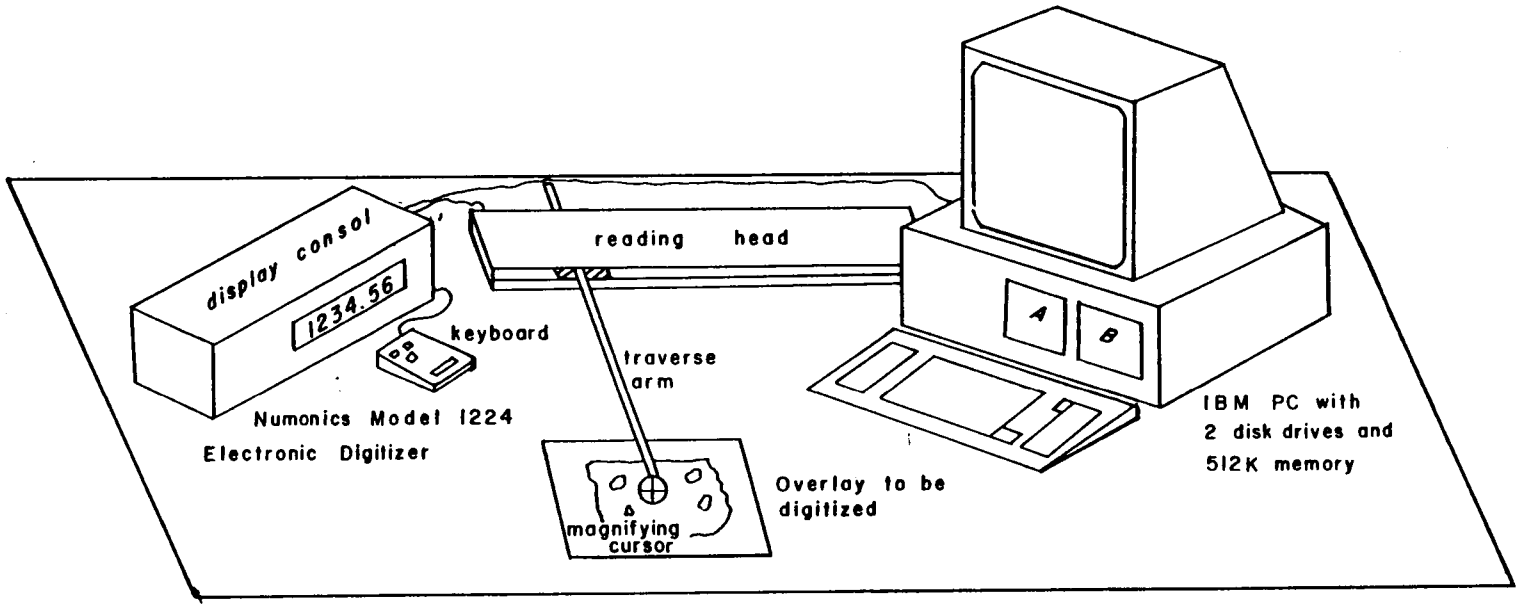


Fig. 63. Hardware for the Epibiont Digitizing Program showing the arrangement of the PC and electronic digitizer.

Most computers are equipped with RS-232 interface cards and adapters for this purpose. The amount of memory necessary to run the EDP depends upon the size of the data set. Each digitized host, with its epibionts, initially is stored as a separate file. Once all of the data have been collected, or when the data set exceeds the memory capabilities of the disk, all of the files are concatenated into a single file.

The EDP has four subroutines. The first subroutine sets the scale of the digitizer to the specimen to be digitized. The second subroutine determines the dimensions of the host fossil. The third subroutine collects data on the epibionts. The last subroutine stores the data. In the data set (see Appendix E), the first ten columns contain the data for the host, and are repeated for each epibiont digitized. The remaining nine columns contain the data collected for each epibiont.

Digitizing Program Running

The EDP begins with a `digitizing program running' prompt (Fig. 64). The first step is to set the scale of the digitizer by registering the scale of the photograph or overlay with the axes of the digitizer. Each time the scale of the fossil tracing changes, the scale of the digitizer must be reset. The scale of the digitizer is the same as the scale of the fossil tracing and is given in the

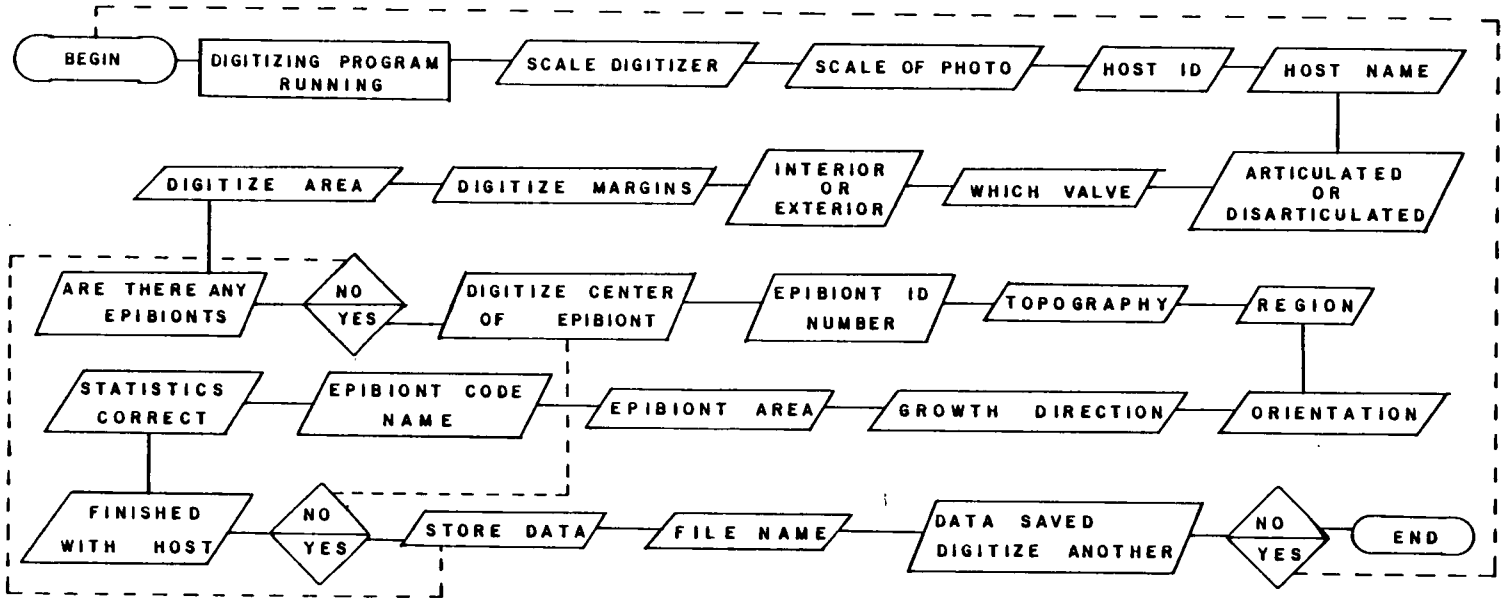


Fig. 64. Flowchart of digitizing procedure. Rectangles refer to non-interactive steps, parallelograms refer to operator input or output steps, diamonds refer to decision points, and ovals refer to terminal steps.

form inches:mm. Once the digitizer scale is set, the`OK to proceed' prompt will register.

Scale of Photograph

The scale of each tracing is entered into the PC by the operator for each new specimen digitized regardless of whether or not the scale has changed. This allows the program to later scale all of the digitized fossils with each other at a scale of 1:1. The scale used in this step should be the same as the scale used to set the digitizer. For example, if two different brachiopod specimens, of different scales and both containing spirorbids, are digitized, the scaling procedure will automatically readjust the area of the spirorbids for the two scales.

Host ID and File Name

Usually more than one surface of a specimen is digitized. To identify and store each surface separately, each host is identified by a three-part code that consists of a combination of letters and numbers. The first set of letters identifies the genus and species of the host. The numbers that follow are the specimen number, and the letters that make up the third part are additional information needed to further separate the surface being digitized. For example, if a disarticulated pedicle valve

of Leptaena acuticuspidata (specimen number 41) is digitized, the host number would read "LA41PI" and "LA41PE" for the pedicle valve interior and exterior respectively. This code is also used as the file name under which the data is stored on the disk.

Host Name

The genus and species name of the host is entered using some variation of the letters in the name. For example, Leptaena acuticuspidata is stored as LACUTI.

Articulated or Disarticulated

The articulated (A) or disarticulated (D) nature of bivalved hosts (brachiopods, bivalves) is recorded. This information can be used to later compare encrustation distribution on the different valves. Where this information is not applicable, such as on crinoid stems, a "." is used as a placeholder.

Which Valve

For bivalved species, such as brachiopds, the valve being digitized is entered. Where this information is not applicable, a "." is used as a placeholder.

Interior or Exterior

The interior (I) or exterior (E) surface being digitized is recorded. This catagory can also be modified for other surface designations as needed. For example, coral surfaces can be designated as oral (O) or aboral (A), top (T) or bottom (B), etc. Where this information is not applicable, a "." is used.

Digitize Margins

Four X,Y coordinates, with respect to some reference point, are digitized for each host to allow the digitizer to plot reference points used in the scaling proceedure and for plotting the distribution of epibionts on the host. The order of digitizing the margins is: origin → bottom margin → left margin → right margin. The origin is designated as some easily identifiable point along the periphery of the host, for example, the tip of the beak on brachiopod. The coordinates are read directly by the PC.

Digitize Area

The digitizer is reconfigured for area computation and the area of each host is determined directly by the digitizer by tracing the outline of the surface being digitized in a clockwise manner. The area is automatically scaled using the scaling factor entered at the beginning of

the EDP. The area measurement is entered by the operator rather than being automatically entered by the digitizer.

Are There Any Epibionts

This prompt signals the end of the second subroutine and the beginning of the third subroutine and represents an operator decision point in the EDP. If no epibionts are present on the host being digitized, `N' is entered and 999 will be registered in the data set signalling that no epibionts are present. The program then skips the epibiont subroutine and proceeds to the storage routine. If epibionts are present, `Y' is entered and the epibiont digitizing subroutine begins. The operator must reconfigure the digitizer for digitizing mode.

Epibiont ID Number

A number is assigned to each epibiont on the tracing and the epibionts are digitized and stored sequentially.

Topography

The location of each epibiont on the host is recorded with respect to the microtopography of the host. Microtopography can be variably defined by the operator; however, in this study, it was defined as a function of shell ornamentation such as ribs, rugae, etc. Three

categories were used: high (H), low (L), and indeterminate (I). Indeterminate locations or locations that span catagores can be designated as either `I' for indeterminate or `HL' for intermediate and combined locations.

Region

Each host is subdivided into regions of various sizes and shapes (1, 2, 3, 4, etc.) that are either arbitrary, reflect a grid system, or reflect larger aspects of shell form, such as geniculation or resupination, or occur at critical functional areas of the shell, such as along the commissure. As many regions as needed can be designated, for example, to separate incurrent from excurrent portions of the commissure, fold and sulcus from lateral margins, etc. Epibionts are located by regions to highlight major patterns of epibiont distribution relative to larger morphological or functional features. Epibionts spanning more than one region are indicated by combinations of region numbers, such as 12, 124, 234, etc.

Orientation

The orientation of epibionts, relative to some point of reference, is accomplished by using a 360° compass system. The reference point is arbitrary depending upon the needs of the operator. In this study, the orientation

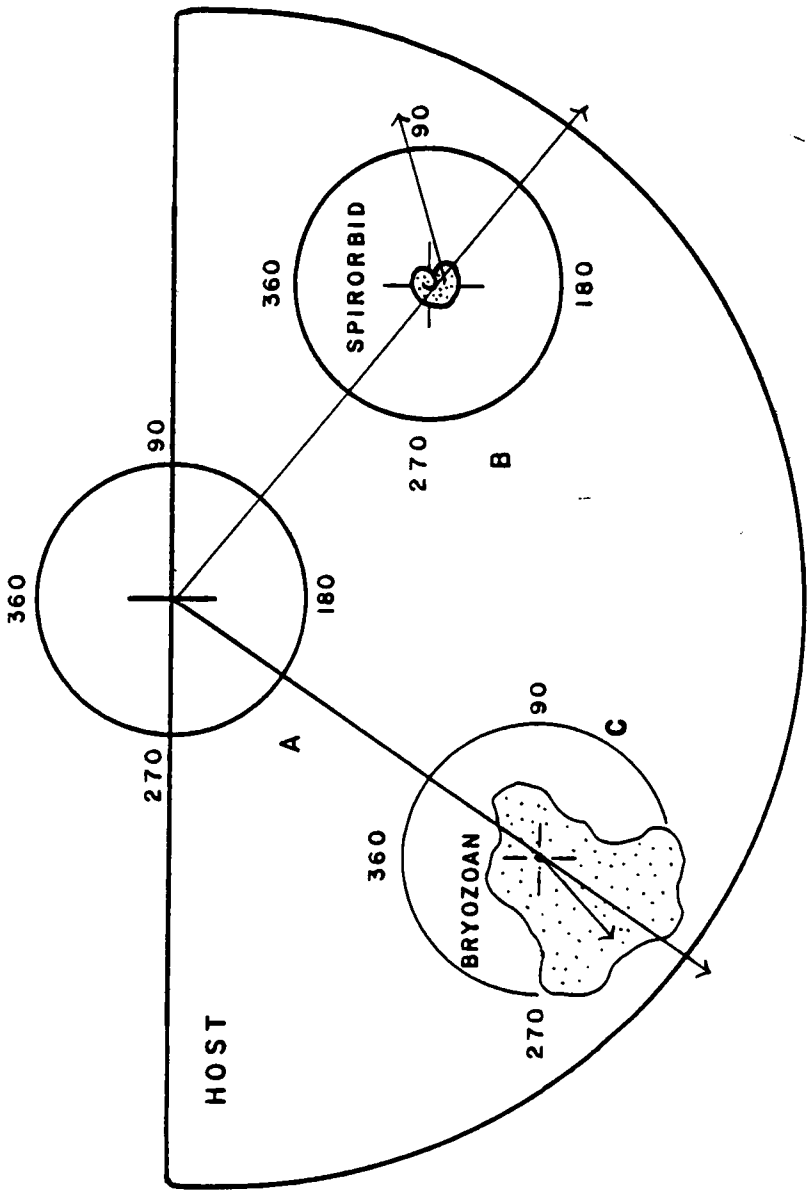
of epibionts was recorded with reference to the origination point of the epibiont, which was taken to represent the point of initial larval attachment. Orientation was measured to the nearest 5°. For example, the initial attachment point of Cornulites served as a reference point and the orientation of the aperture (0-360°) was recorded. The 0° (=360°) direction was always 'up' and coincided with the origin point used to digitize the X,Y coordinate system of the host.

This system allows the operator to either apply the 0-360° system to the whole host or to individual epibionts on the host (Fig. 64). Where orientation was not applicable, for example in bryozoan colonies, a "." is used; however, the default value is 0.

Growth Direction

The direction of growth of colonial epibionts is recorded using the same compass coordinate system used in orientation. Once again, the operator has the option of using the compass system for the entire host or for each individual epibiont. In this study, the system for individual epibionts was used. The point of origin was taken to be the ancestrula of bryozoan colonies and the protocorallite of corals, both of which represent the point of attachment of the larva. The dominant direction of

Fig. 65. Different ways in which orientation can be measured on a host. A. 360° system using a reference point on the host. B. 360° system using center of a solitary epibiont as the reference point and plotting the orientation of the aperture. C. 360° system using dominant direction of growth of colonial organisms. Reference point can be the center of the colony or the ancestrula or protocorallite, if known.


HOST
A
B
C
SPIRORBID
BRYOZOAN
90
180
270
360

growth was taken to be the general direction of greatest colony growth and was measured to the nearest 5°. Where growth direction was not able to be determined, a "." was used; however, the default value is 0.

Epibiont Area

The digitizer is reconfigured for area computation and digitized using the same proceedure as for digitizing the area of the host.

Epibiont Code Name

The taxonomic identity of each epibiont is designated using a code system that can be arbitrarilly defined by the operator.

Statistics Correct

This prompt signals the end of the epibiont subroutine and the beginning of the storage subroutine. The digitized and operator input data is displayed to allow the operator to check the data prior to storage. If the data is incorrect, a `N' is typed and the data for that epibiont is reentered. If the data is correct, a `Y' is typed.

Finished With This Host

If other epibionts are present, `N' is entered and the

epibiont subroutine begins again beginning with digitizing the center of the next epibiont in sequence. If no other epibionts are present, `Y' is typed and the storage prompt is given.

Store Data

This prompt signals the beginning of the fourth subroutine. If the operator wishes to store the data, a `Y' is entered and the file name prompt appears. The file name is then entered. The file name is the same three-part code used for the host number. The data will be stored on the disk as a separate file. If the operator does not wish to save the data, `N' is entered and the data are erased.

Data Has Been Saved On Disc, Digitze Another

Once stored, the EDP asks if the operator wants to digitize another epibiont. A response of `Y' begins the entire program again beginning with the `OK to proceed' prompt. If the answer is `N', the session ends and `ok' appears.

EPIBIONT DIGITIZING PROGRAM (EDP)

```
10 DIM E.ID(200),E.NAME$(200),E.TOPO$(200),E.REGION$(200)
   E.ORIENT(200),E.GRDIR(200),E.AREA(200),E.X(200),E.Y(200)
20 I=1
30 `PROGRAM REQUIRES HARDWARE INTERFACE WITH DIGITIZING DEVICE.
    MOST
40 `MICROCOMPUTERS AND DIGITIZING DEVICES ARE EQUIPPED WITH
    RS-232 INTERFACE
50 `CARDS AND ADAPTERS.  IT IS NECESSARY TO CONFIGURE THE CARDS
    WITH THE 60 `PROPER COMMUNICATION PARAMETERS (BAUD, BITS,
    STOP BIT).
70 CLS
80 PRINT "DIGITIZING PROGRAM RUNNING. REGISTER THE PHOTOGRAPH
    WITH THE"
90 PRINT "AXES OF THE DIGITIZER. REMEMBER TO SCALE THE
    DIGITIZER."
100 PRINT " "
110 INPUT "OK TO PROCEED (Y/N):  ", ANS$
120 INPUT "ENTER SCALE OF PHOTOGRAPH (in mm/in.): ",SCALE
130 INPUT "ENTER HOST ID: ",ID$: INPUT "ENTER HOST NAME:
    ",SPECIES$:
    INPUT "ARTICULATED OR DISARTICULATED: ",ARTIC$: INPUT
    "WHICH VALVE:
    ",VALVE$: INPUT "INTERIOR OR EXTERIOR: ",EXT.INT
140 `****** ROUTINE FOR DETERMINING HOST DIMENSIONS ******
150 OPEN "COM1:1200,E,7,1" AS #1
160 COM(1) ON
170 COM(1) OFF
180 PRINT "PLACE CURSOR ON ORIGIN AND DIGITIZE"
190 INPUT#1, OX, OY
200 CLOSE #1
210 OPEN "COM1:1200,E,7,1" AS #1
220 COM(1) ON
230 COM(1) OFF
240 PRINT "PLACE CURSOR ON OPPOSITE MARGIN AND DIGITIZE"
250 INPUT#1, SX,SY
260 CLOSE #1
270 OPEN "COM1:1200,E,7,1" AS #1
280 COM(1) ON
290 COM(1) OFF
300 PRINT "PLACE CURSOR ON LEFT MARGIN AND DIGITIZE"
310 INPUT#1, LX,LY
320 CLOSE #1
330 OPEN "COM1:1200,E,7,1" AS #1
340 COM(1) ON
350 COM(1) OFF
```

```
360 PRINT "PLACE CURSOR ON RIGHT MARGIN AND DIGITIZE"
370 INPUT#1, RX,RY
380 CLOSE #1
390 LENGTH=OY-SY
400 SWIDTH=RX-LX
410 INPUT "RECONFIGURE DIGITIZER FOR AREA..ENTER AREA OF HOST:
    ",AREA
415 INPUT "ARE THERE ANY EPIBIONTS (Y/N)? ",ANS1$
416 IF ANS1$="N" THEN N=1
417 IF ANS1$="N" THEN E.ID(1)=999
418 IF ANS1$="N" THEN GOTO 840
420 INPUT "RECONFIGURE DIGITIZER FOR DIGITIZING MODE...HIT
    RETURN WHEN
    READY: ",QUE$
430 `ROUTINE FOR INPUTTING DATA ON EPIBIONTS
440 I=1
450 OPEN "COM1:1200,E,7,1" AS #1
460 COM(1) ON
470 COM(1) OFF
480 PRINT "DIGITIZE CENTER OF EPIBIONT"
490 INPUT#1, E.X(I),E.Y(I)
500 CLOSE #1
510 INPUT "EPIBIONT ID NUMBER: ",E.ID(I)
520 INPUT "TOPOGRAPHIC POSITION OF EPIBIONT (H,L,I
    (INDETERMINATE)):
    ",E.TOPO$(I)
530 INPUT "REGION ON HOST...1,2,3, OR COMBINATIONS EG. 12:
    ",E.REGION$(I)
540 INPUT "ORIENTATION ON HOST (360 DEGREES): ",E.ORIENT(I)
550 INPUT "GROWTH DIRECTION (360 DEGREES): ",E.GRDIR(I)
560 INPUT "EPIBIONT AREA..(REMEMBER TO RECONFIGURE DIGITIZER):
    ",E.AREA(I)
570 INPUT "EPIBIONT CODE NAME...ENTER ? IF UNKNOWN:
    ",E.NAME$(I)
580 CLS
590 PRINT "                SUMMARY OF EPIBIONT STATISTICS:"
600 PRINT "_____________________________________________"
610 PRINT "ID:          ",E.ID(I)
620 PRINT "NAME:        ",E.NAME$(I)
630 PRINT "COORDS:      ",E.X(I),E.Y(I)
640 PRINT "TOPO:        ",E.TOPO$(I)
650 PRINT "REGION:      ",E.REGION$(I)
660 PRINT "ORIENT:      ",E.ORIENT(I)
670 PRINT "GRDIR:       ",E.GRDIR(I)
680 PRINT "AREA:        ",E.AREA(I)
690 PRINT ""
700 PRINT "STATISTICS CORRECT"
710 INPUT "ENTER Y OR N... IF N REENTER INFO ON EPIBIONTS:
    ",ANS$
720 IF ANS$="N" OR ANS$="n" GOTO 450
```

```
730 E.ID(I)=I
740 I=I+1
750 N=I
760 INPUT "FINISHED WITH THIS HOST? (Y/N): ", ANS1$
770 IF ANS1$="Y" OR ANS1$="y" GOTO 790
780 GOTO 450
790 `*****FILING SUBROUTINE*****
800 `
810 INPUT "DO YOU WISH TO STORE THE DATA (Y/N): ", ANS3$
820 IF ANS3$="N" OR ANS3$="n" THEN END
830 CLS
840 `ROUTINE TO STORE DATA ON FILE (DISK DRIVE A:)
850 PRINT "DATA FILES:"
860 FILES "*.BNT"
870 INPUT "ENTER A NEW FILENAME";F$
880 F$=F$+".BNT"
890 OPEN "O",#2,F$
900 FOR I=1 TO N
910 WRITE#2,SCALE,ID$,SPECIES$,ARTIC$,VALVE$,EXT.INT$,ORIGIN,
    LENGTH,SWIDTH,AREA,E.ID(I),E.NAME$(I),E.TOPO$(I),
    E.REGION$(I),E.ORIENT(I),E.GRDIR(I),E.AREA(I),E.X(I),E.Y(I)
920 NEXT I
930 CLOSE #2
940 PRINT "DATA HAS BEEN SAVED ON DISK."
950 INPUT "DO YOU WANT TO DIGITIZE ANOTHER HOST (Y/N): ", ANS4$
960 IF ANS4$="Y" OR ANS4$="y" THEN GOTO 20
970 END
```

APPENDIX D

SYTEMATIC PALEONTOLOGY

Introduction

The paleoecological and epibiont analysis discussed in Chapter 4 required identification of both host and epibiont organisms at as low a taxonomic level as possible. Initially, it was necessary to compile and update, where possible, the taxonomic data needed to complete these analyses. The systematic descriptions that follow are not meant to be exhaustive treatments of the fauna of the Birdsong Shale. Rather, the descriptions are meant only to present the basic morphological characteristics that can be readily applied to identifying specimens in the field. Also, this appendix does not contain every fossil taxon known from the Birdsong, only those collected during this study.

The only echinoderms included in this appendix are those that occur as epibionts. The reader is referred to Clement (1988) for a complete treatment of the echinoderms from the Birdsong Shale. The higher classification scheme used is that of the Treatise on Invertebrate Paleontology and may be outdated where revised editions have not been

completed. Only references cited in the synonomy and discussion for each taxon are included in the list of references. The reader is refered to the Treatise for references for the authors and dates of higher taxa.

As noted in Chapter 1, an extensive faunal list from the Birdsong was compiled by Dunbar (1919) using James Hall's reports on the fossils of New York State. This list since has been cited later without change by most other workers. Dunbar (1917b, 1920) described some new species, but since that time, only a few specific groups of the Birdsong fauna have been studied taxonomically. The completeness and quality of these later investigations is variable.

The most extensively studied group from the Ross Formation, since Dunbar's work, is the Brachiopoda. Amsden (1951, 1958), Amsden and Ventress (1963), and Amsden and Boucot (1958) reexamined many of Dunbar's specimens when describing coeval brachiopods from Oklahoma. Echinoderms, especially the crinoids, have been discussed by Springer (1917, 1920a, b, 1926), Strimple (1963, 1975, 1981), MacCintosh (1980), and Broadhead and Strimple (1978). Trilobites were studied by Delo (1940), Eldridge (1973), and Campbell (1977). Ostracodes have been described by Wilson (1935), Petersen (1972), and Lundin and Petersen (1974). Recently, conodonts have been extensively studied

and used to refine the age and biostratigraphy of the Birdsong (McComb and Broadhead, 1980; Capaccioli, 1987; McComb, 1987) and to discuss evolutionary patterns and processes (Broadhead and McComb, 1982).

Other fossil groups from the Birdsong, such as bryozoans and molluscs, have received virtually no attention or revision since Dunbar's original identifications and descriptions of new species. This is particularly true of the bryozoans, which make up the bulk of the epibiont species. Dunbar (1919) recognized only ten species of Bryozoa from the Birdsong. Reid (1983) noted 18 species that occur as epibionts, but she was able to assign only one of her specimens to an already named species. Roger Cuffey (pers. comm., 1987) noted that Lower Devonian bryozoans, as a group, have not received much attention because of the difficulties of identifying bryozoans to the species level. Hall (1874, 1879, 1887), mostly relied on colony form and external characteristics and still represents the best source for identifying species of Lower Devonian Bryozoa (Roger Cuffey, pers. comm., 1987).

Bryozoans described in this appendix are conferred (cf.) to species described from other Lower Devonian units based mostly on external characteristics. This approach was taken because the primary goal of part of this study was to integrate bryozoan data into epibiont analysis, in

which thin section identification of each bryozoan epibiont not only would make the analysis too cumbersome to be useful for standard paleoecological reconstructions but also would result in the destruction of the host specimen.

All specimens described herein were collected from McClanahan's Quarry; however, all of the species described also have been observed at Parsons Quarry. Almost all of the species described can occur as hosts for epibionts, except for the sponges, Spriorbis, Cornulites, and other species too small to support other epibionts. A qualitative estimate of relative abundance of each species, as it occurs in the Birdsong Shale, is given in the discussion of each species. This estimate is based on visual estimation in the field only. The number of specimens used as material for descriptions does not reflect the relative abundance of the species in the Birdsong, but reflects only the number of specimens examined in detail.

SYSTEMATIC PALEONTOLOGY

Phylum Porifera Grant, 1872

Class Demospongia Sollas, 1875

Order Lithistida Schmidt, 1876

Family Astylospongiidae Rauff, 1893

Genus Microspongia Miller, 1878

Microspongia cf. sphaeroidalis (Duncan), 1879

(Plate 1, Figure 1)

Hindia sphaeroidalis Duncan. Duncan, 1879, p. 84, pl. 9; Swartz, 1913, p. 195-198, pl. 17, figs. 1-4.

Description- Spherical mass approximately 25.0 mm in diameter of intercontected spicules; spicules robust, slightly curved, inflated at the ends, and forming tetrads; tetrads unite to form slightly polygonal openings.

Discussion- This was the only species of sponge identified by Dunbar (1919) from the Birdsong Shale and was listed as being very rare. The pyritization and highly weathered nature make a positive identification difficult; therefore, the single specimen has been conferred based upon its spherical shape, robust slightly curved spicules, and the polygonal nature of the openings. De Laubenfels

(1955) noted that Hindia (Duncan) is a synonym of Microspongia. Microspongia does not occur as either a host or an epibiont in the Birdsong Shale.

Material- A single specimen partially embedded in matrix, pyritized, with calcite cement and mud filling.

Phylum Coelenterata Frey and Leuckart, 1847

Subphyllum Cnidaria Hatschek, 1888.

Class Anthozoa Ehrenberg, 1834

Order Tabulata Milne-Edwards and Haime, 1850

Family Auloporidae Milne-Edwards and Haime, 1851

Genus Aulopora Goldfuss, 1826

Aulopora schohariae Hall, 1874

(Plate 1, Figure 6)

Aulopora schohariae Hall. Hall, 1874, p. 110; Hall, 1879, p. 142; Hall, 1887, p. 3, pl. 2, fig. 1-6; Swartz, 1913, p. 219, pl. 26, figs. 2-3.

?Aulopora sp. Reid, 1983, p. 128, pl. D-3, figs. F, Q.

Description- Encrusting reptant corallum composed of elongate tubular corallites that expand toward the aperture and turn upward from the substrate surface; corallites added either in a straight line or by budding into two

series with variable angles of divergence; aperture round with diameters of less than 1.0 mm; length between successive apertures is 4-6.0 mm; internal features not observed.

Discussion- Although Dunbar (1919) listed this species as occurring rarely in the Birdsong, it is common and occurs encrusting other corals, brachiopods, bryozoans, and crinoid stems.

Material- Numerous coralla encrusting brachiopods and corals.

Family Pleurodictyidae Sardeson, 1896

Genus Pleurodictyum Goldfuss, 1829

Pleurodictyum lenticulare (de Koninck), 1841

(Plate 1, Figure 2)

Michelinia lenticularis (de Koninck). Hall, 1874, p. 112; Hall, 1879, p. 145, pl. 3, figs. 1-3, 5; Hall, 1887, p. 7, pl. 3, figs. 1-3, 5.

Pleurodictyum lenticulare (de Koninck). Swartz, 1913, p. 218, pl. 26, fig. 1; Tansey, 1922, p. 180, pl. 42, fig. 9.

Pleurodictyum tennesseensis Amsden. Amsden, 1949, p. 100, pl. 23., figs. 1-3; Reid, 1983, p. 128, pl. D-3, fig.

Description- Corallum hemispherical to slightly flattened with a convex to flattened holotheca-covered base; corallum edges smoothly rounded to lobate when composed of edges of individual corallites; corallites polygonal numbering 7-13 depending upon the age of the corallum, most commonly having one large corallite occupying the central portion of the corallum surrounded by a ring of smaller corallites; corallite walls granulose with occasional spines at the triple junctions between corallites; corallite diameters range from 3 to 8 mm.

Discussion- Reid (1983) assigned her Birdsong specimens to P. tennesseensis Amsden, which was named for two specimens from the Brownsport Formation (Upper Silurian, Ludlow) of western Tennessee (Amsden, 1949). Reid's specimens and the ones of this study more closely resemble P. lenticulare, especially with respect to corallite size and number. This species differs from P. tennesseensis by being larger, posessing a strongly wrinkled holotheca-covered base, and having deeper corallites. Dunbar (1919) listed this species as a common Birdsong fossil.

Material- Four specimens occuring as free living coralla and two as encrusters on brachiopods.

Family Favositidae Dana, 1846

Genus Favosites Lamarck, 1816

Favosites foerstei Dunbar, 1920

(Plate 1, Figure 4a, b, c)

Favosites foerstei Dunbar. Dunbar, 1919, pl. 1, figs. 8-9; Dunbar, 1920, p. 117-118, figs. 3-4.

Description- "Corallum subhemispherical, convex base covered with a thick and concentrically wrinkled epitheca which covers all but the youngest corallites. Upper surface, in the fossil condition, flat or concave. At the center of the base is a small point of attachment about which the corallum is symmetrically developed. The prismatic corallites arise from an undefined central axis and quickly bend outward into a horizontal position, which they maintain to the periphery. The corallites vary in diameter from 1.5 mm to 3.2 mm at the surface, but the majority measure about 2.3 mm. Each side of the corallite bears two vertical rows of round mural pores, of which a row of ten pores occupies a distance of 7mm to 7.4 mm. Tabulae somewhat irregularly arranged, eight to twelve in a distance of 10 mm." (Dunbar, 1920).

Discussion- This is a very common species in the

Birdsong as reported by Dunbar (1919). It occurs as a host for most of the species of epibionts identified from the Birdsong. This species is adapted to living in soft substrata (see Chapter Four) and is unusual in that it possesses an outer covering, pseudoholotheca, composed of early marine fibrous cement, rather than the normal epithecal development of most favositids (Broadhead et al., 1988b).

Material- Twenty coralla of which most have eroded tops.

Favosites conicus Hall, 1874.

(Plate 1, Figure 5a, b, c)

Favosites conica Hall. Hall, 1874, p. 112; Hall, 1879, p. 146, pl. 3, figs. 4, 6, 13.

Favosites conicus Hall. Hall, 1887, p. 9, pl. 3, figs. 4, 6-13; Swartz, 1913, p. 212, pl. 23, figs. 5-7; Tansey, 1922, p. 178-179, pl. 41, figs. 2-7.

Description- Hemispherical corallum, up to 3 cm in diameter; holotheca-covered base, flat to slightly undulating, marked with concentric rugae with faint radiating lines formed by corallite tubes; corallites arise

from center of corallum in a radial pattern; rarely branching more than three times before reaching the corallum surface; corallites polygonal with four to eight sides, diameter of corallites ranges from 1.2 to 4.0 mm; tabulae same thickness as walls, irregularly spaced.

Discussion- This is the most commonly encountered coral in the Birdsong. F. conicus is a host for bryozoans (both surfaces commonly encrusted) and spirorbids (aboral surface encrusted only). This species was adapted to living on firm bottom substrates with rapid to adulthood beteen sedimentation events (see Chapter Four).

Material- This species is represented by over 50 coralla.

Favosites helderbergiae Hall, 1874

(Not Figured)

Favosites helderbergiae Hall. Hall, 1874, p. 111-112; Hall, 1879, p. 145-146, pl. 4-6; Hall, 1887, p. 8-9, pl. 4, figs. 1-2, pl. 5, figs. 1-3, pl. 6, figs. 1-8; Swartz, 1913, p. 208-209, pl. 27, fig. 1; Stewart, 1922, p. 222, pl. 58, fig. 8; Tansey, 1922, p. 177-178, pl. 40, figs. 12-17.

Description- Corallum large, lenticular, with flattened to slightly concave base and a flat to slightly convex upper surface; holotheca present but thin; corallites polygonal in outline; tabulae closely spaced, thickness same as corallite wall thickness; diameter of corallites range from 0.5 to 1.7 mm.

Discussion- Dunbar (1919) reported this species to be a common element of the Birdsong; however, only two partial specimens were found during this study. This species can be distinguished from F. conicus by its larger size, lenticular shape, and flattened surface.

Material- Two partial coralla.

Order Stauriida Verrill, 1865

Family Streptalamatidae Nicholson, 1889

Genus Streptalasma Hall, 1847

Streptelasma strictum Hall, 1874

(Plate 1, Figure 3a, b)

Streptelasma (Petraia) stricta Hall. Hall, 1874, pl 114.

Streptelasma stricta Hall. Hall, 1879, p. 142.

Streptelasma strictum Hall. Hall, 1887, p. 1, pl. 1, figs. 1-10; Weller, 1903, p. 298, pl. 33, figs. 3-4; Swartz, 1913, p. 198, pl. 17, figs. 5-9; Tansey, 1922, p. 177,

pl. 40, figs. 5-11.

Description- Small conical coralla, maximum diameter 14 mm, maximum height 33 mm; straight to trochoid; septa relatively thin, lacking carinae, meeting axially in later growth stages, forming aulos in earlier growth stages; secondary septa long; tabulae few; dissepiments lacking; holotheca thin, surface ornamented with rounded to flat, longitudinal ridges that occasionally branch separated by narrow grooves.

Discussion- The only rugosan Dunbar (1919) recognized from the Birdsong was Enterolasma strictum, which he noted as being a very common element. Although the specimens were not figured or described, specimens assigned to Streptelasma strictum here are probably the same as Dunbar's specimens, especially since Enterolasma was not encountered in this study. Enterolasma differs from Streptolasma by possessing carinae on the septa (Sutherland, 1963).

Material- Twenty-three specimens, all showing some degree of silicification, which is most pervasive in the upper portions of the corallum and causes some distortion of the skeletal features. The deep calyx is generally broken or crushed flat which suggests overturning followed by rapid burial. S. strictum occurs as a host for

bryozoans, spirorbids, and Cornulites.

Phylum Bryozoa Ehrenberg, 1831

Subphylum Ectoprocta Nitsche, 1869

Class Gymnolaemata Allman, 1856

Order Ctenostomata Busk, 1852

Family Ascodictyon Miller, 1889

Genus Eliasopora Bassler, 1952

Eliasopora stellaria Nicholson, 1877

(Plate 3, Figure 4)

Eliasopora sp. Reid, 1983, pl. D-3, fig. k.

Description- Zoarium encrusting with elongate, pyriform zooids connected by threadlike stolon; zooids form radiating cluster of up to five zooids per cluster.

Discussion- This species occurs relatively commonly as epibionts on brachiopods. Usually preserved slightly abraided.

Material- Three specimens of brachiopod with six encrusting zoaria.

Class Stenolaemata Borg, 1926

Order Tubiporata Johnston, 1847 (=Cyclostomata Busk, 1852)

Family Reptariidae Simpson, 1897

Genus Hederella Hall, 1883

Hederella sp.

(Plate 3, Figure 5)

Description- Zoarium encrusting with short, cylindrical to tubular zoecia; zoecia bend from main axis of tubular zoids; surface marked with concentric annulations.

Discussion- This species is relatively rare in the Birdsong and is usually eroded so that only the encrusting bases of the colony remains.

Material- One brachiopod with three encrusting zoaria.

Order Cystoporata Astrova, 1964

Family Ceramoporidae Ulrich, 1882

Genus Ceramopora Hall in Silliman, 1851

Ceramopora cf. parvicella Hall, 1857

(Plate 2, Figure 1)

Ceramopora? parvicella Hall. Hall, 1879, p. 158; Hall, 1887, pl. 16, figs. 3-4.

Description- Encrusting zoarium with short, tubular zooids oriented obliquely to the substrate sometimes forming radiating clusters; overlaping lower zooids alternating or in line forming an imbricated appearance; apertures oblique, proximal aperture forming an overarching hood, rounded to oval to slightly polygonal when eroded; aperture diameter less than 0.5 mm; monticules present but usually not well developed.

Discussion- Reid (1983) assigned specimens with the above characteristics to the family level only based on the descriptions in Bassler (1953). This species is a common encruster on brachiopods forming colonies of various sizes.

Material- Eight zoaria encrusting the brachiopod Atrypa.

Family Fistuliporidae Ulrich, 1882

Genus Fistulipora McCoy, 1849

Fistulipora cf. unilinea Hall, 1887

(Plate 2, Figure 2)

Fistulipora unilinea Hall. Hall, 1887, p. 217-218, pl. 57, figs. 1, 2, 5.

Fistulipora sp. C. Reid, 1983, p. 131, pl. D-3, fig.N.

Description- Massive encrusting zoarium forming hemispherical masses; zooids tubular with circular to oval apertures up to 0.4 mm in diameter; interspace vesiculose; vesicles large up to 0.1 mm in diameter, rounded to polygonal when crowded, usually no more than two between adjacent autozooids; mesopores almost equal in size to autozooids, sometimes impinging becoming polygonal, never more than 1 between adjacent autozooids; surface maked by conspicuous, irregularly arranged monticules in which zooid diameter is the same as normal surface.

Discussion- This species is recognized by its massive growth form with well developed monticules and large diameter mesopores between autozooids. This species tends to be abraided on the surface giving it a smooth highly porous appearance.

Material- Three specimens encrusting two Atrypa.

Fistulipora cf. maculosa (Hall), 1883

(Plate 3, Figure 7)

Lichenalia maculosa Hall. Hall, 1887, p. 30-31, pl. 14, figs. 1-8.

Fistulipora maculosa (Hall). Ulrich and Bassler, 1913, p. 267, pl. 51, figs. 1-2.

Fistulipora sp. B. Reid, 1983 (in part).

Description- Zoarium of encrusting layers, sometimes forming large masses; zooids oval to trilobate with moderately developed lunaria, apertures 0.1 to 0.25 mm in diameter; shallow maculae of irregular shape.

Discussion- Reid (1983) included specimens probably belonging to this species in her discussion of Fistulipora sp. B. In this report, this species has been separated out and conferred to Hall's F. maculosa because of the distinctive nature of the maculae and the large wide interspaces.

Material- Three specimens of Atrypa with four encrusting zoaria.

Fistulipora sp. A

(Plate 2, Figure 4)

Fistulipora sp. A. Reid, 1983, p. 130, pl. D-3, fig. N.

Description- Robust encrusting zoarium, thickness often exceeding 1mm; zooids short, tubular, oriented obliquely forming rows separated by linear interspaces; zooid apertures oriented obliquely, circular to tear-drop

shaped, rimmed by well developed lunaria, and sometimes, a swelled lower rim; aperture diameter 0.25 to 0.5 mm; mesopores absent; interspaces vesiculose.

Discussion- This species occurs as epibionts on numerous hosts, mostly brachiopods. The vesiculate nature of the interspace is best developed in unabraided surfaces; when abraided, the interspaces appear smooth.

Material- Four Atrypa with four encrusting zoaria.

Fistulipora sp. B

(Not Figured)

Fistulipora sp. B. Reid, 1983 (in part), p. 130.

Description- Encrusting zoarium forming low robust mounds; zooids trilobate to oval, apertures uniform in diameter, 0.25 mm maximum; separated by vesicular interspace; monticules present, variable distances apart.

Discussion- This species was reported by Reid (1983), as identified by F.K. McKinney, to be common. It is most easily confused with Reid's F. sp. D; however, that species is very rare and posesses apertures with a diameter of 0.5 to 1.0 mm.

Material- Two Atrypa with two encrusting zoaria.

Genus Buskopora Ulrich, 1886

Buskopora sp.

(Not Figured)

Fistulipora sp. F (Buskopora?). Reid, 1983, p. 131.

Description- Thin to massive encrusting zoarium; zooids trilobate with prominant lunaria with bidenticulate process in unabraided specimens to smoothly oval in abraided specimens; apertures less than 0.15 mm maximum diameter; interspaces vesiculose; surface irregular with broadly rounded monticules.

Discussion- This species is distinguished by its trilobate zooids with prominant bidenticulate lunaria.

Material- One Atrypa encrusted by two zoaria.

Genus Eridopora Ulrich, 1882

Eridopora sp.

(Plate 2, Figure 3)

Fistulipora sp. C (Eridopora?). Reid, 1983, p. 131, pl. D-3, fig. M.

Description- Thin encrusting zoarium; zooids form radiating clusters, inclined forming obliquely alternating series; proximal surface of zooid smooth, formed by prominant overhanging, rounded lunaria of adjacent zooid; zooids separated from adjacent zooids by variable amounts of interspace; apertures triangular to ovoid, 0.1 mm diameter.

Discussion- Reid (1983) tentatively assigned specimens with the above characteristics to the genus Eridopora based upon identifications by F.K. McKinney. This species can be distinguished from Ceramopora cf. parvicella by its small aperture, more tightly imbricated zooid arrangement, and lack of strongly vesiculate interspaces. It can be distinguished from Fistulipora sp. A by its smaller aperture size. Reid reported this species to be absent on Atrypa shells; however, she noted that it could easily be confused with Fistulipora sp. A, thus possibly explaining the apparent absence.

Material- Two zoaria encrusting a single Leptaena.

Family Rhinoporidae Miller, 1889

Genus Lichenalia Hall in Silliman, 1851

Lichenalia cf. serialis Hall, 1879

(Plate 2, Figure 5)

Lichenalia serialis Hall. Hall, 1887, p. 32, pl. 13, figs. 17-18, pl. 15, fig. 6.

Description- Thin frond-like to encrusting zoarium; zooids oblique, tubular, alternating and imbricate; apertures circular to slightly oval, less than 0.5 mm diameter; zooid distribution regular, posterior slightly more elevated than anterior; surface ornamented with smooth maculae without zooids.

Discussion- This is a common species in the Bryozoan zone of the Birdsong.

Material- Two fragmentary zoaria encrusting a fenestrate bryzoan.

Order Cryptostomata Vine, 1884

Family Ptylodictidae Zittel, 1880

Genus Ptylodictya Lonsdale in Murchison, 1839

Ptylodictya tenuis (Hall), 1874

(Plate 3, Figure 6)

Escharopora tenuis Hall. Hall, 1874, p. 99; Hall, 1879, p. 161.

Ptylodictya tenuis (Hall). Hall, 1887, p. 39-40, pl. 17, figs. 7-12, pl. 13, fig. 14, pl. 23A, fig. 15.

Description- Thin, flattened, bifoliate zoarium; width up to 5.0 mm, thickness less than 0.5 mm; zooecia slightly inclined, oval to subquadrate, arranged in parallel longitudinal rows, adjacent zooids may form a straight row or be offset somewhat; two zooids per millimeter longitudinally; marginal zooids usually smaller and more elongate tending to form a flattened border along the margins of the zooarium.

Discussion- This species is distinguished by its flattened bifoliate form, marginal zooidal border, and subquadrate zooids. Rarely found with tapering encrusting base. Base usually occurs as encrustation on brachiopods.

Material- Three fragments.

Family Intraporidae Simpson, 1897

Genus Intrapora Hall, 1883

Intrapora puteolata Hall, 1883

(Plate 2, Figure 7)

Intrapora puteolata Hall. Hall, 1887, p. 97, pl. 29, figs. 18-20.

Description- "Zoarium consisting of a flattened, dichotomously, bifurcating or branching fron, arising from a spreading base. width of branches usually from 2 to 4 mm., but sometimes 20 mm. or more; greatest thickness 1 mm. Cells tubular, for one-half their length essentially parallel with the mesotheca, then turning abruptly outward. Cell apertures oval, length a little more than 0.25 mm., width three-fourths the length; very closely and irregularly disposed, frequently in contact. Peristomes strong, slightly and equally elevated. Inter-apertural space occupied by minute angular pits, generally a single series between adjacent apertures. . . . Intercellular space irregularly vesiculose." (Hall, 1887).

Discussion- This species is common to the Bryozoan zone.

Material- Four fragmented zoaria.

Order Trepostomata Ulrich, 1882

Family Heterotypidae Ulrich, 1890

Genus Leptotrypa Ulrich, 1883

Leptotrypa cf. spinifera (Duncan), 1939

(Plate 2, Figure 8)

Leptotrypella? spinifera Duncan. Duncan, 1939, p. 222, pl. 5, figs. 3-5.

?Leptotrypella sp. Reid, 1983, p. 132, pl. D-3, fig. I.

Description- Encrusting zooarium with thin-walled polygonal zooids in contact with each other; diameter of zooids 0.25-0.50 mm; no mesopores, few diaphrams; monticules present with zooids slightly larger than in other areas; maculae center 3 to 4 mm apart; acanthopores well developed.

Discussion- Reid (1983) assigned specimens with the above characteristics to Leptotrypella based on identifications made by F.K. McKinney. Leptotrypa differs from Leptotrypella by having well developed, spine-like acanthopores.

Material- Four zoaria encrusting three Atrypa.

Genus Leptotrypella Vinassa, 1920

Leptotrypella sp.

(Not Figured)

Description- Massively encrusting zooarium; zooids closely spaced with rounded to slightly polygonal apertures, maximum diameter 0.5 mm; zooids separated by

circular mesopores 0.1 to 0.2 mm in diameter, usually occuring at junction between three adjacent autozooids; interspace consists of smooth surface that meet with the interspace of the adjacent autozooid to form a medial septum thus creating a polygonal shape to the outer part of each autozooid.

Discussion- This species can be distinguished from Leptotrypa cf. spinifera by the lack of well developed acanthopores.

Material- Two zoaria encrusting Atrypa.

Family Batostomellidae Miller, 1889

Genus Eridotrypa Ulrich, 1893

Eridotrypa sp.

(Not Figured)

Eridotrypa sp. Reid, 1983, pl. D-3, fig. D.

Description- Massively encrusting zooarium; zooid diameters less than 0.25 mm; zooids irregularly arranged, closely spaced; apertures oval to slightly polygonal when closely spaced; interspace narrow to absent appearing vesiculose in abraided specimens; surface irregular and undulating with low monticules or undifferentiated zooids.

Discussion- This species resembles some species of Fistulipora because abraided specimens appear vesiculose. Reid (1983) figured, but did not describe, this species which was identified by F.K. McKinney.

Material- Two encrusting zooaria on Atrypa.

Family Stenoporidae Waagen and Wentzel, 1886

Genus Lioclema Ulrich, 1882

Lioclema cf. pulchellum Ulrich and Bassler, 1913

(Not Figured)

Lioclema pulchellum Ulrich and Bassler. Ulrich and Bassler, 1913, p. 274-275, pl. 43, figs. 9-12.

Description- Thin encrusting zoarium; zooids subcirular to ovate to slightly petaloid in outline; interspace with one to three rows of even sized, small, angular mesopores with thin walls; monticules and maculae absent; surface smooth; acanthopores indistinct but present.

Discussion- This species can be distinguished by its large zooids and polygonal mesopores. It is rare in the Birdsong.

Material- Two encrusting zooaria on one

Rhipidomelloides.

Family Trematoporidae Miller, 1889

Genus Monotrypa Nicholson, 1879

Monotrypa cf. tabulata (Hall), 1883

(Plate 2, Figure 6)

Monotrypa tabulata (Hall). Ulrich and Bassler, 1913, p. 278-279, pl. 50, figs. 1-4.

Description- Hemispherical encrusting zoarium; zooids polygonal with thin walls; aperture 0.25 to 0.4 mm diameter.

Discussion- This species is very rare in the Birdsong.

Material- One zoarium encrusting Atrypa.

Order Fenestrata Boardman, 1983

Family Fenestellidae King, 1850

Genus Semicoscinium Prout, 1859

Semicoscinium sp.

(Not Figured)

Description- Fragmented fan-shaped frond; zooids on one side only, six to nine per centemeter; zooids arranged in linear rows with elongate oval fenestrules separated by irregular wavy vertical zooid series; dissepiments short.

Discussion- This species is very rare in the Birdsong.

Material- One specimen.

Phylum Brachiopoda Dumeril, 1806

Class Articulata Huxley, 1969

Order Orthida Schuchert and Cooper, 1932

Family Orthidae Woodward, 1852

Genus Orthostrophia Hall, 1883

?Orthostrophia strophomenoides (Hall), 1857

(Plate 3, Figure 1)

Orthis halli Safford. Safford, 1869, p. 328, 553.

Orthostrophia strophomenoides (Hall). Weller, 1903, p. 300, pl. 34, figs. 6-8; Dunbar, 1919, fig. 2, fig. 16; Schuchert and Maynard, 1913, p. 297, pl. 53, figs. 20-23.

Description- Shell outline transversely elongate to suboval, greatest width of shell at or just anterior to hingeline; pedicle valve unknown; brachial valve convex;

faint low sulcus extends medially from beak to commissure, beak slightly incurved, hingeline straight; surface with radiating striae that increase distally by bifurcation.

Discussion- Dunbar (1919) reported this species to be very rare in the Birdsong. Amsden and Boucot (1958) compared their Oklahoma species to the specimens collected from the Birdsong which Safford (1869) had named Orthis halli. According to Amsden and Boucot (1958), Hall and Clarke (1892) concluded that O. halli is conspecific with O. strophomenoides. Amsden and Boucot (1958) also looked at Dunbar's specimens and found that his specimens were comparable to their own. Commonly encrusted by epibionts.

Material- Two disarticulated brachial valves.

Family Dalmanellidae Schuchert, 1913

Genus Dalmanella Hall and Clarke, 1892

Dalmanella concinna (Hall), 1859

(Plate 4, Fig. 1)

Orthis concinna Hall. Hall, 1859, p. 172; Hall, 1861, pl. 10a, figs. 1-3.

Dalmanella concinna (Hall). Schuchert and Maynard, 1913, p. 301-302, pl. 54, figs. 11-13.

Description- "Shell longitudinally semielliptical: valves unequally convex: hinge-line straight, with the extremities subangular. Dorsal valve convex, with a depression from beak to base, on each side of which the shell is more convex, and thence sloping somewhat abruptly to the sides: beak small and scarcely incurved. Ventral valve more convex, gibbous, and almost subcarinate in the middle: beak prominent, much elevated above the hinge-line, and neatly incurved over the area. Area comparatively large, the length greater than half the width of the shell. Surface very finely and evenly striated." (Hall, 1859, in Schuchert and Maynard, 1913).

Discussion- Dunbar (1919) reported this species to be very rare in the Birdsong.

Material- One pedicle valve.

Family Dicoelosiidae Cloud, 1948

Genus Dicoelosia King, 1958

Dicoelosia varica (Conrad), 1842

(Not Figured)

Dicoelosia varica (Conrad). Amsden, 1958, p. 50-51, pl. 1, figs. 29-31.

Description- Shell very small, less than 1 cm in width or length, subequally biconvex; shell outline subtriangular with anterior margin deeply indented causing the bilobed appearance; bilobed appearance results from a pedicle and brachial sulcus that meet, thus truncating the anterior margin; surface ornamented with very fine radial costellae.

Discussion- As noted by Amsden and Boucot (1958), this genus was known as Bilobites until 1948 when Cloud demonstrated that this name was incorrect. For a more full discussion of the nomenclatural history of this genus, see Cloud (1948) and Amsden and Boucot (1958). Although Amsden and Boucot (1958) mentioned Dunbar's specimens, they did not compare them with their own. Dunbar (1919) reported this species to be very common in the Birdsong; however, it was rarely encountered in this study.

Material- Two articulated specimens.

Family Rhipidomellidae Schuchert, 1913

Genus Rhipidomelloides Boucot and Amsden, 1958

Rhipidomelloides oblata (Hall), 1857

(Plate 3, Figure 2a, b, c, d)

Rhipidomella oblata (Hall). Weller, 1903, p. 304, pl. 35, figs. 9-13, p. 350, pl. 46, figs. 5-7; Schuchert and

Maynard, 1913, p. 303-304, pl. 55, figs. 4-16; Dunbar, 1919, pl. 1, fig. 1.

Rhipidomelloides oblata (Hall). Amsden, 1958, p. 54-50, pl. 1, figs. 2-9; Boucot and Amsden, 1958, p. 165-169, pl. 12, figs. 1-4.

Description- Unequally biconvex shell with subcircular to elliptical outline; greatest width of the shell near midvalve; hingeline short; cardinal extremities rounded, more so on the brachial valve; brachial valve more inflated than pedicle with a prominent rounded cardinal process that fills the notothyrium; pedicle valve less inflated with a prominant triangular delythyrium; pedicle scars extending one-third to two-third valve length, expanding quickly, triangular outline with rounded posterior margin; plicate surface ornamented with bifuricating fine costellae, anterior plications show crenulations that bisect each plica.

Discussion- Boucot and Amsden (1958) revised the genus Rhipidomella, to which Dunbar (1920) had assigned Ross brachiopods with the above characteristics. They erected the new genus Rhipidomelloides to include all Rhipidomella-like brachiopods of Early Devonian age (pre-Hamilton) with rectangular marginal crenulations rather than rounded marginal crenulations. They looked at

Dunbar's specimens and noted no differences with their Oklahoma specimens. Dunbar (1919) reported this species to be very common in the Birdsong.

Material- 26 disarticulated specimens displaying excellent preservatiom and detail.

Rhipidomelloides emarginata (Hall), 1859

(Plate 3, Figure 3)

Rhipidomella oblata var. emarginata (Hall). Hall, 1859, p. 164; Hall, 1861, pl. 10A, figs. 4-6.

Rhipidomella emarginata (Hall). Schuchert and Maynard, 1913, p. 302-303, pl. 55, figs. 1-8; Dunbar, 1919, pl. 2, fig. 1.

Rhipidomelloides emarginata (Hall). Boucot and Amsden, 1958, p. 165-169, pl. 2, fig. 10.

Description- Features same as for Rhipidomelloides oblata except for anterior margin; brachial valve shallowly sulcate begining at beak, anterior margin with a deep indentation coincident with the shallow sulcus.

Discussion- This species resembles R. oblata in all respects except for the anterior margin. Typically this species is very small, rarely more than 1 cm wide. Dunbar

(1919) reported this species to be very common in the Birdsong.

Material- Three disarticulated brachial valves.

Order Strophomenida Opik, 1934

Family Strophomenidae King, 1846

Genus Leptaenisca Beecher, 1890

Liljevallia adnascans (Hall and Clarke), 1892

(Not Figured)

Leptaenisca adnascans Hall and Clarke. Hall and Clarke, 1892, p. 352, pl. 52A, figs. 22-23.

Liljevallia adnascans (Hall and Clarke). Cooper, 1944b, p. 343.

?Leptaena sp. Reid, 1983, pl. D-3, fig. E.

Description- Shell, outline transversely elliptical to subquadrate; encrusting pedicle valve; valves concavo-convex; shells small, usually less than 1 cm in length, usually 3 to 4 mm wide; other features not observed.

Discussion- This species was reported by Dunbar (1919) to be very common in the Birdsong. Amsden and Boucot (1958) noted that juvenile Leptaena concava (not present in

the Birdsong) is often confused with Leptaenisca adnascans. They also pointed out that specimens belonging to L. adnascans are now refered to the genus Liljevallia based on work by Cooper (1944b). Amsden and Boucot (1958) noted that Dunbar (1919) had reported this species from the Birdsong, but they did not study his specimens.

Material- Two pedicle valves encrusted on brachiopod hosts, two on crinoid stems, and several on the lower surface ofFavosites foerstei.

Family Leptaenidae Hall and Clarke, 1894

Genus Leptaena Dalman, 1828

Leptaena acuticuspidata Amsden, 1958

(Plate 4, Figure 2a, b, c, d)

Leptaena rhomboidalis Wilkens. Weller, 1903, p. 228, pl. 20, fig. 10, p. 278-279, pl. 27, fig. 9, p. 302, pl. 33, fig. 10; Schuchert and Maynard, 1913, p. 308-309, pl. 56, figs. 13-17; Dunbar, 1919, pl. 2, fig. 17; Tansey, 1922, p. 186-187, pl. 46, figs. 26-32; Prouty and Swartz, 1923, p. 418-419, pl. 15, figs. 23-24; Morse, 1930, pl. 2, figs. 4-5; Wilson, 1949, pl. 27, figs. 10-12.

Leptaena acuticuspidata Amsden. Amsden and Boucot, 1958, p.

84-88, pl. 3, figs. 1-9.

Description- Shell alate, rectangular in outline, hingeline usually extending to points representing maximum shell width; beak extending slightly above hingeline; shells concavo-convex and geniculate with angle of geniculation ranging from 70 to 90 degrees; exterior of shell strongly rugate, numbering 7 to 13 rugae prior to geniculation of the pedical valve, rugae regular to slightly sinuous; exterior also with radiating costellae numbering between 18 and 22 at 5 mm from the umbo; pedicle interior convex with deeply impressed muscle scars, scars triangular shaped with straight to rounded anterior margin seperated by faint median septum; brachial interior concave, muscle field less distinct, brachiophore bases prominant and divergent.

Discussion- Amsden (1958) and Amsden and Boucot (1958) note that most workers assign Hunton specimens to the species L. rhomboidalis. Dunbar (1919) did the same for his Ross specimens. L. rhomboidalis differs by being much larger, less alate, and with a greater number of rugae prior to the geniculation (Amsden, 1958). Amsden and Boucot (1958) point out, however, that juveniles of L. rhomboidalis can resemble L. acuticuspidata. Reid (1983) assigned her specimens to L. acuticuspidata rather than L.

rhomboidalis as did Dunbar (1919). She also noted the extreme variability present among the Birdsong specimens and constructed L/W ratio histograms to determine if more than one species existed. She found a unimodal curve and concluded that only one species was present in the Birdsong. She also plotted L/W ratios against L to determine whether or not her data were ontogentically biased. Her data indicated that all of her specimens were mature adults and that the size variation was due either to (1) sexual dimorphism, (2) sampling bias, or most likely (3) the presence of dwarfed assemblages in the Birdsong. Dunbar (1919) reported this species (here equal to his L. rhomboidalis) to be very common.

Material- Five articulated specimens and eight disarticulated specimens.

Leptaena rhomboidalis (Wilkens), 1769

(Plate 4, Figure 3)

Leptaena cf. rhomboidalis (Wilkens). Amsden, 1958, p. 62-66, pl. 2, figs. 12-15; Amsden and Boucot, 1958, pl. 3, figs. 10-14.

Description- Like L. acuticuspidata except much larger up to 61 mm wide, slightly more alate rectangular to slightly rounded in outline; musculature less developed; rugae bifurcate and less distinct numbering greater than 21 prior to geniculation; geniculate up to right angles; costellae less distinct numbering 19 per 5 mm at geniculation.

Discussion- This species is easily distinguished from L. acuticuspidata by its larger size and more numerous rugae.

Material- Six articulated specimen.

Family Strophodontidae Castor, 1939

Genus Strophonella Hall, 1879

Subgenus Strophonella (Strophonella) Hall, 1879

Strophonella (Strophonella) punctulifera holladayi Dunbar, 1920

(Plate 4, Figure 4)

Strophonella punctulifera holladayi Dunbar. Dunbar, 1920, p. 127-128, pl. 2, figs. 18-19.

Description- Shell nearly semicircular, nearly as long as wide; hingeline straight; greatest width of shell near

hingeline; interarea narrow, striated vertically; surface ornamented with up to thirty fine, wide spaced costae; area between striations flattened with finer costellae; large costae thread-like, increase by bifurcation in umbo region only, secondary costellae numbering up to 12 between each larger costae; fine concentric growth lines also occur.

Discussion- Dunbar (1920) and Amsden and Boucot (1958) noted that this species is distinct from other species of Strophonella (Strophonella) by possesing costae of two ranks. Dunbar (1919) reported this subspecies to be very rare in the Birdsong and S. (P.) punctulifera to be very common; however, no specimens of the later were found in this study.

Material- Two incomplete specimens.

Genus Leptostrophia Hall and Clarke, 1892

Leptostrophia beckii beckii (Hall), 1859

(Plate 4, Figure 5a, b)

Stropheodonta beckii Hall. Hall, 1859, p. 191; Hall, 1861, pl. 22, fig. 1, pl. 23, fig. 3; Weller, 1903, p. 300, pl. 33, figs. 7-8.

Stropheodonta (Leptostrophia) beckii Hall. Hall and Clarke, 1892, pl. 13, figs. 23-24; Schuchert and Maynard,

1913, p. 314-315, pl. 57, figs. 12-13.

Leptostrophia beckii beckii (Hall). Morse, 1930, pl. 2, fig. 8.

Description- Shell typically flat to slightly curved, up to 60 mm in width along the hingeline, very thin and fragile; greatest width occurs anywhere from the hingeline to half the shell length, hingeline straight; shell outline broadly rounded to subquadrate; ornamented with regular, concentric, rounded, faint rugae of uneven height, rugae extend through to the inner surface of the shell; surface also ornamented radiating costellae.

Discussion- This species is easily distinguished by its irregularly wrinkled rugae. Amsden and Boucot (1958) discussed the nomenclatural history of the genus Leptostrophia, and in particular, Dunbar's specimens of L. beckii and L. beckii tennesseensis concluding that the tennesseensis subspecies described by Dunbar (1920) represents an unusual variation that occurs in both the Birdsong and the Hunton. Dunbar (1919) reported this species to be a common element of the Birdsong.

Material- Eight partial specimens of pedicle and brachial valves.

Leptostrophia beckii tennesseensis Dunbar, 1920

(Not Figured)

Leptostrophia beckii tennesseensis Dunbar. Dunbar, 1920, p. 129, pl. 3, fig. 18; Amsden, 1958, p. 58-59, pl. 2, figs. 7-9; Amsden and Boucot, 1958, p. 78-80, pl. 3, figs. 15-20, pl. 6, fig. 1, pl. 11, figs. 27-28.

Description- "This fine large Leptostrophia is distinguished from L. beckii only by the character of the corrugations which ornament its surface. Instead of the fairly regular and even-crested concentric corrugations of L. beckii, this variety is marked by concentric ridges that are not only crooked but also undulate in height. The result is the characteristic 'dimpled' surface . . . ." (Dunbar, 1920).

Discussion- The history of this species is discussed under L. beckii. Dunbar (1919) considered this species to be very rare.

Material- One incomplete specimen. Both species are generally preserved as disarticulated or fractured valves.

Family Schuchertellidae Williams, 1953

Genus Schuchertella Girty, 1904

Schuchertella woolworthana (Hall), 1859

(Not Figured)

Strophomena woolworthana (Hall). Weller, 1903, p. 274, pl. 27, fig. 5.

Schuchertella woolworthana (Hall). Schuchert and Maynard, 1913, p. 328-329, pl. 60, figs. 4-9.

Description- Planoconvex, transversely elliptical to subquadrate shell; straight to moderately arched hingeline, greatest width of valves at midvalve; cardinal extremeties angular to rounded; surface ornamented with fine radiating costae that bifurcate.

Discussion- This genus is sometimes confused with Orthostrophia, especially with respect to external morphology, but differs by having finer costae and not being sulcate. Amsden and Boucot (1958) examined Dunbar's specimens comparing them to Schellwienella marcidula Amsden. They concluded that Dunbar's specimens were much larger (up to 5 cm in length) and differed from Schellwienella by possessing receding dental plates in the pedicle valve. Dunbar (1919) found this species to be common in the Birdsong.

Material- Two disarticulated and two articulated

specimens.

Order Pentamerida Schuchert and Cooper, 1931

Family Pentameridae M'Coy, 1844

Genus Gypidula Hall, 1867

Gypidula multicostata Dunbar, 1920

(Plate 4, Figure 7)

Gypidula multicostata Dunbar. Dunbar, 1919, pl. 2, fig. 22; Dunbar, 1920, p. 131-132, pl. 3, figs. 12-13; Tansey, 1922, p. 191-192, pl. 48, figs. 10-19; Amsden and Boucot, 1958, p. 69, pl. 2, fig. 17.

Description- "Shell subtrigonal in outline. Ventral valve strongly convex and much larger than dorsal. Its beak narrow and strongly arched, but not incurved over that of the opposite valve. The sides diverge regularly to their greatest width at abouth three-fourths to four-fifths the distance to the front of the shell, then round abruptly into the broad and very slightly emarginate anterior margin, so that the outline is almost an isosceles triangle. Dorsal valve transversely elliptical and gently convex. A broad but low flat fold occupies the median half of the ventral valve, becoming obsolete before reaching the

beak, and a corresponding sinus is present on the dorsal valve. The fold and sinus bear each ten to twelve slender, sharp, angular plications separated by angular grooves of equal width, while the inner parth of each lateral slope is marked by four or five obscure plications . . . ." (Dunbar, 1920).

Discussion- This species is common and is generally poorly preserved. Dunbar (1919) reported it to be very common in the Birdsong. Amsden and Boucot (1958) reported fragments of this species in the Haragan Formation of Oklahoma.

Material- Six disarticlated valves.

Order Rynchonellida Kuhn, 1849

Family Trigonirhynchiidae McLaren, 1965

Genus Trigonirhynchia Cooper, 1942

Trigonirhynchia acuticostella Amsden, 1958

(Plate 4, Figure 8)

Trigonirhynchia acuticostella Amsden. Amsden and Boucot, 1958, p. 104-105, pl. 13, figs. 1-7.

Description- Subpentagonal to subtrigonal shell outline with pedicle beak pointed and extending well above

the hingeline; lateral and ventral outlines smoothly rounded, pedicle valve slightly sulcate; surface ornamented with slightly curving radiating costae with costae being narrow, round, and seperated by slightly angular troughs.

Discussion- Amsden and Boucot (1958) erected this species for specimens belonging to the Henryhouse Formation of Oklahoma. They noted that T. acuticostella resembles Sphaerirhynchia lindenensis (Dunbar) in gross morphology, but differs by having a much less inflated brachial valve and an erect, sharply pointed beak.

Material- Two specimens, one disarticulated pedicle valve and one articulated specimen with a broken brachial valve.

Genus Obturamentella Amsden, 1958

Obturamentella wadei (Dunbar), 1920

(Not Figured)

Wilsonia wadei Dunbar. Dunbar, 1919, pl. 2, fig. 8; Dunbar, 1920, p. 133, pl. 3, figs. 3-4; Tansey, 1922, p. 195, pl. 49, figs. 35-48, pl. 50, figs. 1-4.

Obturamentella wadei (Dunbar). Amsden, 1958, p. 70-71, pl. 3, figs. 17-24; Amsden and Boucot, 1958, p. 100-103, pl. 6, figs. 15-22, pl. 11, figs. 29-30, pl. 14, fig.

1.

Description- "Shell small, subglobular or subpentahedral in form; deepest and strongly truncate at the front margin; length, breadth, and height about equal. Ventral valve depressed convex, but sharply deflected, almost angulated along the margins; beak short and small, neatly incurved. A medial sinus begins about the middle of the valve and is produced anteriorly into a narrow linguliform extension that is sharply deflected at right angles to the plane of the valve. Dorsal valve about as deep as the ventral, also gently convex and steeply angulated at the margins. A fold on the anterior portion corresponds to the sinus of the opposite valve. The surface bears low rounded plications, of which one occupies the sinus, two the fold, and three each lateral slope. Rarely in large specimens there are two plications on the sinus and three on the fold. The plications become obsolescent near the beak." (Dunbar, 1920).

Discussion- Amsden and Boucot (1958) describe O. wadei from the Hunton Group of Oklahoma and examined Dunbar's specimens in the process. They designated the specimen pictured without description by Dunbar (1919), as the lectotype for the type species for their new genus. This species is most easily confused with Sphaerirhynchia

lindenensis, but can be distinguished by its much smaller size and fewer plications within the sulcus. Dunbar (1919) reported this species to be a common Birdsong element.

Material- Four articulated specimens.

Genus Sphaerirhynchia Cooper and Miur-Wood, 1951

Sphaerirhynchia lindenensis (Dunbar), 1920

(Plate 4, Figure 6a, b)

Uncinulus lindenensis Dunbar. Dunbar, 1919, pl. 2, fig. 20; Dunbar, 1920, p. 133-134, pl. 3, figs. 5-6.

Sphaerirhynchia lindenensis (Dunbar). Amsden, 1958, p. 67-70, pl. 5, figs. 1-14; Amsden and Boucot, 1958, p. 97-99, pl. 7, figs. 23-28, pl. 11, figs. 15-16, pl. 13, figs. 21-23.

Description- "Shell of medium size, subpentahedral in form, subtriangular to subpentagonal in outline, as wide as or wider than long. Ventral valve almost flat, shallow and steeply angulated at the margins. A flat shallow sinus is visible only near the anterior margin, where it is produced into a very long linguliform extension, sharply deflected at right angles to the valve. Dorsal valve very deep, sharply deflected at the margins into the deep, nearly

vertical sides, highest in front, and sloping with depressed convexity to the beak. Beaks small, and posterio-lateral sides often concave. Surface marked by rounded plications, of which three or four occupy the sinus, four or five the fold, and five or six each lateral slope. Anteriorly the plications are marked with a fine median line." (Dunbar, 1920).

Discussion- This species is very common in the Birdsong, as reported by Dunbar (1919), and is generally found articulated and often in living position. Amsden (1958) and Amsden and Boucot (1958) found no differences between their Oklahoma specimens and Dunbar's specimens.

Material- Fourteen articulated specimens.

Family Camarotoechiidae Schuchert and LeVene, 1929

Genus Camarotoechia Hall and Clarke, 1893

Camarotoechia bialveata (Hall), 1857

(Not Figured)

Rhynchonella(?) bialveata Hall. Schuchert and Maynard, 1913, p. 377, pl. 66, fig. 4; Tansey, 1922, p. 195-196, pl. 50, figs. 21-24.

Camarotoechia bialveata (Hall). Dunbar, 1919, pl. 2, fig. 6.

Description- Shell elongate, subtriangular, subequally biconvex with slightly more inflated pedicle valve; pedicle beak recurved and pointed, hooked over brachial beak; posterior margins straight and steeply inclined; fold and sulcus well developed; surface ornamented with up to fourteen slightly curved, radiating, angular to slightly rounded plicae with three plicae occuring within the fold and sulcus region.

Discussion- Dunbar (1919) considered this species to be a "New Scotland" guide fossil confined to and common in the Birdsong; however, this species actually extends into the Rockhouse Limestone. Amsden and Boucot (1958) compared their C.(?) haraganensis to Dunbar's figured specimens of C. bialveata and suggested that the two may be the same species, but did not study Dunbar's actual specimens.

Material- Three articulated specimens.

Camarotoechia transversa (Hall), 1859

(Plate 4, Figure 9)

Rhynchonella transversa Hall. Hall, 1859, p. 234, pl. 34, figs. 9-16; Weller, 1903, p. 283, pl. 29, figs. 28-31; Tansey, 1922, p. 195, pl. 50, figs. 5-20.

Description- Shell small, short, longitudinally expanded; pedicle beak recurved and pointed, hooking over brachial; posterior margin straight and inclined; fold and sulcus well developed; surface ornamented with up to eleven angular plicae.

Discussion- Hall and Clarke (1894) revised the genus Rhynchonella and erected the new genus Camarotoechia. Subsequent authors such as Amsden and Boucot (1958) have assigned the above described species to this genus. This species is distinguished from C. bialveata by its smaller size, more longitudinal expansion, and very angular plicae. Dunbar (1919) reported this species to be very common in the Birdsong.

Material- One articulated specimen.

Order Spiriferida Waagen, 1883

Family Atrypidae Gill, 1871

Genus Atrypina Hall and Clarke, 1893

Atrypina imbricata (Hall), 1857

(Plate 5, Figure 2)

Atrypina imbricata (Hall). Hall, 1857, p. 108; Hall, 1859, p. 246, pl. 38, figs. 8-13; Hall and Clarke, 1894, p.

353, pl. 56, figs. 8-10; Schuchert and Maynard, 1913, p. 395-396, pl. 68, figs. 4-6; Dunbar, 1919, pl. 2, fig. 2; Tansey, 1922, p. 197-198, pl. 50, figs. 27-29.

Description- Planoconvex shell with brachial valve nearly flat; pedicle beak slightly elevated and recurved over brachial; hingeline slightly angular with sharp lateral margins; greatest width of shell near midvalve; shell slightly wider than long; fold and sulcus poorly developed; surface ornamented with five to six broad rounded plicae that form lobate nature to the anterior margin; also with very coarse, concentric, wavy growth lines creating an imbricated appearance; the two plications in the fold and sulcus are the best developed.

Discussion- Amsden and Boucot (1958) compared their A. hami to Dunbar's (1919) figured specimen of A. imbricata and noted that Dunbar's specimen was very similar and was possibly conspecific with the Oklahoma species. Dunbar (1919) reported this species to be a very common element of the Birdsong.

Material- Two articulated specimens.

Genus Atrypa Dallman, 1828

Atrypa reticularis (Linne), 1758

(Plate 5, Figure 3a, b, c, d)

Atrypa reticularis (Linne). Hall, 1859, p. 253; Hall, 1861, pl. 42, fig. 1; Hall, 1867, p. 312-327, pl. 51, figs. 10-24, pl. 52, figs. 1-12; Hall and Clarke, 1894, p. 162-175, pl. 55, figs. 1-17; Weller, 1903, p. 236, pl. 21, figs. 35-37, p. 286, pl. 30, figs. 11-18; Schuchert and Maynard, 1913, p. 392-393,pl. 67, figs. 20-28; Prouty and Schwartz, 1923, p. 444-446, pl. 21, figs. 24-25; Branson, 1922, p. 97-98, pl. 21, figs. 6-7; Tansey, 1922, p. 198-199, pl. 50, figs. 30-40; p. 245, pl. 65, fig. 2; Morse, 1930, pl. 2, figs. 1-2; Savage, 1931, pl. 28, fig. 7; Wilson, 1949, pl. 26, figs. 15-17; Boucot, Johnson, and Stanton, 1964, pl. 126, figs. 1-5.

Description- Shell unequally biconvex, variable in outline ranging from subrounded to triangular (slightly wider than long) to suboval (slightly longer than wide); brachial beak recurved over pedicle; brachial valve inflated, with commissure forming a depressed sulcus best developed along the anterior margin; pedicle valve flattened to slightly geniculate with a prominant fold in the anterior margin that coincides with the brachial trough; lateral and anterior margins often recurved in the

direction of the pedicle valve; surface ornamented with strong radiating costae separated by rounded interspaces, this is overlain by faint to coarse concentric lamellae creating the reticulated pattern.

Discussion- Although Dunbar (1919) assigned his Birdsong specimens to this species, Reid (1983) chose to assign her specimens to A. tennesseensis based on the discription of that species from the Brownsport Formation (Silurian) of Tennessee by Amsden (1949). In this report, the Birdsong specimens are assigned to A. reticularis following Dunbar's original assignment because there does not appear to be any difference between figured specimens of A. reticularis reported from other Lower Devonian areas. Amsden and Boucot (1958) discussed the nomenclatural history of this species and noted that this species shows a very wide range of morphology. Their reason for this was that there is a great geographic separation between Tennessee and Gotland, where A. reticularis was described. Reid (1983) constructed L/W histogram for her specimens and noted that only one species was present, but that this species shows a wide, but continuous, gradation in L/W ratio. This species is very common in the Birdsong.

Material- Over fifty articulated and disarticulated specimens.

Family Retziidae Waagen, 1883

Genus Trematospira Hall, 1859

Trematospira costata angusta Dunbar, 1920

(Plate 5, Figure 1)

Trematospira costata angusta Dunbar. Dunbar, 1920, p. 141, pl. 4, figs. 6-7; Amsden and Boucot, 1958, p. 136-137, pl. 11, fig. 31.

Description- "This variety of T. costata . . . differs from the New York form chiefly in proportion of length to breadth. In New York, the shells are less than half as long as wide, and each lateral slope bears five or commonly six plications; in Tennessee, the length is about three-fourths the width, and the lateral slopes have only five plications. This narrower and elongate form is therefore a clearly distinguished variety, though in all its other characters it agrees fully with Hall's specimens." (Dunbar, 1920).

Discussion- Amsden and Boucot (1958) compared Dunbar's specimens with their T. cf. hipplyte and concluded that, although very similar, T. costata angusta differs by having a more transversely expanded shell. They also compared a T. sp. to the Birdsong specimens and concluded that their

specimens represented a different species based on a pustulose nature to the shell. Dunbar (1919) found that this species was very rare in the Birdsong.

Material- One articulated specimen.

Family Rhynchospirinidae Schuchert and LeVene, 1929

Genus Rhynchospirina Schuchert and LeVene, 1929

Rhynchospirina formosa (Hall), 1859

(Plate 5, Figure 4)

Trematospira formosa Hall. Hall, 1859, p. 215-216; Hall, 1861, pl. 36, fig. 2.

Rhynchospira formosa (Hall). Weller, 1903, p. 240, pl. 21, figs. 30-34, p. 289, pl. 31, figs. 9-11; Schuchert and Maynard, 1913, p. 426, pl. 72, figs. 26-30; Tansey, 1922, p. 201, pl. 52, figs. 5-18.

Rhynchospirina formosa (Hall). Scbuchert and LeVene, 1929, p. xx; Amsden and Boucot, 1958, p. 138-142.

Description- Shell longitudinally ovate, biconvex; pedicle beak prominant, rounded, curved and truncated by a round pedicle foramen; anterior margin smoothly rounded; surface ornamented with eighteen rounded radiating plications; anterior commissure very slightly sulcate.

Discussion- The Birdsong specimens very closely match figured specimens of T. formosa of Hall (1861). Schuchert and LeVene (1929) noted that Rhynchospira was a homynym of Rhynchospirina. Amsden and Boucot (1958) figured specimens of Rhynchospirina maxwelli which they compared to Dunbar's Birdsong specimens. They noted a strong similarity between the three species but failed to explain specific differences, leaving the distinguishing characteristics uncertain. One major difference between Amsden and Boucot's and Dunbar's specimens is easily seen in the figured specimens, that is, Dunbar's specimens do not posess the sulcate anterior margin unlike the Oklahoma specimens. Specimens collected in the present study have a smoothly rounded anterior margin. This species was reported by Dunbar (1919) to be very common in the Birdsong.

Material- Three articulated specimens.

Rhynchospirina globosa (Hall), 1857

(Plate 5, Figure 5a, b)

Rhynchospira globosa (Hall). Schuchert and Maynard, 1913, p. 425-426, pl. 72, figs. 16-25; Prouty and Swartz, 1923, p. 456, pl. 24, figs. 16-25

Rhynchospirina globosa (Hall). Shuchert and LeVene, 1929, p. xx.

Description- Shell large, subtrigonal to expanding globose in outline, slightly longer than wide, up to 19 mm in width with inflated valves; pedicle beak prominant, rounded with a small circular foramen; anterior margin slightly orthogonal and flattened; fold and sulcus present; surface ornamented with approximately 21 smoothly rounded, radiating plications with up to four plications occuring within the sulcus region.

Discussion- Schuchert and LeVene (1929) noted that the genus Rhynchospira was a homynym of Rhynchospirina Although similar to R. formosa, this species is distinguished by its larger size, orthogonal anterior margin, and more prominant sulcus. Dunbar (1919) reported this species to be common in the Birdsong.

Material- Four articulated specimens.

Family Meristellidae Waagen, 1883

Genus Meristella Hall, 1859

Meristella atoka Girty, 1899

(Plate 5, Figure 6a, b)

Meristella atoka Girty. Dunbar, 1919, pl. 1, fig. 11, pl. 2, fig. 3; Tansey, 1922, p. 204, pl. 53, figs. 7-20;. Amsden, 1958, p. 84-85, pl. 4, figs. 1-14; Amsden and Boucot, 1958, p. 128-133, pl. 10, figs. 1-15.

Description- Subtriangular shell with greatest width located one half to two-thirds distance from the beak; shell usually slightly wider than long; margins straight from beak to greatest shell width, then smoothly rounded; biconvex shell with brachial valve slightly less convex than pedicle; pedicle beak small, pointed, hooked over brachial umbo; pedicle sulcus deep and brachial fold pronounced, smoothly rounded; surface smooth except for growth lines becoming more pronounced along anterior margin.

Discussion- Dunbar (1919) considered this species to be very common in the Birdsong. Amsden and Boucot (1958) noted that Hall had described Meristella meeki in 1857 from rocks that they presumed to represent the Ross Limestone in Tennessee. They believed that Dunbar and Wilson both overlooked Hall's specimens and referred all subsequent Tennessee specimens to M. atoka or to M. arcuata. Amsden and Boucot (1958) looked at Dunbar's specimens and concluded that M. meeki was not present and that these specimens belonged either to M. atoka or to M. arcuata. M.

meeki differs from M. atoka by being larger and more transversely expanded.

Material- Five articulated specimens.

Meristella laevis (Hall), 1859

(Not Figured)

Meristella laevis (Hall). Hall, 1859, p. 247; Hall, 1861, pl. 39, figs. 1-4; Safford, 1869, p. 324, fig. 12; Safford and Killebrew, 1897, fig. 37, no. 12; Weller, 1903, p. 290, pl. 31, figs. 1-8, p. 317, pl. 37, figs. 11-18; Tansey, 1922, p. 202, pl. 52, figs. 34-44.

Description- Shell outline oval; pedicle valve slightly larger than brachial, with shallow median sulcus that becomes attenuated as it reaches the umbo; beak prominant and incurved over brachial beak; brachial valve convex without well developed fold; surface smooth except for faint concentric growth lines.

Discussion- This species was reported by Dunbar (1919) to be very rare in the Birdsong.

Material- One articulated specimen.

Family Cyrtiidae Frederiks, 1919

Genus Macropleura Boucot, 1963

Macropleura macropleura (Conrad), 1840

(Plate 5, Figure 8)

Spirifer macropleura Conrad. Safford and Killebrew, 1897, fig. 39, no. 9.

Spirifer macropleurus (Conrad). Safford, 1869, p. 324, fig. 9; Weller, 1903, p. 288, pl. 30, fig. 1, p. 313, pl. 37, figs. 1-3; Schuchert and Maynard, 1913, p. 396, pl. 68, figs. 1-3.

Eospirifer macropleura (Conrad). Dunbar, 1919, pl. 2, fig. 21.

Macropleura macropleura (Conrad). Boucot, 1963, p. 690-693, pl. 98, figs. 1-8, pl. 99, figs. 1, 2, 5, 7-9.

Description- Shell very large, up to 70mm in length, biconvex; strophic hingeline with prominant beak extending well beyond hinge; interarea large, slightly concave with open delethyrium, cardinal extremeties rounded; widest portion of shell one-fourth to one-half distance anterior to the hingeline; posterior margin broadly rounded; pedicle sulcus broadly U-shaped, diverging from beak at a forty degree angle; commissure region of sulcus poorly plicate; brachial fold broadly rounded, divergent at a twenty-five

degree angle; four broadly rounded plications flank the sulcus becoming indistinct near the anterior margin and hingeline; plicaions slightly arcuate away from sulcus and cause a slightly rounded crenulate commissure; three plications flank the fold becoming indistinct toward the anterior margin and toward the hingeline; surface ornamented with fine beaded costellae.

Discussion- This species is very common in the Birdsong. Specimens are usually preserved fractured or otherwise deformed. Boucot (1963) revised the Eospiriferidae and erected the genus Macropleura based on the elliptical shell outline and three to four lateral plications with broad rounded troughs. In his revision, he looked at Dunbar's specimens from the Birdsong and included them in this genus.

Material- Eight articulated and disarticulated specimens.

Family Delthyrididae Waagen, 1883

Genus Kozlowskiellina Boucot, 1957

Kozlowskiellina (Megakozlowskiellina) parmellosa (Hall), 1857

(Plate 5, Figure 9a, b)

Spirifer parmellosa Hall. Hall, 1857, p. 57, figs. 1-5.

Delthyris parmellosa (Hall). Dunbar, 1919, pl. 1, fig. 4.

Delthyris parmellosus (Hall). Tansey, 1922, p. 199, pl. 50, figs. 41-49.

Kozlowskiellina (Megakozlowskiellina) parmellosa (Hall). Boucot, 1958, in Amsden and Boucot, 1948, p. xx.

Description- Shell outline slightly rounded to alate with greatest width at or just anterior to the hingeline; brachial beak overhanging hingeline; interarea narrow, laying horizontally; surface ornamented with plicae displaying well developed concentric lamellae, three to four plications on either side of the fold and sulcus, plications slightly arcuate laterally; sulcus angular with concentric lamellae.

Discussion- As discussed by Amsden and Boucot (1958) the genus Kozlowskiella was erected by Boucot (in Amsden and Boucot, 1958) into which he placed Delthyris parmellosa. Amsden and Boucot (1958) described specimens belonging to K. (M.) velata from Oklahoma and compared them to Dunbar's specimens from the Birdsong. They noted that Dunbar's Delthyris parmellosa differed by being larger than their species. Boucot (1958) substituted the name Kozlowskiellina for Kozlowskiella because the latter was already occupied as a genus of ostracod. Dunbar (1919)

reported this species to be very common in the Birdsong.

Material- Three articulated specimens.

Kozlowskiellina (Megakozlowskiellina) cyrtinoides
Dunbar, 1920
(Not Figured)

Delthyris cyrtinoides Dunbar. Dunbar, 1920, p. 138, pl. 4, figs. 1-3.

Kozlowskeillina (Megakozlowskiellina) cyrtinoides Dunbar, 1920. Amsden and Boucot, 1958, p. ss.

Description- "External aspect indentical with the less alate forms of D. parmellosa. Hinge-line varying from slightly less to a little greater than the width of the shell below. Cardinal angles varying from sharp to slightly rounded. Area one-fourth to one-third as high as long. Deltidium very narrow. Surface marked by three or four strong narrow plications on each fold and sinus, which are crossed by strong concentric imbricating lamellae as in D. parmellosa." (Dunbar, 1920).

Discussion- Dunbar (1920) reported this species to be from the Rockhouse Shale only; however, in this study, one specimen was found in the Birdsong Shale. This species is

distinguished from other related species by its more robust shape, very prominant interarea, and sharp well developed fold and sulcus. Amsden and Boucot (1958) compared this species to their K. (M.) velata and noted that, although the two species resembled each other externally, the spondylium differs significantly.

Material- One articulated specimen.

Kozlowskiellina (Megakozlowskiellina) octocostata tennesseensis Dunbar, 1920

(Plate 5, Figure 11)

Delthyris octocostata tennesseensis Dunbar. Dunbar, 1920, p. 139-140, pl. 4, figs. 8-9.

Description- "This common Spirifer of the Linden group in western Tennessee very closely resembles the earlier Delthyris octocostata of the Keyser formation of Maryland. It differs from the later in being proportionaly shorter and more transverse, the ratio of length to breadth being 3 to 5 as compared with 4 to 5 in the Maryland form. There is also tendency to have more plications which diverge rapidly, the mutation frequently developing eight and occasionally ten, whereas the species usually has six and

rarely eight. The ventral beak is more erect, the cardinal area is proportionately larger, more clearly defined, less curved, and more nearly in the plane of the valve. The deltidium is wider. The dorsal valve is proportionately smaller and its beak less prominant." (Dunbar, 1920).

Discussion- Amsden and Boucot (1958) compared Dunbar's specimens to their K. (M.) velata also. The later differed by having broader, more rounded costae and closer spaced lamellae. Dunbar (1919) reported this species to be a common Birdsong element.

Material- Two disarticulated specimens.

Order Terebratulida Waagen, 1883

Family Centronellidae Waagen, 1882

Genus Rensselaerina Dunbar, 1917

Rensselaerina medioplicata Dunbar, 1917

(Plate 5, Figure 7)

Rensselaerina medioplicata Dunbar. Dunbar, 1917c, p. 466-470, pl. 2, figs. 1-9; Dunbar, 1919, pl. 2, fig. 12; Tansey, 1922, p. 196-197, pl. 50, figs. 25-26.

Description- The genus is described as having a ". . . shell decidedly elongate oval, often nearly cylindrical,

but otherwise having the general form of the later Renssaelerinas, though always less broad-shouldered. Shell substance very finely punctate. Of the exterior surface, the posterior half and the lateral slopes of the shell are entirely smooth; but anteriorly the median portion of both valves bears a few simple, rounded, conspicuous plications which are separated by well-defined concave interspaces that are at least as wide as the plications themselves. There is no cardinal area and the cardinal and lateral slopes are rounded . . . . The minute beak of the dorsal valve is concealed by that of the ventral valve, which is strongly incurved and closely appressed; the pedicle foramen is minute and neither resorbed nor abraded through the umbo." (Dunbar, 1917c).

The species R. medioplicata is described as a . . . "shell with the characters of the genus; length of a mature individual 24 mm, width 14 mm, thickness 11 mm. Six to eight plications on the middle of the ventral valve and one more on the dorsal. About three of these plications in a width of 5 mm on the anterior margin. Hinge-plate extremely variable, being in some specimens excavate, in other raised into a median process." (Dunbar, 1917c).

Discussion- Dunbar (1919) found this species to be very common in the Birdsong. Amsden and Boucot (1958) noted that Dunbar's species is similar to R. haraganensis

from the Boid D'arc of Oklahoma; however, the basic differences between the two, as cited by Cloud (1949), were in the internal features, in particular, the loop structure. They concluded that the differences cited by Cloud were significant enough that the two species were justified and emphasized that the external similarities were not marked.

Material- Three articulated, but partially weathered, specimens.

Phylum Annelida Larmarck, 1809

Class Polychaeta Grube, 1850

Order Sedentaria Lamarck, 1818

Family Serpulidae Burmeister, 1837

Genus Spirorbis Daudin, 1800

Spirorbis laxus Hall, 1859

(Plate 6, Figure 5)

Spirorbis laxus Hall. Hall, 1959, p. 349, pl. 54, figs. 18a-c.

Description- Shell encrusting, circular to discoid in outline, small; dextrally spiraled with two to four whorls; umbilicus deep; aperture rounded with a flattened base

where encrusted onto substrate, slightly upturned at the end; surface ornamented with strong concentric ridges and finer striae between ridges.

Discussion- This species is very common. Often, only the encrusting base remains.

Material- Numerous specimens encrusting brachiopods.

Family Cornulitidae Fischer, 1962

Genus Cornulites Schlotheim, 1820

Cornulites sp.

(Not Figured)

Description- Large, up to 4.0 mm in length, sinuous conical shell marked by coarse, irregularly spaced annulations of variable width; annulations ornamented with thin parallel longitudinal striae; apex generally recurved.

Discussion- Dunbar (1919) listed two species of Cornulites (C. chrysalis and C. n. sp.) from the Birdsong failing to describe the new species. The species described above differs from C. chrysalis by not possessing regular cross-spaced annulations that appear as inverted truncate cones.

Material- Three specimens encrusting brachiopods.

Phylum Mollusca

Class Cricoconarida Fisher, 1962

Order Tentaculitida Lyashenko, 1955

Family Tentaculitidae Walcott, 1886

Genus Tentaculites Schlotheim, 1820

Tentaculites aculus Hall, 1858

(Plate 6, Figure 1)

Tentaculites aculus Hall. Hall, 1888, p. 6, pl. 114, figs. 15-17; Ohern and Maynard, 1913, p. 485, pl. 87, figs. 6-7.

Description- Uniformly tapering, straight, conical shell up to 15mm in length; ornamented with concentric transverse rings that increase in distance from each other and in prominance toward the aperture; shell surface between transverse rings with finer thread-like concentric striae which increase in number according to the width of the spacings occupied.

Discussion- This is the only species of Tentaculites reported from the Birdsong (Dunbar, 1919).

Material- Only one slab containing numerous alligned shells has been found from the upper portion of the Birdsong in the Bryozoan Zone. The shells are generally

well preserved except for some collapse in the more distal portions that give the shell the appearance of being ornamented by a bisected invagination that is oriented roughly parallel to the shell margins.

Class Gastropoda Cuvier, 1797

Order Archeogastropoda Thiele, 1925

Family Platyceratidae Hall, 1859

Genus Platyceras Conrad, 1840

Platyceras (Platyceras) multisinuatum Hall, 1861

(Plate 6, Figure 2a, b)

Platyceras multisinuatum Hall. Hall, 1861, p. 319-320, pl. 58, figs. 8a-c, 9a-b; Ohern and Maynard, 1913, p. 477, pl. 85, figs. 4-6.

Platyceras cf. multisinuatum Hall. Branson, 1922, p. 257-258, pl. 69, fig. 1.

Description- Discoidal evolute shell with three whorls; dorsal surface nearly flat; earlier whorls smooth, dorsal surface of last whorl marked by ridges and shallow depressions with growth lines becomming more prominant toward the aperture; lower surface of last whorl expanded to become slightly angular in outline.

Discussion- This is a difficult species to identify because most specimens are crushed or are only partially preserved; however, the ridges on the last whorl are distinctive. Dunbar (1919) listed this species as being rare.

Material- Eleven specimens were found and are generally preserved as dark gray shell material flattened and crushed in shale matrix.

Platyceras (Platyceras) tenuiliratum Hall, 1861

(Plate 6, Figure 3)

Platyceras tenuiliratum Hall. Hall, 1861, p. 317-318, pl. 58, figs. 1-5, pl. 59, fig. 6a,b; Ohern and Maynard, 1913, p. 476, pl. 85, figs. 1-2.

Description- Shell usually very small, evolute, subovoid in outline; dorsal surface flattened with two to three rounded whorls separated by deep sutures; last whorl expanding rapidly; apex only slightly raised; surface marked by very fine growth lines.

Discussion- Dunbar (1919) listed this species as rare. This species is similar to P. (P.) multisinuatum except for its smaller size, lack of plications, and more subdued

ornimentation.

Material- Nine complete specimens preserved as dark gray shell material flattened and crushed in shale matrix.

Platyceras (Orthonychia) spirale Hall, 1961

(Plate 6, Figure 4)

Platyceras spirale Hall. Hall, 1961, p. 331, pl. 63, figs. 4-9; Ohern and Maynard, 1913, p. 478, pl. 85, figs. 8-9.

Description- Very loosely coiled, high spiraled, conical shell; aperture rounded to oval; surface smooth except for faint growth lines.

Discussion- Hall (1858) described older specimens of P. spirale as having plications with undulating striae; however, this feature is poorly developed in the Birdsong specimens.

Material- Six specimens preserved as dark gray shell material in shale. Usually as poorly preserved fragments

or crushed specimens with apex and aperture broken and missing.

Class Bivalvia Linne, 1758

Order Pteroida Newell, 1965

Family Pteriidae Gray, 1847

Genus Actinopteria Hall, 1859

Actinopteria reticulata Weller, 1903

(Not Figured)

Actinopteria reticulata Weller. Weller, 1903, p. 245, pl. 22, fig. 3; Ohern and Maynard, 1913, p. 459, pl. 76, fig. 6.

Description- Large convex shell, greater than 5cm from umbo to broken anterior margin; surface ornamented with very conspicuous concentric growthlines becoming wider spaced anteriorly; surface also ornamented with coarse radiating costae that curve slightly as they approach the anterior margin.

Discussion- Although none of the diagnostic features to assign this specimen to any specific family or genus are present, the combination of the coarse concentric growthlines and the radiating costae give the shell surface a strong reticulate pattern. This pattern does not occur on any other species of fossil recorded for the Lower Devonian and can therefore be used to assign the specimens

described herein to the Actinopteria reticulata. Ohern and Maynard (1913) identified this same species from the Keyser Formation of Maryland using this same criterion.

Material- One partial left valve interior.

Phylum Echinodermata

Class Crinoidea Miller, 1821

Family Edriocrinidae Miller, 1821

Genus Edriocrinus Hall, 1858

Edriocrinus adnascans Dunbar, 1920

(Plate 5, Figure 10)

Edriocrinus adnascans Dunbar. Dunbar, 1920, p. 120-121, pl. 2, fig. 3.

Description- "Base flat and cemented to some foreign object, usually a brachiopod shell. The central portion is occupied by a broad and very shallow depression, bounded by a low rim, outside of which the surface is concave as it slopes away to the margin. The rim of the shallow basal cup is scalloped by six slight, concave depressions for the insertion of the five radials and the anal plate. . . . These scallops continue to the center of the visceral cup

as shallow, concave, radial depressions." (Dunbar, 1920).

Discussion- Edriocrinus adnascans is common in the Birdsong as epibionts on brachiopods and crinoid stems. Only the cemented bases are found.

Material- Two specimens attached to brachiopods form the basis for this identification. This species is generally preserved as dark gray shell material that is slightly worn.

Phylum Arthropoda Siebold and Stanius, 1845

Class Trilobita Walch, 1771

Order Phacopida Salter, 1864

Family Phacopidae Hawle and Corda, 1847

Genus Paciphacops (Paciphacops) Makismova, 1972

Paciphacops (Paciphacops) logani (Hall), 1859

(Not Figured)

Phacops logani (Hall). Hall, 1859, p. 353; Hall, 1861, pl. 23, figs. 15-25; Weller, 1903, p. 231, pl. 11, figs. 3-4; Ohern and Maynard, 1913, p. 497-498, pl. 91, figs. 1-4

Paciphacops (Paciphacops) logani (Hall). Campbell, 1977, p. 49, pl. 12, figs. 1-4, pl. 13, figs. 3-4.

Description- "General form elliptical. Head semielliptical in outline, broadly concave above, with the posterior angles curved and declining more abruptly. Glabella somewhat pentagonal; length and greatest breadth nearly in the proportion of three to four; very prominent in front, projecting behond the rudimentary frontal limb, which becomes more developed on each side, and below which is a defined groove, marking the limits of the lower side of the cephalic test. Upper surface convex, gibbous in front, having two pairs of transverse grooves, the middle and posterior ones of which are but faintly defined; while the third or anterior ones, extending from the inner angle of the eye backwards, and a little inwards, are scarcely conspicuous, and, on many specimens, not observable. First annular furrow strongly defined, and sometimes with a small turbercle at the summit: first or intercalated annulation narrow and well defined and terminated at each extremity by a strong oblong tubercle, which is wider than the annulations, and usually marked by two pustules at the summit one on each side of the center. Occipital furrow wider and more strongly defined than the intercalated one, slightly sinuous, and terminating in a deep cavity on each extremity; occipital annulation broad and strong, slightly sinuate at the extremities, and when entire, marked by one larger central pustule and several smaller ones.

Eyes of medium size, their summit less elevated than the glabella, extending backwards to the line of the occipital furrow, composed of seventeen vertical ranges of lenses. . . .

The axis of the thorax is prominent and narrower than each of the lateral lobes; the annulations furnished with a prominent node at each extremity. The lateral lobes are flat or somewhat concave towards the axis. . . . Pygidium semicircular; the axis prominent, with about nine annulations; the lateral lobes having about five or six ribs, each with a groove along the center. . . ." (Hall, 1859).

Discussion- Campbell (1977) thoroughly evaluated the Lower Devonian trilobites of Oklahoma and he recognized two forms of this species based upon the size of the eye lenses. The specimen described by Hall belongs to his small-eyed form because it contains only 16 files with no greater than seven lenses in the longest file. Campbell also recognized a second species, P. (P.) birdsongensis, from Dunbar's (1919) trilobite zone near Big Sandy Creek. The most distinguishing characteristic that separates the latter species is the presence of strong furrows in the posterior portion of the glabella.

Material- Two complete specimens.

Family Dalmanitidae Vogdes, 1890

Genus Dalmanites Barrande, 1852

Dalmanites retusus Dunbar, 1920

(Plate 6, Figure 7)

Dalmanites retusus Dunbar. Dunbar, 1920, p. 149, pl. 5, fig. 3.

Description- "Species known only from the pygidium, which is semi-elliptical in outline, broader than long, and evenly rounded behind without any spinose extension. Axis low, only slightly arched, rapidly tapering, marked by fourteen or fifteen annulations, the last of which are very indistinct as the axis becomes obsolete posteriorly. Pleura gently arched, marked by ten or eleven broad ribs separated by narrower grooves, all of which become obsolete before reaching the edge, leaving a smooth margin about 4 mm wide." (Dunbar, 1920).

Discussion- Campbell (1977) redefined the genus Dalmanites and created the new genus Huntonia with the subgenus (H.) (Huntonia). Although he assigned Dalmanites purduei Dunbar to this new genus, he did not include D. retusus. The distinguishing characteristic of Huntonia is the presence of a pygidial spine. The lack of this spine

and the smoothly elliptical outline of the pygidium distinguishes the Birdsong species.

Material- Ten pygidia.

Genus Huntonia Campbell, 1977

Huntonia (Huntonia) lindenensis (Delo), 1940

(Plate 6, Figure 6)

Odontochile lindenensis Delo. Delo, 1940, p. 57-58, pl. 4, fig. 26.

Huntonia (Huntonia) lindenensis (Delo). Campbell, 1977, p. 95-96 (in discussion under H. (H.) purduei purduei), pl. 29, figs. 4-5.

Description- Cephalon moderately convex, large measuring greater than 6.0 cm across posterior to glabella; outline semi-elliptical with genal spines extending 1.0 cm posteriorly; glabella large, smooth, slightly flattened and sloping anteriorly; first glabellar furrow deep extending three-fourths distance to the axis, succeding furrows extending closer to axis and more norrow; cheeks with arched slopes and occipital furrows bordering eyes; eyes large, elevated.

Discussion- This species was first described by Delo

(1940) based upon a single pygidium from the Birdsong near Pace, TN. No formal description for the cephalon exists. Campbell (1977), in his revision of the subfamily Dalmanitinae, erected the new genus and subgenus Huntonia (Huntonia) to which he assigned Odontochile lindenensis. Campbell did not include a systematic description of this species, but he did figure two chephala and also briefly discussed this species in his discussion of H (H.) purduei purduei. The former can be distinguished from the latter, which occurs in the Ross Formation, by its less convex ventral surface on the cephalon and very fine granulations between larger granulations of the cephalon. These details are not well developed on our specimen; however, the lack of shallow subcircular pits on the glabella and the very large eyes are sufficient to distinguish H. (H.) lindenensis from the other species.

Material- One complete cephalon.

Huntonia (Huntonia) sp.

(Plate 6, Figure 5)

Description- Only fragmentary pygidium known; subtriangular with smooth margin, convexity less than 8 mm, maximum width 3.0 cm, pygidium terminates in a slightly

upturned point with a rudimentary spine; twelve or more fused plurae occur in slightly arched plural lobe, plurae asymmetrically angular, sloping toward thorax and separated by deep furrows.

Discussion- The rudimentary upturned spine, smaller size, subtriangular outline, and asymmetrical angular plurae distinguish this species from Dalmanites retusus. The rudimentary spine places this species within the genus Huntonia and the twelve plurae are characteristic of the subgenus H. (Huntonia).

Material- Two pygidia.

Ichnogenus Irmena Boekschoten, 1970

Irmena sp.

(Plate 6, Figure 8)

Description- Small slit-like borings; up to 1.0 mm in length; forming a band or patch of randomly oriented excavations on shells.

Discussion- This species is common, especially on brachiopods. Boekschoten (1970) interpreted Irmena as the borings of ctenostome bryozoans.

Material- Four specimens in two rugosan corals and two Leptaena.

Ichnogenus Rhizocorallium Zenker, 1836

Rhizocorallium sp.

(Plate 6, Figure 10)

Description- Straight to slightly arcuate, indistinct, U-shaped tube with prominant spreite; oriented horizontal to bedding, tube diameter 2 mm; diameter between tubes 1.0-1.5 cm; maximum observed length 16 cm.

Discussion- The most distinctive feature of this trace is its spreite. The tubes are generally indistinct.

Material- One slab which contains mostly spreite without the U-shaped tube. Traces occur in gray shale laminae within wackestone-packstone from the lower part of the upper Birdsong.

Ichnogenus Helminthopsis Heer, 1877

?Helminthopsis sp.

(Plate 6, Figure 9)

Description- Simple, horizontal, meandering, smooth trails; diameter very regular, maximum width 1 mm; meanders with tight 180° turns to form loops.

Discussion- Trace appears as a slightly lighter colored discoloration on slab surface.

Material- One slab preserved as gray traces in hyporelief in yellow-brown silty mudstone.

Plate 1

SPONGES (1) AND CORALS (2-6)

1. Microspongia cf. spinifera (Duncan), 1879, x 1.0.

2. Pleurodictyum lenticulare (de Koninck), 1841, calical view, x 1.5

3. Streptelasma strictum Hall, 1874.
   a. Side view, x 1.5
   b. transverse section, x. 2.0

4. Favosites foerstei Dunbar, 1920.
   a. Aboral view of pseudoholotheca showing irregular concentric banding and successive ovelaps of younger bands, x 1.5.
   b. Oral view of weathered specimen showing corallites and tabulae, x 1.5.
   c. Transverse section, x 1.3.

5. Favosites conicus Hall, 1874.
   a. Transverse section, x 2.5.
   b. Aboral view of holotheca, x 2.5.
   c. Oral view showing polygonal corallites and epibiotic cystoporate bryozoan, x 2.0

6. Aulopora schohariae Hall, 1874, x 10.

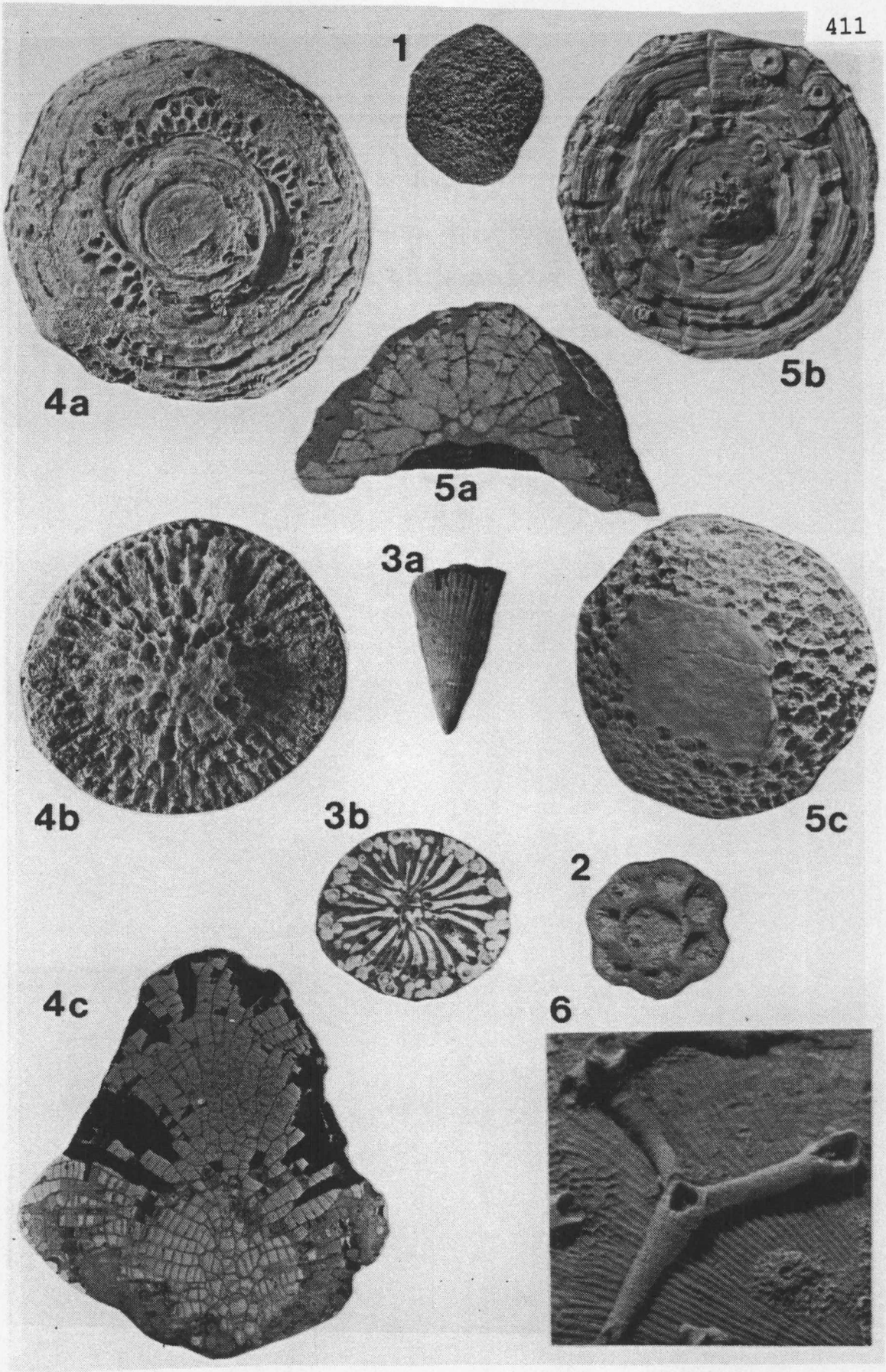

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5b
5a
3a
4b
5c
3b
2
4c
6

PLATE 2

BRYOZOANS

All are dominantly encrusting forms.

1. Ceramopora cf. parvicella Hall, 1857, x 20.
2. Fistulipora cf. unilinea Hall, 1857, x 18.
3. Eridopora sp., x 18.
4. Fistulipora sp. A, x 18.
5. Lichenalia cf. serialis Hall, 1879, x 12.
6. Monotrypa cf. tabulata (Hall), 1883, x 14.
7. Intrapora puteolata Hall, 1883, x 22.
8. Leptotrypa cf. spinifera (Duncan), 1939, x 18.

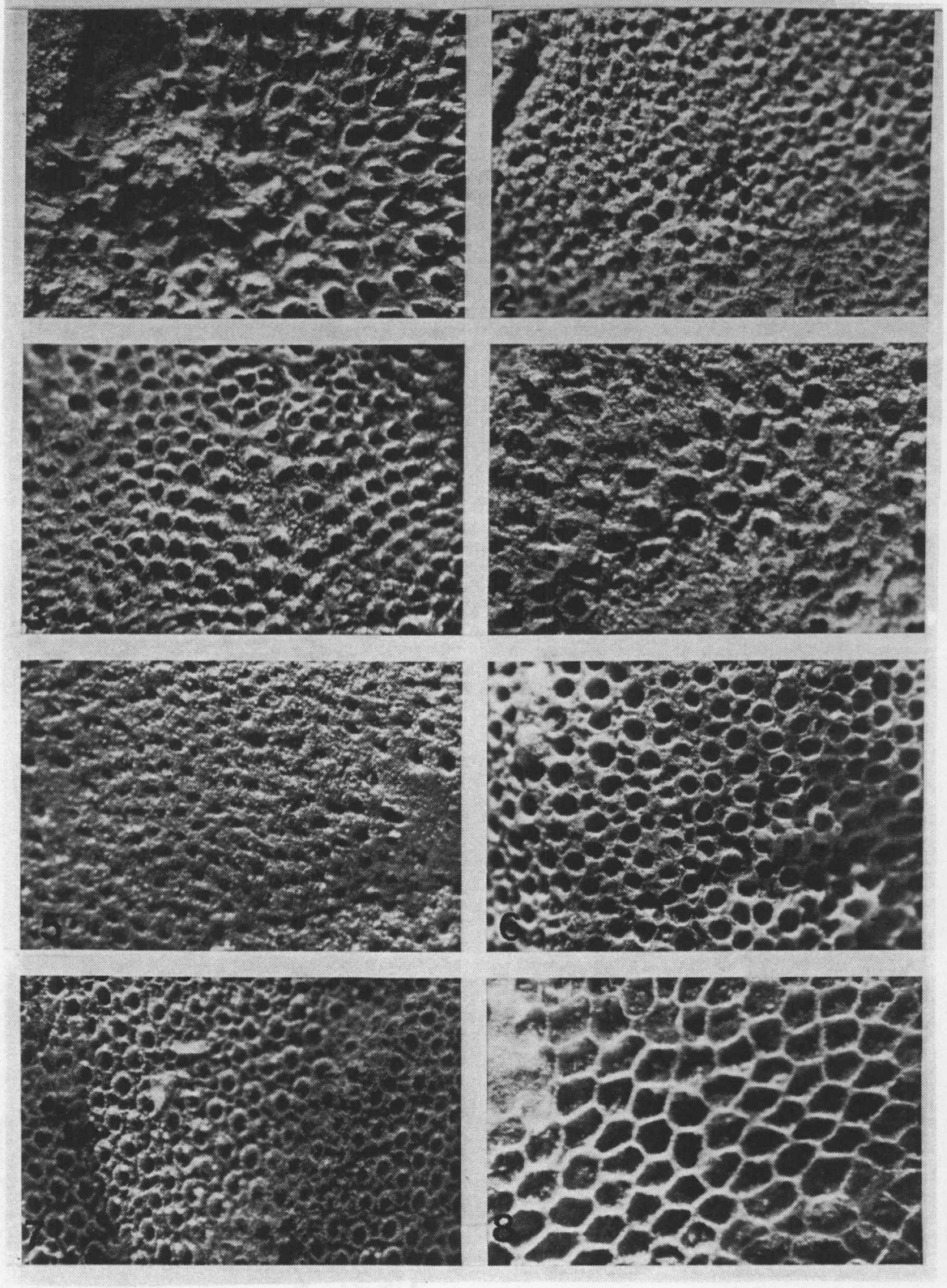


PLATE 3

BRYOZOANS (4-7) AND ORTHID (2-3) AND STROPHOMENID (1) BRACHIPODS

1. ?Orthostrophia strophomenoides (Hall), 1857, brachial exterior, x 1.5

2. Rhipidomelloides oblata (Hall), 1857.
   a. Pedicle exterior, x 1.5.
   b. Brachial interior, x 1.5.
   c. Pedicle interior, x 1.5.
   d. Brachial exterior, x 1.5.

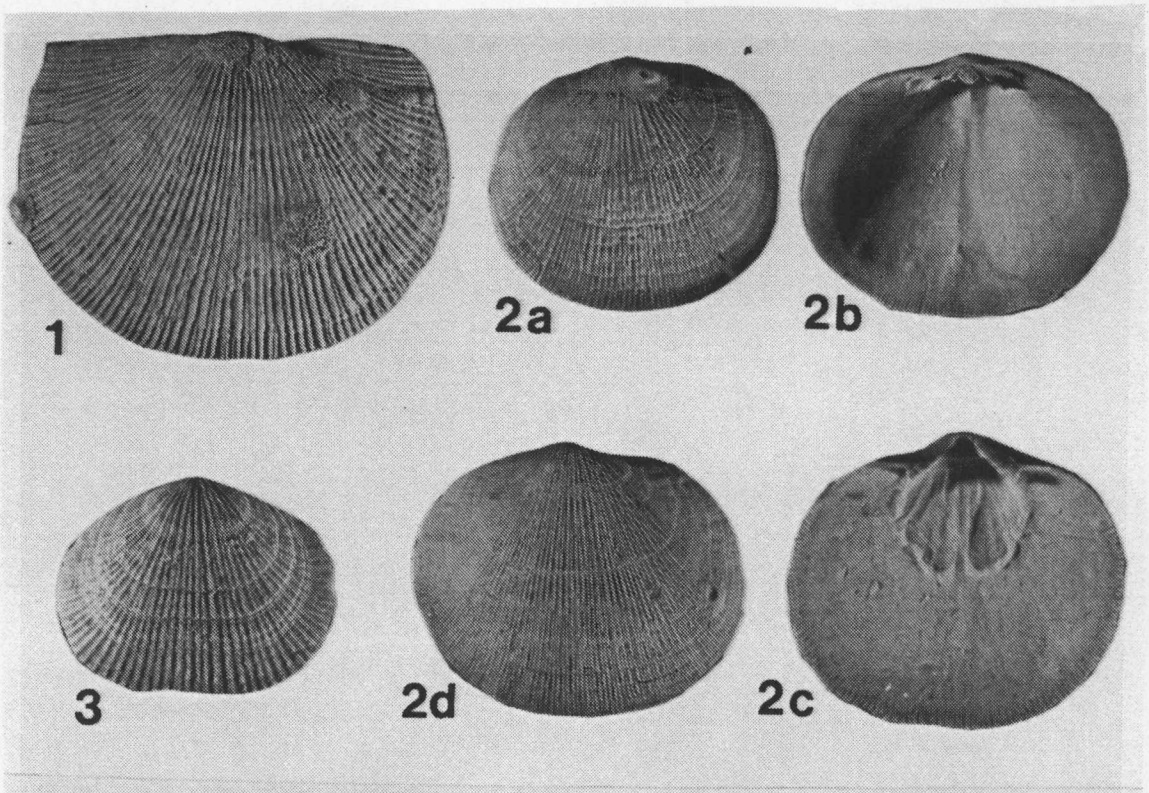
3. Rhipidomelloides emarginata (Hall), 1859, x 3.

4. Eliasopora stellaria Nicholson, 1877, x 15.

5. Hederella sp. on R. oblata, x 3.5.

6. Ptylodictya tenuis (Hall), 1874, x 22.

7. Fistulipora cf. maculosa (Hall), 1883, x 18.


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2c

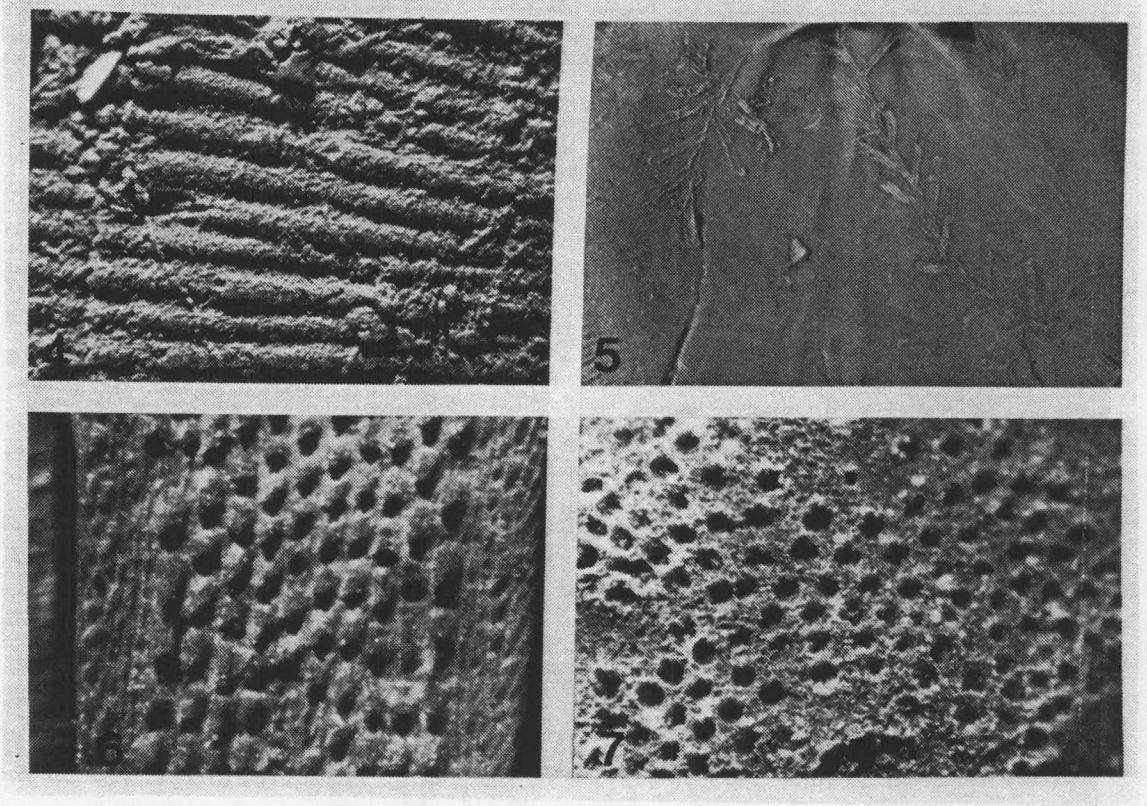

4
5
6
7

PLATE 4

ORTHID (1), STROPHOMENID (2-5), RHYNCHONELLID (6, 8, 9), AND PENTAMERID (7) BRACHIOPODS.

1. Dalmanella concinna (Hall), 1859, pedicle exterior, x 3.0.

2. Leptaena acuticuspidata Amsden, 1958.
   a. Brachial interior, x 1.5.
   b. Brachial exterior, x 1.5.
   c. Pedicle exterior, x 1.5.
   d. Pedicle interior, x 1.5.

3. Leptaena rhomboidalis, brachial exterior, x 1.5.

4. Strophonella punctulifera holladayi Dunbar, 1920, pedicle exterior, x 1.5.

5. Leptostrophia beckii (Hall), 1859.
   a. Brachial exterior, x 1.0.
   b. Pedicle exterior, x 1.0.

6. Sphaerirhynchia lindenensis (Dunbar), 1920.
   a. Brachial exterior, x 2.0.
   b. Pedicle exterior, x 2.0.

7. Gypidula multicostata Dunbar, 1920, pedicle exterior, x 2.0.

8. Trigonorhynchia acuticostella Amsden, 1958, pedicle exterior, x 2.0.

9. Camarotoechia transversa (Hall), 1859, pedicle exterior, x 3.

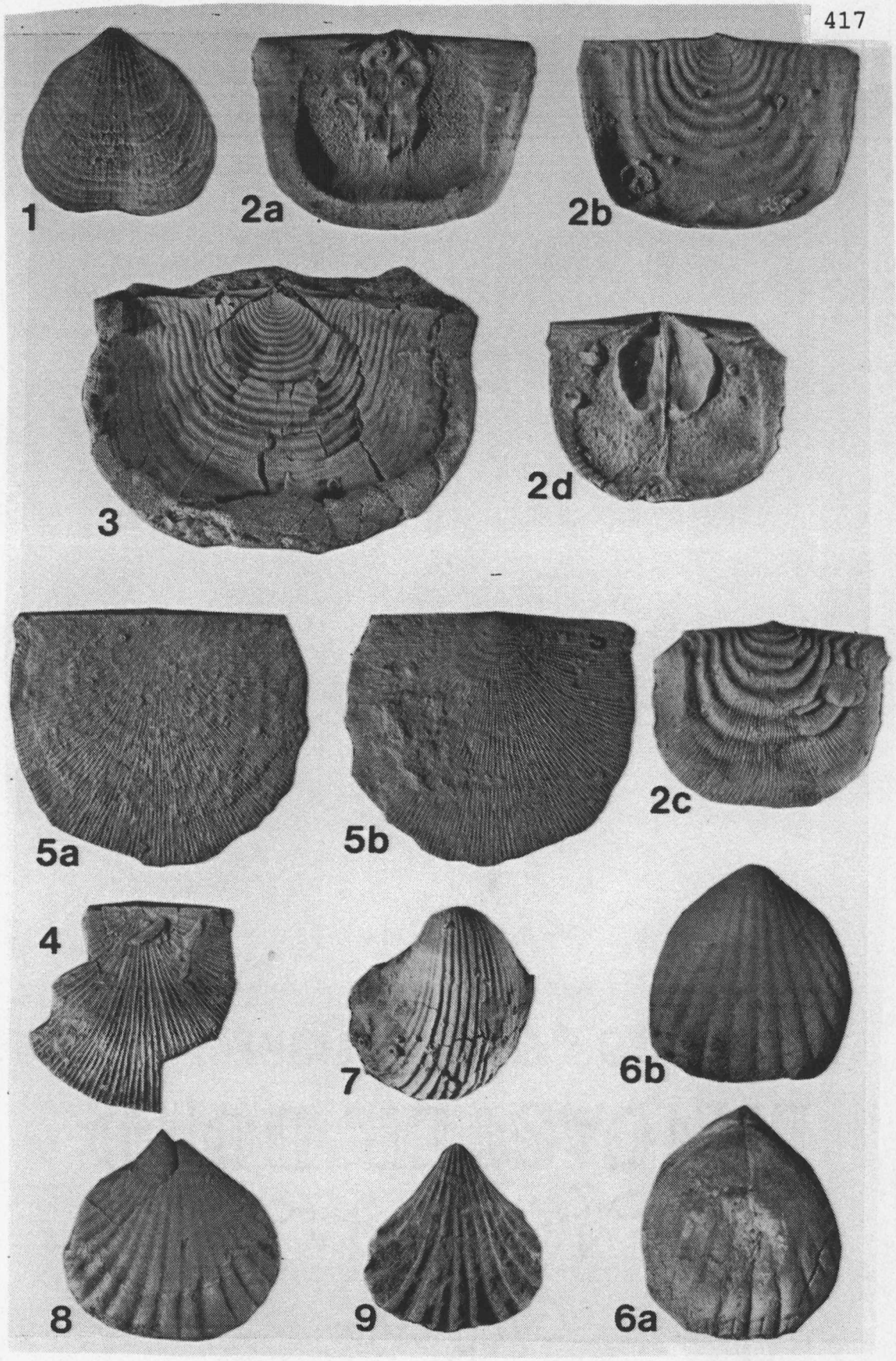

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2c
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7
6b
8
9
6a

PLATE 5

SPIRIFERIDA (1, 6, 8, 9), ATRYPID (2, 3), RHYNCHONELLID (4, 5), AND TEREBRATULID (7) BRACHIOPODS, CRINOIDS (10).

1. Trematospira costata angusta, Dunbar, 1920, brachial exterior, x 3.0.

2. Atrypina imbricata (Hall), 1857, pedicle exterior, x 3.

3. Atrypa reticularis (Linne), 1758.
   a. Brachial interior, x 1.8.
   b. Brachial exterior, x 1.8.
   c. Pedicle exterior, x 1.8.
   d. Pedicle interior, x 1.8.

4. Rynchospirina formosa (Hall), 1859, brachial exterior, x 3.0.

5. Rynchospirina globosa (Hall), 1857.
   a. Brachial exterior, x 2.0.
   b. Pedicle exterior, x 2.0.

6. Meristella atoka Girty, 1899.
   a. Brachial exterior, x 1.5.
   b. Pedicle exterior, x 1.5.

7. Rensselaerina medioplicata Dunbar, 1917, pedicle exterior, x 1.5.

8. Macropleura macropleura (Conrad), 1840, pedicle exterior, x 1.0.

9. Kozlowskiellina (Megakozlowskiellina) parmellosa (Hall), 1857.
   a. Pedicle exterior, x 1.5.
   b. Brachial exterior, x 1.5.

10. Edriocrinus adnascans Dunbar, 1920, base encrusting brachiopod, x 2.0.

11. Kozlowskiellina (Megakozlowskiellina) octacostata tennesseensis Dunbar, 1920, pedicle exterior, x 1.8.

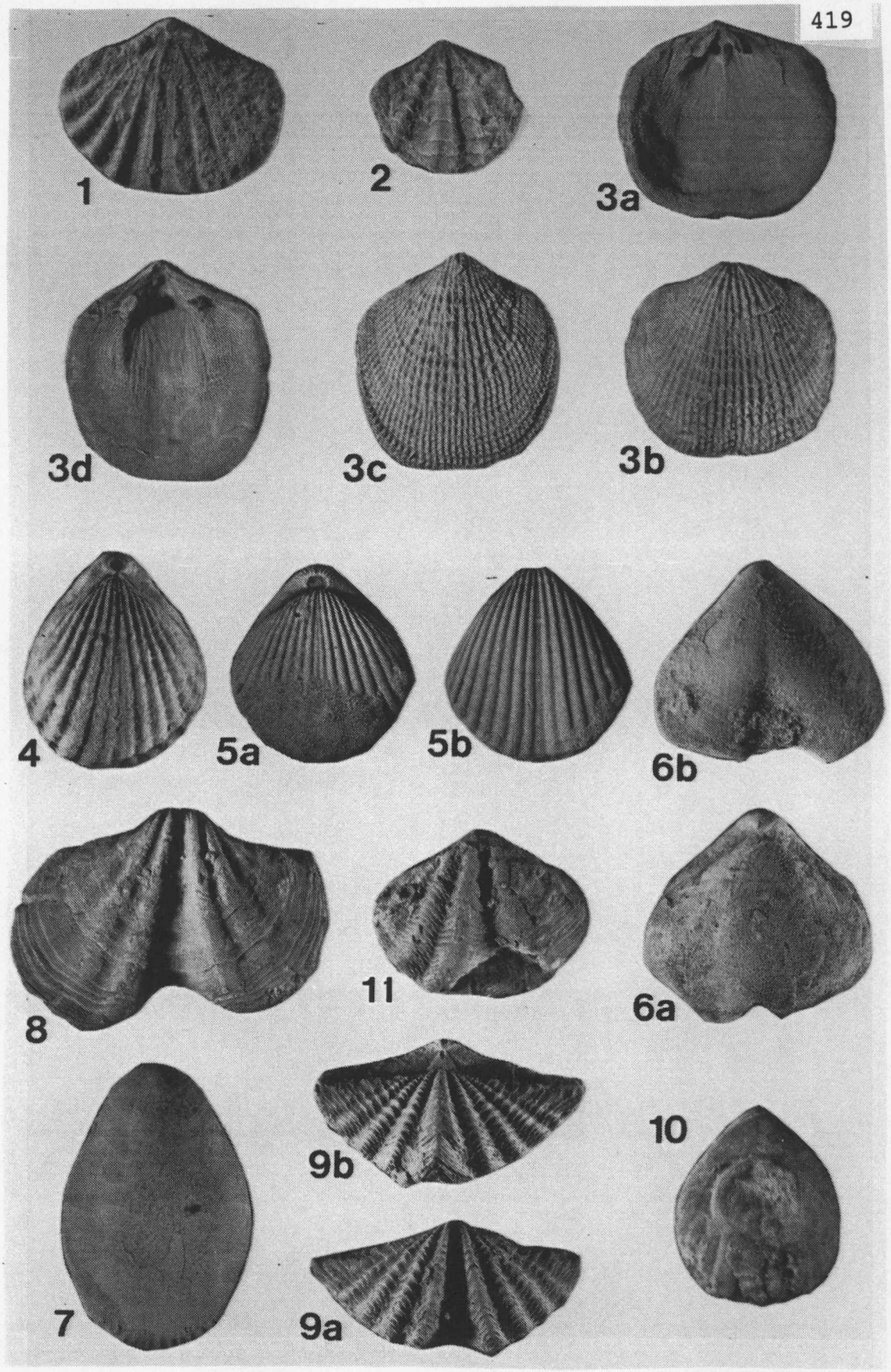

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6b
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9a

PLATE 6

SPIRIFERID BRACHIOPODS (1, 2), GASTROPODS (3, 6, 7), CRICOCONARIDS (4), ANNELIDS (5), CRINOIDS (8), AND TRILOBITES (9-11).

1. Tentaculites aculus Hall, 1858, SEM photo, x 35.0.

2. Platyceras (Platyceras) multisinuatum Hall, 1861.
   a. Apertural view, x 1.25.
   b. Apical view, x 1.25.

3. Platyceras (Platyceras) Tenuiliratum Hall, 1861.
   a. Side view, x 1.5.
   b. Apical view, x 1.5.

4. Platyceras (Orthonychia) spirale Hall, 1861, fragment missing apex and aperture, x 1.5.

5. Huntonia (Huntonia) sp., x 1.3.

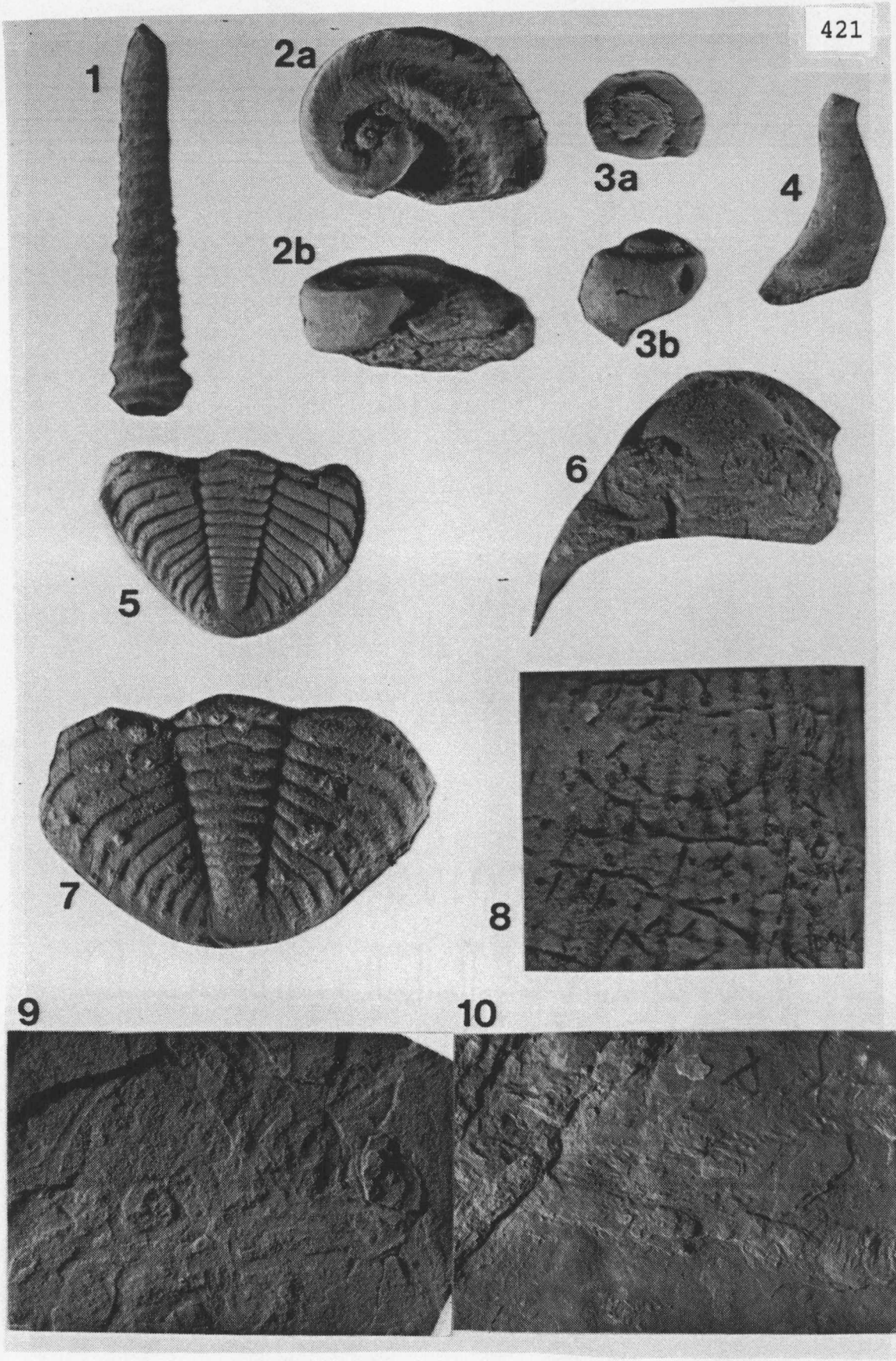
6. Huntonia (Huntonia) lindenensis (Delo), 1940, cephalon, x 1.0.

7. Dalmanites retusus Dunbar, 1920, pygidium, x 1.5.

8. Irmena sp., x 38.

9. Rhizocorallum sp., x 1.0.

10. ?Helminthopsis sp., x 1.5.


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2a
2b
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3b
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VITA

Michael A. Gibson was born on June 14, 1957 in Williamsburg, Virginia. After graduating from Lafayette High School in 1975, he attended the College of William and Mary, where in 1979, he graduated with a Bachelor of Science degree in geology. Michael began working toward his Master of Science degree in geology at Auburn University in 1981. While at Auburn, he was employed as a graduate teaching assistant in the Department of Geology and as a subcontracted exploration geologist for Callahan Mining Corporation (1981-1984). Soon after completing his M.S. degree, in 1983, Michael married Edie A. Bolton of Thoedore, Alabama. He was then employed by the Department of Geology at Auburn as an Instructor during the 1983-1984 academic year. In the fall of 1984, he accepted a graduate teaching assistantship in the Department of Geological Sciences at The University of Tennessee at Knoxville to work on his Doctor of Philosophy degree in geology. Michael served as secretary and graduate council representative for the Gamma Gamma Chapter of Sigma Gamma Epsilon and guest editor for the Gamma Gamma issue of The Compass. In addition, he was editorial associate for the UTK Department of Geological Sciences Short Course Note series. In 1987, Michael received the Chancellor's Citation for Extraordinary Professional Promise.

completing his Doctor of Philosophy degree in August of 1988, Michael was hired by The University of Tennessee at Martin as Assistant Professor of Geology.