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The application of filtration theory to the paleoecology of Crinoids from the Lansing Group (Missourian, upper Pennsylvanian), midcontinent North America

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University of Cincinnati, 1993

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THE APPLICATION OF FILTRATION THEORY TO THE PALEOECOLOGY OF CRINOIDS FROM THE LANSING GROUP (MISSOURIAN, UPPER PENNSYLVANIAN), MIDCONTINENT NORTH AMERICA

A Dissertation submitted to the

Division of Research and Advanced Studies
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requirements for the degree of

DOCTOR OF PHILOSOPHY

in the Department of Geology
of the College of Arts and Sciences

1993

by

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UNIVERSITY OF CINCINNATI

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I, Peter F. Holterhoff ,
hereby submit this as part of the requirements for the degree of:

Doctor of Philosophy

in Geology Department

It is entitled The Application of Filtration
Theory to the Paleoecology of Crinoids from
the Lansing Group (Upper Pennsylvanian),
Midcontinent, North America.

Approved by:

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THE APPLICATION OF FILTRATION THEORY TO THE PALEOECOLOGY OF CRINOIDS FROM THE LANSING GROUP (MISSOURIAN, UPPER PENNSYLVANIAN), MIDCONTINENT NORTH AMERICA.

Peter F. Holterhoff

Abstract - Filtration theory was developed by engineers to model the removal of particulate matter from industrial gases. Recently, it has been used by biologists and paleo-biologists to model the capture of food particles by filter feeding organisms. The purpose of this study was to test paleosynecologic (biofacies - level) and paleoautecologic (species - level) models of crinoid distribution utilizing filtration theory. These models were tested by analyzing the crinoid faunas of three transgressive - regressive sequences from the Upper Pennsylvanian Lansing Group of midcontinent North America.

The results of this study confirm general patterns of crinoid distribution noted for modern and Mississippian crinoids: dense mesh filtration fan crinoids are most abundant in higher energy, nearshore facies while open mesh filtration fan crinoids are most abundant in low energy, offshore facies. Crinoid taxa within these functional groups, or guilds, are structured into five recurrent biofacies that are arrayed along the onshore - offshore depth gradient. These are, moving offshore: 1) the Dense Fan Crinoid Biofacies; 2) the High Guild Diversity Crinoid Biofacies; 3) the Open Fan Crinoid Biofacies; 4) the Small, Pinnulate Crinoid Biofacies; 5) Dysaerobic Mature Molluscan Biofacies. While multivariate techniques consistently identify these biofacies, it is also clear that these biofacies grade into one another. Review of the position of these biofacies within the three cyclothems also reveals that these biofacies are not symmetrically disposed about the maximum flooding horizon. Thus, although crinoids consistently recur in the same environments from cycle to cycle, the intergradation and asymmetry of biofacies within cycles indicate that these organisms are not organized into interlocked communities which track rise and fall of sea - level. Instead, they appear to migrate in accord with their own ecological requirements and form recurrent biofacies as environmental conditions dictate.

Examination of nearshore and offshore populations of the dense fan crinoid *Delocrinus subhemisphericus* demonstrates that growth rates decrease, juvenile mortality rates increase, and adults are stunted offshore compared to nearshore. This reduction in fitness offshore is consistent with filtration theory which predicts that feeding efficiency decreases offshore for this species. The response of this species provides a model for interpreting the integration of many species into the observed onshore - offshore biofacies pattern.

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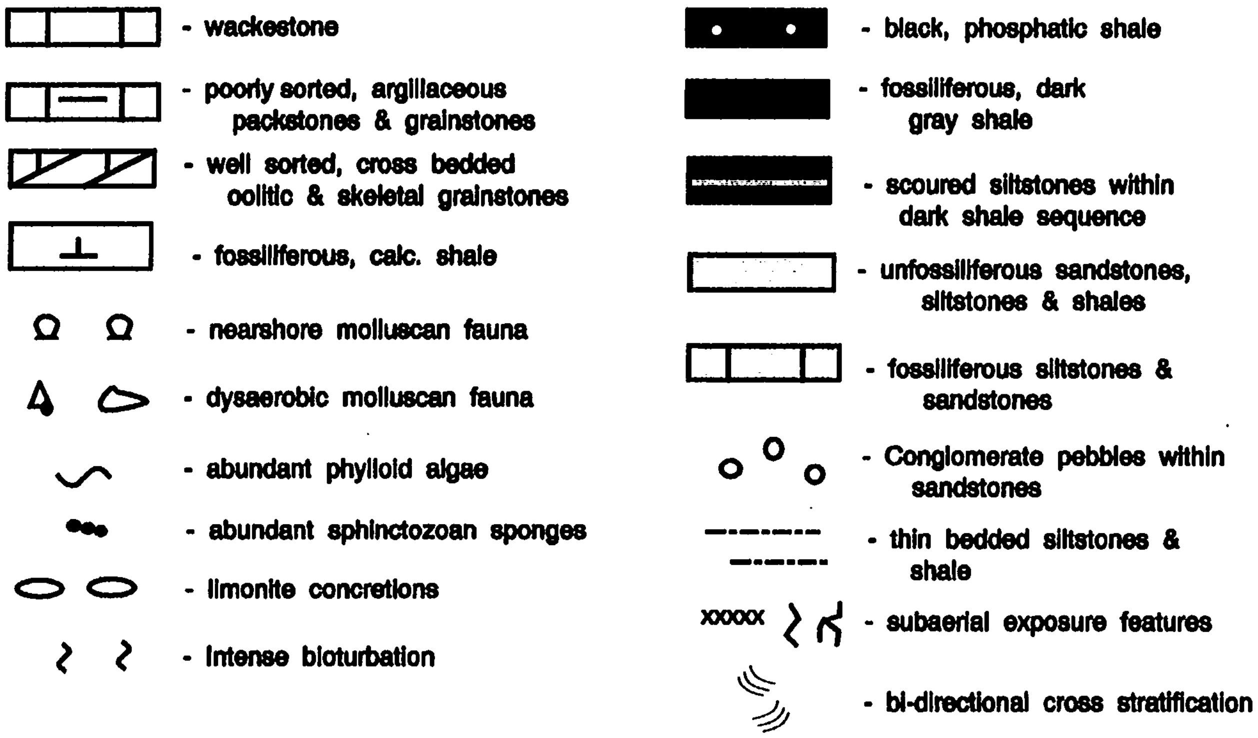


- wackestone
- poorly sorted, argillaceous packstones & grainstones
- well sorted, cross bedded oolitic & skeletal grainstones
- fossiliferous, calc. shale
- nearshore molluscan fauna
- dysaerobic molluscan fauna
- abundant phylloid algae
- abundant sphinctozoan sponges
- limonite concretions
- intense bioturbation
- black, phosphatic shale
- fossiliferous, dark gray shale
- scoured siltstones within dark shale sequence
- unfossiliferous sandstones, siltstones & shales
- fossiliferous siltstones & sandstones
- Conglomerate pebbles within sandstones
- thin bedded siltstones & shale
- subaerial exposure features
- bi-directional cross stratification

RST - Regressive Systems Tract

HST - Highstand Systems Tract

MFH - Maximum Flooding Horizon

lTST - late Transgressive Systems Tract

eTST - early Transgressive Systems Tract

CHAPTER 1

INTRODUCTION

Filtration theory was developed by engineers to model the removal of particulate matter from industrial gases. Recently, it has been used by biologists and paleobiologists to model the capture of food particles by filter feeding organisms. The purpose of this study was to analyze crinoid distribution and stress response patterns utilizing filtration theory. This analysis was performed on the crinoid faunas of three transgressive - regressive sequences from the Upper Pennsylvanian Lansing Group of midcontinent North America. These cycles not only provide a myriad of facies to examine the paleoecology of crinoids, but also provide recurrent sequences of facies by which to study the persistence of these patterns.

The proximate goals of this study are: 1) to document the distribution of crinoid morphotypes within the transgressive - regressive facies mosaic of the Upper Pennsylvanian Stanton Formation and to define biofacies based on the diagnostic co-occurrence of taxa, 2) to assess the persistence of these biofacies by examining distributional patterns in the three cycles of the Lansing Group and 3) to determine environmental stress gradients and document ecophenotypic differentiation in *Delocrinus subhemisphericus*. The ultimate goal is to assess whether there is a monotonic relationship between crinoid filtration fan morphology and depth-controlled energy gradients. If there is a strong connection between crinoid morphology, ecology, and environmental energy regimes, then it is highly likely that this relationship structures crinoid biofacies and influences phenotypic divergence within species. Put in more general terms, the question is: *how was the evolutionary ecology of crinoids controlled by Late Paleozoic sea - level change?*

CHAPTER 2

STRATIGRAPHY AND DEPOSITIONAL SYSTEMS OF THE LANSING GROUP (MISSOURIAN, UPPER PENNSYLVANIAN), MIDCONTINENT NORTH AMERICA: FRAMEWORK FOR THE ANALYSIS OF CRINOID PALEOECOLOGY.

Introduction

Moore (1964) noted that the Pennsylvanian and Permian of the midcontinent are ideally suited to paleoecological analysis because a wide range of marine environments are developed within a single cyclothem. Additionally, the systematic repetition of facies resulting in stacked cyclothems presents an excellent opportunity to study the response of organisms to fluctuations in sea - level.

The focus of this study is to investigate how crinoids responded to this cyclical change in sea - level. The Missourian Lansing Group of the midcontinent was selected because crinoids are abundant from a wide array of facies. However, before a paleoecological analysis can be undertaken, the processes controlling this cyclicity need to be established. A detailed stratigraphic and depositional framework can then be constructed and the environmental relationships of the crinoid - bearing localities determined.

Late Paleozoic Cyclicity and Cyclothems

The upper Paleozoic of midcontinent North America has long been recognized for its cyclicity (Weller, 1930; Wanless and Weller, 1932). Although individual cycles of diverse litho- and biofacies, or cyclothems, were identified as genetically related sequences, depositional interpretations and sea - level histories remained controversial (see Heckel, 1979). It has now become clear that a simple "Kansas - type" cyclothem represents a single, extensive marine transgression (with maximum inundation represented by the "core", or middle, shale member) and regression (with maximum regression represented by regional paleosols and incised shelf edge fan systems)(Fig. 2.1; Heckel, 1977; Boardman et al., 1984; Watney et al., 1989a; Brown et al., 1990). The Upper Pennsylvanian Missourian Stage of the midcontinent is composed of numerous cyclothems stacked in succession and represents repeated cycles of transgression and regression (Heckel, 1986).

Wanless and Shepard (1936) recognized that Upper Paleozoic strata across the globe are cyclic and proposed that glacio-eustatic transgression and regression were responsible for their formation. There is indeed abundant evidence that Gondwanan glaciation reached a maximum during the Mid to

Late Carboniferous and Early Permian, coincident with pronounced cyclic sedimentation in Euramerica (Crowell, 1978; Powell and Veevers, 1987; Veevers and Powell, 1987; Visser, 1990). However, they did not demonstrate the interbasinal synchroneity of individual cycles necessary to substantiate a global eustatic mechanism (Galloway, 1989).

Recent detailed paleontological analyses have demonstrated that individual cyclothems are biostratigraphically unique (Boardman and Barrick, 1989). This has facilitated cyclothem mapping across profound facies transitions along the midcontinent outcrop belt and, more significantly, has provided a framework for detailed correlations between basins. Boardman and Heckel (1989) provide biostratigraphic diagnoses of cyclothems from the midcontinent and north - central Texas and demonstrated the close match of facies development and extent of inundation for cycles between the two basins. Connolly and Stanton (1992) also provide cycle for cycle correlations between southeastern Arizona and the midcontinent. Additional preliminary studies involving these regions and the Illinois Basin (Heckel and Weibel, 1991) and the Appalachian Basin (Anderson and Boardman, 1989) also show a strong correlation between major upper Middle and Upper Pennsylvanian cyclothems.

The abundance of Late Paleozoic glacial deposits on Gondwana, the interbasinal correlation of individual cyclothems, and the tracing of individual cyclothems across diverse tectono - stratigraphic regions (stable craton to foreland basin) clearly demonstrate the glacio - eustatic origin for these cycles. Other proposed mechanisms of cyclothem formation cannot encompass all of these observed phenomena. Autogenic processes such as delta switching (Ferm, 1970; Brown et al., 1973) cannot explain regional subaerial exposure of platform carbonates, shelf edge incision and basinal delta building (Brown, 1982; Brown et al., 1990); however delta progradation can be a significant depositional process during sea - level highstand and fall. Tectonic effects have recently been proposed as a controlling mechanism in tectonically active regions (Klein and Willard, 1989). Bennison (1984, 1985) has shown that although the depositional and stratigraphic motif of individual cycles change across tectonically stable to unstable regions, the cycles themselves are intact and correlatable. Additionally, it has not been demonstrated in Upper Pennsylvanian deposits associated with tectonically active regions, such as north-central Texas and the Arkoma Basin, that local, major cyclothems are intercalated between interbasinally extensive cyclothems. Thus, tectonics control the overall depositional milieu by dictating subsidence and sedimentation rates but are not driving the cycles themselves.

An additional factor which needs to be addressed is the periodicity of these cycles. Pleistocene glacial cycles are apparently driven by changes in northern mid-latitude summer insolation (Denton and Hughes, 1983). Waxing and waning of northern continental glaciers in turn affects sea level, which can have a major impact on marine ice sheet behavior, which can amplify sea - level changes (Denton and Hughes, 1983; Anderson and Thomas, 1991). This linkage and feedback system is ultimately controlled by Milankovitch orbital parameters, which control solar insolation (Denton and Hughes, 1983; Imbrie, 1985). These orbital parameters are precession of the orbital axis, which cycles approximately every 20,000 years, axial tilt, or obliquity, which cycles approximately every 40,000 years, and orbital eccentricity with a 100,000 year period (Imbrie, 1985). A secondary, or long, eccentricity cycle has also been identified with a periodicity of approximately 400,000 years (Briskin and Harrell, 1980; Imbrie, 1985).

By dividing the number of Late Pennsylvanian cycles by the interval duration, Heckel (1986) arrived at an average periodicity for cyclothems at approximately 400,000 years, corresponding to the Milankovitch secondary eccentricity cycle. Although some have questioned this methodology (Klein, 1990), it is clear that by virtually any method and using any reasonable assumptions, Late Pennsylvanian cyclothem periodicities fall within Milankovitch band durations (Heckel, 1991a; Connolly and Stanton, 1992).

Although smaller, flooding surface - bounded packages can sometimes be identified within these cyclothems (Busch et al., 1985; Busch and West, 1987), and attempts have been made to cluster midcontinent cyclothems into larger packages (van Veen and Simonsen, 1991), the Kansas - type cyclothem is the most prominent organizational unit of Upper Pennsylvanian sedimentation in the midcontinent. These cyclothems can readily be recast within a sequence stratigraphic framework (Watney et al., 1989a) and although stratigraphic sequences have classically encompassed intervals of one to two million years, higher frequency sequences can have durations of approximately 500,000 years, accommodating Late Paleozoic cyclothems (Mitchum and Van Wagoner, 1991).

One final note concerns potential magnitudes of eustatic sea - level change. While sea-level changes may have been as great as 200 m (Heckel, 1977), recent estimates using isotopic analyses (Adlis et al., 1988) and climate/ice volume models (Crowley and Baum, 1991) hover between >70 m and 60±15 m, respectively. These are certainly large magnitude fluctuations on par with Pleistocene sea - level variations (Imbrie, 1985; Carter et al., 1986).

Thus, midcontinent Upper Pennsylvanian cyclothems are stratigraphic sequences recording high amplitude, high frequency changes in sea level driven by glacio-eustacy. The three cyclothems of the Lansing Group are no exception and these units form the basis of this investigation.

Vertical Sequences and Depositional Models

The Lansing Group in its type area of northeastern Kansas and northward into Nebraska consists of five named formations (Fig. 2.2). The Lansing Group is bounded by the Bonner Springs Shale Formation below and the Weston Shale Member, Stranger Formation above. The three limestone formations (Plattsburg, Stanton, South Bend) are each composed of three members which correspond to the lower transgressive limestone, middle "core" shale, and upper regressive limestone of the model cyclothem (Figs. 2.1, 2.2). The nearshore shale units of the model cyclothem correspond to the shale formations (Bonner Springs, Vilas, Rock Lake, Weston [Member])(Figs. 2.1, 2.2). An examination of the vertical sequence through the Lansing Group in northeastern Kansas provides a starting point for discussion of the depositional systems producing cyclothems (Fig. 2.3).

Initial Flooding - eTST. The transition from non-marine to marine deposition often occurs within the nearshore shale formations and represent the early components of the transgressive systems tracts (Fig. 2.3). These include fossiliferous clastics between underlying subaerial facies and overlying transgressive carbonates (Bonner Springs - Merriam transition, Enos and Herman, 1989; Rock Lake - Little Kaw transition, Joeckel, 1989), silty shale facies overlying subaerially exposed carbonates (Stoner - Rock Lake transition north of Kansas City), and sand-rich sequences dominated by physical sedimentary structures overlain by silty, bioturbated, fossiliferous shales (mid Vilas transition). Many of these early transgressive deposits may be filling depressions on the underlying units (Bonner Springs channel, Enos and Herman, 1989).

Facies transitions which involve a switch from non-fossiliferous to fossiliferous clastics may indeed involve autogenic processes of shifting depocenters and subsequent biotic colonization. However, the transition from subaerial to subaqueous facies clearly indicates an increase in accommodation space heralding the oncoming eustatic transgression.

Flooding Carbonates - ITST. The initial flooding deposits are highly variable spatially and may not be developed to any significant thickness. The transgressive limestones are, by contrast, extremely aerially extensive and represent the main proportion of the transgressive systems tract (Fig. 2.3). Even in areas of high clastic input, rising sea level drowns source areas and permits the development of carbonate depositional systems. These carbonates can range from condensed skeletal grainstones to expanded mud-rich wackestones.

In northeastern Kansas, these units can have high energy and/or coated grain facies developed at their base, but all of these units are characterized by dense, darker gray, skeletal wackestones, particularly towards their top. This transition clearly indicates a shift from nearshore to offshore carbonate deposition (Heckel, 1977). These flooding carbonates are also consistently thin units, ranging from a few centimeters to a few meters thick (Watney et al., 1989).

Quaternary sea level histories provide some views into the mechanisms producing these thin, extensive, and often abrupt facies sequences. Foraminiferal oxygen isotope records reveal that major glacial intervals are terminated by very rapid ice sheet decay and replenishment of light oxygen into the marine system (Broecker and Denton, 1989). These rates range from 2.5 to 10 m/1,000 years (Watney et al., 1989b) while short term rates may have been as high as 3 to 5 cm/year (Anderson and Thomas, 1991). By way of comparison, ice build up is stepped and much slower, and corresponding sea - level fall generally less than 1 m/1,000 years (Broecker and Denton, 1989; Watney et al., 1989b). These rapid rates of flooding not only narrow the temporal window during which depth - and strand line - related facies can equilibrate, but may also produce conditions retarding carbonate sedimentation.

While rising sea - level reduces clastic sedimentation, it also floods extensive land areas (Heckel, 1980). Additionally, flooding continental interiors can have a potentially profound influence on precipitation rates in the surrounding hinterlands. Flooding can therefore dramatically raise the level of terrestrial nutrient input into the marine setting (Neumann and McIntyre, 1985; Hallock and Schlanger, 1986). Increased nutrient supply can cause more frequent and intense phytoplankton productivity, which in turn can reduce the effective depth of the photic zone (Hallock and Schlanger, 1986). Because most organisms producing appreciable carbonate sediment are photosynthetic, reducing the photic zone can inhibit carbonate sedimentation; Watney et al. (1989b) state that accumulation rates for Quaternary sea - level rises are about an order of magnitude less than for stable conditions.

Thus, transgressive systems are generally thin due to decreased rates of both carbonate and clastic sedimentation, widespread due to pervasive depositional system disequilibrium, and are destined to become drowned because of ever increasing water column depth and inhibited aggradation ability.

Core Shale - MFH/HST. The core shales of these Missourian cyclothems represent the maximum flooding horizon and early highstand of the cycle (Fig. 2.3). Core shales, like flooding carbonates, are aerially extensive and represent deposition during the final rapid phases of transgression when sedimentation rates were outstripped by sea - level rise. Ultimately the bottom passed through the photic zone into water deep enough to preclude any carbonate sedimentation (Heckel, 1977). However, core shales have been variously interpreted and these differences have fundamental implications for cyclothem models. In particular, black core shales have been the focus of much controversy (Heckel, 1977, 1979) and the recent realization that there are different types of black shales associated with Middle and Late Pennsylvanian cyclothems has helped to clarify some of the confusion (Heckel and Swade, 1977; Coveney et al., 1991; Schultz and Coveney, 1992).

Midcontinent Missourian black shales are fissile, have virtually no benthic fauna, contain appreciable amounts of phosphate (Kidder, 1985; Schultz and Coveney, 1992), and contain an abundant and diverse pelagic fauna of fish debris (Watney et al., 1989a), conodonts (Heckel, 1977), and radiolarians (Nodine-Zeller et al., 1979). These shales also contain appreciable amounts of uranium (Watney, 1984) and have uniformly light sulfur isotope ratios (Coveney and Schaffer, 1988; Schultz and Coveney, 1992). These are all characteristics of sediment - starved, low oxygen, deep marine sedimentation.

The black shale facies often grades laterally into gray shales coincident with either structurally or sedimentologically controlled features elevating these localities above the coeval black shale facies (Heckel, 1978; Watney, 1985).

These thin, starved gray shales still contain a diverse pelagic microfauna and significant phosphate concentrations as well as developing an epifaunal benthic fauna (Heckel, 1978).

Virtually all models now used to explain these black shales evoke some kind of water mass stratification to isolate bottom waters producing anoxia (Heckel, 1977, 1991b; Boardman et al., 1984; Watney, 1985). As mentioned earlier, rising sea level flooded the continental interior, potentially increasing hinterland precipitation rates. Transgression also brought cooler basinal waters onto the shelf. This combination may have allowed development of a pycnocline separating cooler, more saline bottom waters from warmer, fresher surface waters (Heckel, 1991b). This boundary was penetrated by topographic features which, although sediment starved, were not anoxic. Two features of these black shales may indicate seasonality or periodic breakdown of the pycnocline: 1) Bedding planes within the black shales are sometimes bioturbated (Watney et al., 1989b) and 2) DOP values for these shales are not diagnostic of anoxia (Schultz and Coveney, 1992). Periodic incursions of oxygenated waters may have allowed bottom colonization of the black muds by opportunistic infauna and concomitant oxidation of sulfides within the muds. In any event, black shales associated with these cyclothems represent very hostile, sediment - starved, offshore conditions.

In the study interval, the Eudora Shale Member of the Stanton Formation is the only core shale that develops a black facies. The Hickory Creek Shale Member of the Plattsburg Formation locally develops a very dark gray facies where it fills topographic lows. However it, along with the Gretna Shale Member of the South Bend Formation, are generally medium gray, fossiliferous shales.

Gray core shales are similar to the lateral and vertical gray shale facies of black core shales. While phosphate is variably developed, all contain the diagnostic diverse and abundant pelagic fauna (Heckel and Baesemann, 1975). A high diversity benthic epifauna is sometimes associated with these shales, although in topographic lows and regions of high terrigenous input, a distinctive molluscan fauna is associated with gray core shales (Boardman et al, 1984). The position of this fauna within the cyclothem between normal, epifaunal benthos and its close proximity to black core shales (where developed) or maximum flooding horizons is indicative of dysaerobic conditions. Indeed this fauna bears a strong resemblance to Devonian and Mississippian dysaerobic basinal faunas (Kammer et al., 1986). Cyclothems with gray core shales thus represent less extensive transgressions compared to black shale - bearing cyclothems (Heckel, 1986). This is substantiated by lateral pinch - out of these cyclothems compared to the greater extent of black shale bearing cyclothems.

Regressive Carbonates and Clastics - RST. The regressive systems tract is the thickest portion of the cyclothem, usually being ten's of meters thick (Fig. 2.3). Eustatic regression is suggested in many cyclothems by the presence of skeletal grainstones and phosphatic pebble lags at the tops of core shales demonstrating truncation by storm wave base impinging on offshore muds. These "precursor beds" (C. Brett, pers. comm.) indicate lowering of sea level and storm wave base on a basically starved sea floor and not aggradation to wave base.

Regressive systems tracts are highly variable due to the vagaries of terrigenous dispersal systems and the sensitivity of carbonate depositional systems to clastic influx and topography (Boardman et al., 1984; Boardman and Malinky, 1985). Regressive carbonates are floored by argillaceous wackestones with a diverse marine fauna grading upward into often algal-dominated wackestones and clean skeletal wackestones and packstones. These carbonates are capped by high energy grainstone facies or low energy mudstone facies.

If regression proceeds to completion, the shoaling carbonate sequence can be exposed subaerially (Watney, 1980; Joeckel, 1989). However, at any point during regression, terrigenous influx can convert the carbonate system into a shoaling siliciclastic system (Heckel, 1977). This is demonstrated by the South Bend regression, in which the entire Kitaki Limestone Member "shales out" between Nebraska and northeastern Kansas. The Gretna Shale Member is thus only identifiable as a mollusk - bearing marine shale at the base of the thick Weston Shale Member of the Stranger Formation, the lower portion of which is equivalent to the Kitaki. Continued regression and siliciclastic progradation causes the strand line to migrate basinward, potentially exposing the siliciclastics to incision and pedogenesis (Enos et al., 1989).

Paleogeography of Lansing Group Cyclothems

In the midcontinent, numerous local and regional tectonic features and sources of siliciclastic input controlled the paleogeographic variability of these cyclothems (Fig. 2.4). Mountain building to the south and adjacent foreland basins to their north basically divides the midcontinent into two major tectono-stratigraphic regions. The northern midcontinent is characterized by carbonate - dominated and mixed carbonate - siliciclastic cycles encompassing a carbonate shelf region on the North American craton. The terrigenous basin region lies within the Anadarko and Arkoma basins of Oklahoma and southernmost Kansas (Heckel, 1977; Bennison, 1985).

The development of two major facies regions was probably a product of differences in regional subsidence rates as well as proximity to siliciclastic source areas. Tectonic reconstructions of the midcontinent during the Missourian indicate steadily increasing subsidence rates southward across east-central Kansas into the Arkoma/Anadarko basins (Kluth, 1986). While this north - south subsidence gradient controlled the thicknesses of depositional sequences, siliciclastics of the northern shelf and northern portions of the southern basins were not derived from a northern source and transported parallel to the subsidence gradient. The geometry of siliciclastic wedges (Heckel, 1978; Arvidson, 1990) and sediment transport structures (Moussavi - Harami, 1990) strongly indicate that siliciclastic source areas lay to the east and entered the midcontinent from the east - northeast, oblique to dip (Fig. 2.4). This interplay of regional subsidence and siliciclastic input subdivided the two major tectono - stratigraphic regions into four facies belts (Fig. 2.5).

The over - riding control subsidence rates had on cyclothem development is illustrated by regional cross sections of the carbonate shelf (Fig. 2.6) and terrigenous basin (Fig. 2.7). The northward thinning of cycles onto the stable craton and southern thickening of cycles into the Arkoma Basin is paralleled by the Lansing Group in the western Kansas subsurface (Watney, 1980). Structurally - and sedimentologically - controlled changes in elevation and siliciclastic input superimposed on the subsidence gradient also had a significant impact on depositional processes. Specific cyclothem motifs associated with each facies belt are discussed below.

Northern Shoreward Facies Belt. The northern shoreward facies belt of

Iowa and Nebraska is the proximal shelf facies as cycles begin to pinch out onto the stable craton (Figs. 2.5, 2.6, *1,2*). Cycles tend to be quite thin; the members of the Plattsburg Formation cannot be differentiated in Iowa as the entire formation is barely 1 meter thick and composed of argillaceous skeletal wackestones, packstones, well sorted grainstones and conglomerates (Heckel, 1992). Cycles also tend to be carbonate - dominated, especially in Nebraska. For example, the only regressive limestone developed in the South Bend Formation (Kitaki Limestone Member) occurs in Nebraska, demonstrating this area's isolation from siliciclastics. Regressive carbonates are dominated by packstone/grainstone and laminated mudstone facies. These carbonates are also invariably topped by pronounced exposure surfaces and paleosols (Joeckel, 1989).

Open Marine Facies Belt. The open marine facies belt of northeastern Kansas is a mid-shelf embayment, basinward of the shoreward facies and behind the distal shelf buildups (Fig. 2.5). Cyclothems tend to be well developed and are also thicker than shoreward cycles (Fig. 2.3, 2.6, *3,4*). Siliciclastic input was more important during regressive intervals in this area, but are still variably developed, depending on local topography and proximity to local point sources. Carbonates tend to be dominated by skeletal wackestone/packstone facies, although most regressive units do develop grainstone and/or mudstone caps. Exposure features are only sporadically developed and some cycle tops show no evidence of exposure separating it from the next cycle. Compared to the shoreward facies belt, this area was consistently deeper and allowed a thicker accumulation of each cycle phase, indicating the greater accommodation space provided by increased subsidence (Watney, 1985).

Algal Mound Facies Belt. The transition from the Open Marine Facies Belt to the Algal Mound Facies Belt is marked by a substantial increase in cumulative thickness of the Lansing Group (Fig. 2.6, *5,6,7*). Additionally, subsidence rates appear to be increasing at an increasing rate toward the basin as the interval thickens over shorter distances compared to the northern shoreward - open marine transition. The Algal Mound Facies Belt represents rapidly accumulating distal shelf carbonate buildups and obliquely migrating shelf margin clastic wedges developed over previous mound complexes or shelf margin wedges on a rapidly subsiding shelf or ramp.

In the Stanton and South Bend Formations, the transgressive carbonates (Captain Creek and Little Kaw, respectively) were able to "keep up" with rising sea level and high subsidence rates, producing thick, aggradational mound complexes (Fig. 2.6; Heckel, 1978; Neumann and McIntyre, 1985). The core shale of the Stanton Formation (Eudora) reflects this increased thickness by developing a fossiliferous, phosphatic gray shale facies rather than the black, fissile shale facies (Heckel, 1978). Regressive mound complexes are also developed in this region with some developing impressive tidal channel facies (Heckel, 1978). Although siliciclastics can be very thick, they are confined to topographic lows between mound complexes and are thus generally very thin over mound complexes. Additionally, no regressive systems tracts have been observed to display exposure features of any kind, although mound complexes show a wide variety of diagenetic fabrics (Heckel, 1978).

Terrigenous Detrital Facies Belt. This facies belt represents a fundamental shift in the character of midcontinent cyclothems. Not only do sequences continue to increase dramatically in thickness, but carbonates virtually disappear as well (Fig. 2.7). It is therefore appropriate to develop a modified cyclothem model to accommodate these differences.

Subsidence rates in the Anadarko Basin reached a maximum during the Missourian (Goldstein, 1982; Watney, 1985), producing sediment starved conditions through this interval (Watney et al., 1989a). Submarine fan and slope deposits were a dominant mode of basin filling when prograding margins finally reached the basin center (Kumar and Slatt, 1984). The Arkoma Basin, or Trough (Bennison, 1985), was closer to clastic source areas and may have been a major conduit for clastics derived from eastern sources transported as axial fans and deltas (sensu Morris, 1974; Houseknect, 1986) as well as a major locus of sedimentation from the Ouachitas to the south.

Heckel (1975), Boardman et al. (1984), and Bennison (1985) recognized the relationship between these basinal cycles and classic Kansas cyclothems and developed a modified cyclothem model for terrigenous basinal sequences (Fig. 2.8). The proximity to clastic source areas precluded the production and accumulation of substantial thicknesses of carbonates. Eustatically - controlled avulsion of clastics, coupled with fairly rapid basinal subsidence and eustatic sea-level rise, generated a substantial transgressive water column. This transgressive event is preserved as a thin, but distinctive, condensed horizon. In areas subject to very high sedimentation rates, deposition of suspended fine clastics during highstand can potentially expand the normally thin core shale interval (Boardman and Malinky, 1985; Watney et al., 1989a). Subsequent regression filled this accommodation space with thick coarsening-upward siliciclastic regressive systems tracts. Thus, basinal cyclothems are very asymmetrical, with thin, condensed transgressive systems tracts and very thick highstand and regressive systems tracts (Fig. 2.8; Bennison, 1985).

The northernmost basinal localities (Fig. 2.8, *8*) are not only thin compared to other areas within the basin, but are also thinner than many shelf margin localities (Fig. 2.7, *6,7*). This may be an indication that while carbonate production was effectively suppressed, terrigenous sedimentation was not able to substantially fill the accommodation space; this area may have been the bathymetric center of the basin. Southward, very thick regressive packages indicate sedimentation rates high enough to overcome rapid basinal subsidence, producing a southern terrigenous ramp or shelf (Bennison, 1985). Southward, southern ramp facies are dominated by fluvial and deltaic facies against which the marine portions of the intermediate cyclothems begin to pinch out (Fig. 2.8, *9-11*).

As a brief aside, correlations between the shelf and basinal regions have historically been problematic, but recognition of the significance of flooding intervals for interregional correlation combined with the unique suites of biostratigraphic markers present in each cycle has allowed a reassessment of these correlations (Bennison, 1985). Ongoing work by P. Heckel, D. Boardman, A. Bennison, and many others, while making significant strides, has also pointed out that there are many problems with current correlations and stratigraphic arrangements in Oklahoma. The Oklahoma formations correlative to the Lansing Group do not have the same genetic underpinnings as the structure of formations and members in Kansas (Fig. 2.9). While these Kansas cycles can be identified in Oklahoma, applying an Oklahoma name to these genetic sequences becomes intractable. This study seeks to retain the fidelity and uniformity of the study sequences across the entire region and while Oklahoma marker horizons are used, references shall be made to the transgressive systems tracts and maximum flooding horizons of the formations as identified and named in Kansas and correlated into Oklahoma.

Depositional Settings of Crinoid - Bearing Localities

The South Bend Formation is an intermediate cycle at the top of the Lansing Group (Fig. 2.3; Heckel, 1986). Four principal crinoid localities were examined for this study and are presented below from north to south.

LXQN. L-X Quarry, Cass County, Nebraska: NW, Sec. 18, T.12N, R.12E - Crinoids collected from a prominent shale unit near the middle of the regressive Kitaki Limestone Member of the northern shoreward facies belt (Figs. 2.2, 2.4; Heckel et al., 1979). Significantly, the limestones above and below this shale are grainstones dominated by fusulinids and osagid coated grains. Osagid coatings are algal - foraminiferal associations indicative of shallow, well agitated environments (Toomey et al., 1989). Thus, this unit represents a terrigenous pulse into a shallow carbonate environment during mid regression on the northern shoreward margin.

ERQK. Elk River Quarry, Montgomery County, Kansas: NE, SW, Sec. 17, T.32S, R.14E - Crinoids collected from algal mound facies of Little Kaw Limestone Member (Fig. 2.10). This was an aggrading carbonate bank deposited at the shelf margin edge during transgression (Heckel, 1975a). Subsidence and eustatic transgression apparently never allowed aggradation into higher energy bathymetric zones.

RRWK. Railroad Cut, Wayside, Montgomery County, Kansas: NW, NW, Sec. 3, T.34S, R.14E - Crinoids collected from the upper surface of the sponge - dominated dense wackestone facies of the Little Kaw Limestone Member (Fig. 2.10). The Little Kaw is very thin here reflecting the retardation of carbonate deposition within the basinal facies. A dysaerobic molluscan fauna has been collected from the shales immediately overlying the Little Kaw in this area. The crinoids are therefore associated with the latest transgressive phases before core shale deposition. The distinctive sphinctozoan sponge fauna associated with these crinoids also occurs in other transgressive systems tracts of the underlying cyclothems within the basinal facies belt and seems to be quite diagnostic of the transgressive systems tract in this area.

ARCK. Anderson Ranch, Caney, Montgomery County, Kansas: SW, NW, Sec. 6, T.35S, R.14E - Crinoids collected from upper portion of highly argillaceous sponge - dominated packstones and wackestones between basal conglomerate and overlying calcareous sponge - rich shales of the Little Kaw Limestone (Fig. 2.10). Like RRWK, Little Kaw is thin and overlain by dysaerobic core shales, however no sponge - dominated dense wackestone is developed here; it appears to be shaling out southward. The crinoids therefore seem to be coming from an earlier phase of transgression compared to RRWK.

ERQK, RRWK, and ARCK are arrayed along a north to south, shelf margin to basin transect (Fig. 2.10). The observed pattern of thinning is consistent with broader scale patterns discussed earlier. The paleogeographic position, stratigraphic position, and sponge - dominated faunas of the southern basinal localities are all indicative of very low energy conditions compared to the shelf margin locality. All of these localities represent lower energy conditions compared to LXQN in the northern shoreward facies belt.

The Stanton Formation is the second of three cyclothems which compose the Lansing Group and the last major cycle of the Missourian Stage (Fig. 2.3; Heckel, 1986; Heckel and Boardman, 1989). Twenty principal crinoid localities and several ancillary localities were examined for this study and are presented below from north to south.

PRQN. Platte River Quarries, Louisville area, Cass and Sarpy counties, Nebraska: (Rock Lake Quarry; SE, NW, Sec. 3, T.12N, R.10E) (Derby Quarry; NE, NW, Sec. 16, T.12N, R.11E)(Ash Grove Quarry; NW, Sec. 18, T.12N, R.12E) - Crinoids collected from this area are all from the Kiewitz Shale Bed of the Stoner Limestone Member exposed in quarries along the Platte River Valley near Louisville, Nebraska (Figs. 2.2; 2.4, 2). The Kiewitz is a very uniform bed in this area, both faunally and lithologically, and it was therefore deemed appropriate to pool these samples into a single "locality" (Heckel et al., 1979). It is a light gray, slightly to strongly calcareous shale with an abundant and diverse fauna (see Pabian and Strimple, 1979 for a faunal list). Skeletal material, including fusulinids, is often concentrated into thin beds or gutter casts with scoured bottoms and planar tops. The depositional setting of the upper Stoner Limestone in the northern midcontinent is best described as a shoalling carbonate ramp. The Kiewitz Bed represents a distal ramp setting forward of a fusulind shoal. Behind the fusulinid shoal, carbonate muds give way upward to burrowed foreshore and beach grainstones and finally to laminated supratidal carbonates with exposure features and ultimately a well developed paleosol (Joeckel, 1989). Thus, crinoids from the Kiewitz Shale Bed inhabited a moderate energy setting during early mid regression along the northern shoreward margin.

LKCK, UKCK. Lower and Upper Kill Creek, Kansas Rt. 10, DeSoto, Johnson County, Kansas: SE, SE, Sec. 33, T.12S, R.22E - Crinoids were collected from two horizons within the transgressive Captain Creek Limestone. The Stanton Formation at this locality in the Open Marine Facies Belt rests upon a thickened interval of Vilas Formation siliciclastics (P. Heckel, pers. comm.; J. French, pers. comm.). This bathymetric high produced uncharacteristically high energy facies within the lower half of the Captain Creek Limestone. The maximum flooding Eudora Shale, normally black, fissile, and phosphatic in this region, is a dark gray clay shale with an abundant dysaerobic molluscan fauna at this locality, reflecting its elevated position.

LKCK is from a shale parting and bedding plane 30 cm below the top of the Captain Creek. The limestones flooring the bedding plane are fragmented skeletal wackestones and packstones. UKCK is from the uppermost 2 - 3 cm of the Captain Creek. This is an extensive bedding plane of argillaceous, whole and unabraded fossil packstones transitional between the dense wackestones below and the dysaerobic shales above. Thus, LKCK is a fairly high energy carbonate setting perched on a local high during mid transgression. UKCK represents the last vestiges of carbonate deposition and epifaunal benthos during latest transgression before core shale deposition.

WLQK. Wilson County Lake Quarry, Buffalo, Wilson County, Kansas: SE, SE, Sec. 17, T.27S, R.16E - Crinoids collected from whole fossil grainstones and shales of the basal Stoner Limestone Member in the Algal Mound Facies Belt (Fig. 2.5). These beds overlie the thin, gray, phosphatic shale of the Eudora Shale, which has lost its black shale facies over the tops of the Captain Creek algal mound complex (Heckel, 1978). These whole fossil grainstones and shales probably represent highstand and earliest regressive accumulations of diverse epifaunal assemblages in a fairly low energy setting.

TMQK. Table Mound Quarry, Elk City Lake State Park, Montgomery County, Kansas: NE, Sec. 16, T.32S, R.15E - Crinoids collected from intermound argillaceous packstones and grainstones in the middle to upper portions of the Captain Creek algal mound complex (Fig. 2.11). The Captain Creek mound complex at the Table Mound Quarry has a tremendous amount of topography developed in its upper portions, with algal wackestone and packstone highs flanked by argillaceous packstones filling lows. These units were evidently deposited near the end of the Captain Creek transgression at a prominent position along the shelf margin edge.

WINK. West Independence road cut on U.S. Rt. 160, Montgomery County, Kansas: NW, NW, Sec. 36, T.32S, R14E - Crinoids collected from highest fossiliferous shales beneath the Timber Hill Siltstone Bed (Fig. 11; Heckel, 1975). This thick shale unit is classified as the Eudora Shale simply because the Stoner Limestone has pinched out between here and the Elk City State Lake dam (Figs. 2.11). Thus, this is the northernmost extent of the terrigenous basinal facies for the Stanton Formation. The thin limestone stringers in this fossiliferous section represent a temporary clearing of the muddy bottom fairly late in regression before rapid detrital influx and deltaic progradation deposited the overlying unfossiliferous Timber Hill Siltstone Bed and Onion Creek Sandstone (Heckel, 1975; Moussavi - Harami, 1990).

PHFK, BNFK, 75BK. (Patterson Hog Farm pond - NE, NE, Sec.23; Bolton North Farm pond - SW, SW, Sec. 25; U.S. Rt. 75 cut - NW, NW, Sec. 36), T.33S, R.14E; Bolton, Montgomery County, Kansas - Crinoids from these localities are all from the sponge - rich dense wackestone facies of the Captain Creek Limestone (Fig. 2.11). The Captain Creek is very thin here and is typical of the condensed transgressive systems tracts found in the terrigenous basin. This unit is immediately overlain by the black fissile shale facies of the Eudora Shale. Additionally, this area is within an offshore embayment, forward of the shelf margin and behind a basinal rise produced by activation of the Chautauqua Arch (Fig. 2.12; Heckel, 1975; Bennison, in prep.). Thus, these crinoids are from a very low energy offshore embayment facies deposited late in transgression.

PGSK, RFPK. (Patterson Ground Silo - NW, NW, Sec. 24; Rollins Farm Pond - NW, NW, Sec. 25), T.33S, R.14E; Montgomery County, Kansas - Crinoids collected from the upper portion of the Eudora Shale below the Bolton Bed (Fig. 2.11). These crinoids occur in the gray shale facies of the Eudora with an abundant dysaerobic molluscan fauna (Boardman et al., 1984). The overlying Bolton Bed is a packstone/ grainstone composed of unabraded fossil material and may represent the eustatically forced impingement of storm wave base on the muddy bottom and concomitant colonization of bottom by epifaunal suspension feeders. The overlying Onion Creek Sandstone represents rapid deltaic progradation into the basin from the east (Heckel, 1975; Moussavi-Harami, 1990). Thus, this unit was deposited during later highstand in an offshore (below storm wave base), dysaerobic environment.

TOQK, ETQK. Tyro Quarry, Montgomery County, Kansas: SW, SE, Sec. 30, T.34S, R.15E - Crinoids were collected from two horizons at the quarry north of Tyro, Kansas (Fig. 2.11). During Stanton Formation deposition, this area was subject to flexure along the crest of the Chautauqua Arch which generated a basinal rise (Figs. 2.11, 2.12; Bennison, in prep.). This rise developed a localized oolite shoal during transgression: this is the Tyro Oolite (Heckel, 1975; Bennison, in prep.). TOQK is from a thin wackestone horizon at the top of the Tyro Oolite, transitional with the overlying gray, phosphatic shales of the Eudora. The Eudora has a lower gray shale facies and an overlying black shale facies developed at the Tyro Quarry. Malinky and Mapes (1982) report on the unique dysaerobic fauna from the Eudora here, including the crinoids. ETQK is from the lower gray shale facies of the Eudora report by them. Continued flexure through the subsequent regression allowed storm wave base to incise the arch and truncate the underlying systems tracts, including much of the Eudora at the Tyro Quarry (Bennison, in prep.). TOQK crinoids thus inhabited a drowned oolite shoal on a basinal rise fairly late in transgression. ETQK crinoids inhabited the same site except under more hostile, late transgressive, dysaerobic conditions transitional to maximum flooding anoxia.

LTDO, UTDO. Lower and Upper Tank Dike, Copan, Washington County, Oklahoma: NW, SW, Sec. 10, T.28N, R.13E - Crinoids collected from the Tank Dike are from the middle portion of the Barnsdall Formation, which is equivalent to the Stanton Formation (Fig. 2.9). A local structural cross section shows anomalous high dip to the north at this locality and indicates that it either lies within a small structural syncline, or that the unit runs up over a structurally or sedimentologically controlled rise to the south, or all of the above (Fig. 2.13). A well developed limestone at the top of the unit to the south suggests that this locality was perched above surrounding basinal clastics, much like Gulf of Mexico reefs are perched on salt domes above the nepheloid layer (Manner, 1990). In any event, the high dip makes precise stratigraphic positioning of these samples within this cycle difficult, although they are both generally within the middle of the regressive systems tract. LTDO occurs several meters below UTDO and may be quite close to the underlying dysaerobic molluscan fauna. UTDO occurs close to a nearshore molluscan limestone stringer, above which nonfossiliferous shales and sandstones cap the cycle. Thus, LTDO represents the transition from strongly dysaerobic highstand facies to muddy, normal marine facies while UTDO is near the top of the fossiliferous marine section, being overlain by rapidly deposited clastic facies.

LCWO, UCWO. Lower and Upper Copan West, Copan Lake, Washington County, Oklahoma: NW, Sec. 18, T.28N, R.13E - Crinoids collected from two horizons within the transgressive systems tract of the Stanton Formation equivalent Barnsdall Formation (Fig. 2.14). This unit outcrops anomalously far west and a local structural cross section roughly along strike (north-northeast, south-southwest) demonstrates this. The top of the underlying cycle (Torpedo Sandstone) outcrops at roughly the same elevation at the north end of Copan Hill (Fig. 2.13), Copan East, and North Copan East (Fig. 2.14). However, these localities lie several miles down regional dip from one another. The thick, argillaceous packstone sequence developed at Copan West is not characteristic of starved basinal transgressive systems tracts and reflects the elevated position and increased carbonate production this area enjoyed during flooding (Fig. 2.14). Like the Tyro Quarry section, a fossiliferous conglomerate is developed over this structure in the regressive systems tract, indicating potentially active flexure during Stanton deposition (Fig. 2.14). These units then dip to the south, *against* regional dip, into a thick, fossiliferous shale sequence in the Bar-Dew Lake area (Fig. 2.14).

LCWO was deposited during early transgression on a subtle basin rise. That this feature was relatively subdued is indicated by the shale - rich, whole fossil taphonomy of these units compared to the cross bedded oolite developed over the more pronounced Chautauqua Arch. UCWO was deposited over this same feature near the end of Stanton transgression and therefore in deeper water conditions.

NTSO. North Torpedo Switch, Osage County, Oklahoma: NE, SE, Sec. 7, T.26N, R.12E - Crinoids collected from the upper portion of early regressive shale of Stanton equivalent Barnsdall Formation (Fig. 14). This is an attenuated sequence which lies atop the Backius Anticline (Rascoe, 1975). This feature, along with other local structural features in western Washington and eastern Osage counties, are the product of differential compaction over irregular Precambrian basement (Ireland, 1955; Gay, 1989). There is the possibility that these structures were mildly active during Late Pennsylvanian time in that they seemed to have been able to maintain different patterns of sedimentation over the structures compared to surrounding areas.

At NTSO, the transgressive systems tract is quite thin and may reflect higher energy conditions winnowing this skeletal material compared to Copan West. No overlying core black shale facies is developed, also indicating the elevated position of this locality. The fairly thin fossiliferous shale unit is overlain by nonfossiliferous shales and upward silts and sands. The thin fossiliferous shale sequence represents muddy, moderate energy conditions on a pronounced positive feature during highstand and early regression.

BCQO, SLWO. (Bull Creek Quarry - SE, SE, Sec. 4; Skiatook Lake West - NE, NW, Sec. 21), T.22N, R.10E: Osage County, Oklahoma - Crinoids collected from the condensed, transgressive argillaceous packstones of the Stanton equivalent Barnsdall Formation (Fig. 2.7, *11*). The overlying core shale does not develop a black, fissile facies, but rather is a thick dysaerobic shale with an abundant molluscan fauna. In this area a thick regressive carbonate, the Wildhorse Dolomite, is developed which is roughly equivalent to the Stoner Limestone. This carbonate may be associated with a regional structural feature, the Caney River Arch (Chenoweth, 1965), which would have perched this area enough to allow carbonate deposition. Additionally, in this portion of the Arkoma Basin sedimentation rates were apparently very high, judging from sediment thicknesses between marine zones (Fig. 2.7). Marine flooding units begin to lap out against these clastic wedges forming a southern shelf facies. BCQO and SLWO represent fairly high energy marine conditions on a north facing southern shelf during early transgression.

The Plattsburg Formation is the lowest formation of the Lansing Group (Fig. 2.3). Ten principal crinoid localities were examined for this study and are presented below north to south.

CCQN. Cedar Creek Quarry, Cass County, Nebraska: SW, Sec. 7, T.12N, R.12E - Crinoids were collected from the top of the middle Merriam Limestone Member. This is the transgressive limestone of this intermediate cycle (Fig. 2.2; Heckel, 1986; Boardman and Heckel, 1989) at a position along it northern shoreward margin (Fig. 2.5, 2). The lower Merriam is composed of thin bedded, pectin - dominated packstones and interbedded shales. The middle Merriam Limestone is a very fine grained, well sorted skeletal - pelletal grainstone which is overlain by thin bedded osagid - coated grain packstones and interbedded shale with whole fossils of the upper Merriam. Near the top of this unit, osagid coatings become quite thick and encompass other coated grains.

The Merriam here is a deepening upward unit of bay, shoal, and foreshoal facies. Crinoids from CCQN are at the transition from well sorted shoal grainstones to foreshoal coated - grain packstones and shales. Thus, these crinoids inhabited a fairly high energy carbonate environment during mid transgression at the northern shoreward margin of this cycle.

O75K. Old U.S. Rt. 75, north Altoona, Wilson County, Kansas: NE, NW, Sec. 28, T.28S, R.16E - Crinoids from this locality were collected from the middle to upper units of the regressive Spring Hill Limestone Member in the Algal Mound Facies Belt (Fig. 2.15). Unfortunately, some of the sample may have come from the underlying core shale, however the specimens from museum collection seem to be dominated by material from the Spring Hill. The Spring Hill here is not thickened into a regressive algal mound complex and indeed neither is the transgressive limestone, the Merriam. The Spring·Hill appears to be coming down off of the Bourbon Arch, where it does develop algal - biostromal facies (Fig. 2.6, *4*). Although the Plattsburg in this area has dropped into an embayment, the overlying Vilas Shale is a thick clastic wedge which infills this relief prior to Stanton algal mound deposition (Fig. 2.6).

O75K crinoids are from skeletal wackestones and interbedded shales deposited during mid regression in an apparently broad embayment before rapid deposition of late regressive siliciclastics.

N75K, K47K, K96K, NFDK, BRQK. (New U.S. Rt. 75 - SE, NE, Sec. 28, T.28S, R.16E; Kansas Rt. 47 - NW, NW, Sec. 17, T.29S, R.16E; Kansas Rt. 96 and Neodesha Farm Ditch - SE, SW, Sec. 23, T.30S, R.15E; Brickton Quarry - NE, NE, Sec. 1, T.31S, R.15E), Wilson and Montgomery counties, Kansas - Crinoids from all of these localities were collected from the Hickory Creek Shale Member in the Algal Mound Facies Belt (Fig. 2.15). In this area, the flooding carbonate of the Plattsburg Formation (Merriam) did not thicken into an aggradational mound complex, however its upper surface is developed as a algal - foraminiferal boundstone hardground (Fig. 2.15; Holterhoff, 1991). This surface is bored and encrusted by epifaunal macroinvertebrates and represents both terrigenous and muddy carbonate starvation during maximum rates of transgression. The overlying Hickory Creek core shale varies in thickness across this area. A nearby eastern clastic source expanded the thickness of the core shale, producing a small rise (Fig. 2.15). Subsequent regression allowed algal carbonates to become established and aggrade rapidly on this rise while the prograding clastics diverged around this high, similar to the development of perched reefs on salt domes in the Gulf of Mexico (Fig. 2.15; Minnery, 1990).

NFDK is from the lowest horizons of the expanded Hickory Creek Shale and represents the maximum flooding/earliest highstand facies of this cycle and therefore the deepest conditions of these samples. BRQK, K47K and N75K are from higher in the Hickory Creek Shale and represent later highstand/early regressive conditions. K96K comes from the transition of the Hickory Creek Shale into the mound facies of the Spring Hill Limestone and therefore are into the regressive systems tract. All of these localities and samples occur in medium gray shales with thin skeletal grainstone layers and are associated with an abundant sphinctozoan sponge fauna.

TMBO. Top of The Mound, Bartlesville, Osage County, Oklahoma: SE, Sec 3, T.26N, R.12E - Crinoids were collected from the lower portion of the transgressive facies of the Plattsburg equivalent Upper Wann cycle (Fig. 2.9).

This locality is on the Dewey Faulted Flexure, a basement related structure within the basinal facies belt (Fig. 2.16; Ireland, 1955; Rascoe, 1975). Although a prominent feature, it is not clear if this was an actual rise during deposition of this cyclothem. However this cycle does contrast strongly to the facies developed in the Rice Creek Syncline located to the south (Fig. 2.16). The upper Wann here crops out in an outlier within the syncline and the cycle appears to be extraordinarily thick (Rascoe, 1975). Thus, TMBO represents the initial flooding deposits within the basin on a high along the northern border of a prominent structural low.

HPTO. Hairpin Turn on county road, Osage County, Oklahoma: SW, Sec. 15, T.25N, R.12E - Crinoids collected here are from the upper portions of the flooding unit of the Plattsburg equivalent upper Wann Formation (Fig. 2.16). This area may be affected by a small anticline immediately south of the Rice Creek Syncline (Oakes, 1940). The unit is dominantly argillaceous wackestones and interbedded shales and carries an abundant sponge fauna towards the top. It is overlain by a dysaerobic molluscan fauna. Thus, HPTO represents the later transgressive systems tract within the basin, potentially on a slope or rise bordering a northern depression.

CBMO. Crystal Bay Marina, Skiatook Lake, Osage County, Oklahoma: NE, Sec. 21, T.22N, R.11E - Crinoids collected from this locality are from the medial shale of a thin limestone horizon equivalent to the Plattsburg Formation within the upper Wann Formation (Fig. 2.16). The fossiliferous shale unit lies between two skeletal grainstones and represents the maximum flooding core shale in this region. This marine unit is overlain by a very thick, cross bedded sandstone which cuts out the unit along outcrop.

This is the southernmost exposure of this marine cycle yet identified (P. Heckel, pers. comm.) and represents the southern shoreward pinchout of the Plattsburg cyclothem. CBMO represents fairly high energy, shallow marine conditions along the southern shore.

Summary

The Upper Pennsylvanian Lansing Group of the midcontinent is composed of three cycles of glacio - eustatically controlled transgression and regression: the intermediate South Bend cyclothem, the major Stanton cyclothem, and the intermediate Plattsburg cyclothem (Fig. 2.3; Heckel, 1986; Heckel and Boardman, 1989). The unique biostratigraphic character of each cyclothem and the association of these faunas with the laterally extensive flooding units of each cycle has allowed precise correlation of these cycles across tectono - stratigraphic regions.

Cyclothems of the northern midcontinent are dominated by carbonate depositional systems with siliciclastics punctuating late regressive phases and starved, flooded shelf phases. Different starved shelf facies are developed depending on the extent of transgression and topographic relief. Anoxic black shale deposition is only associated with major cycles in topographic lows while gray dysaerobic to aerobic core shales are associated with major cycles over topographic highs and intermediate inundations (Heckel, 1977, 1978; Boardman and Malinky, 1985). Transgressions were more rapid than regressions and this is demonstrated by most cycles by their marked asymmetry. However, midshelf cycles can be roughly symmetrical due to high aggradation rates of algal carbonates.

Correlative cyclothems of the terrigenous basin are highly asymmetric with transgressive systems generally highly condensed and the cycle dominated by highstand and regressive, shoaling - upward siliciclastics. Although structural features within the basin can have a profound effect on cycle thickness and facies development, these cycles can still be identified and individual systems tracts recognized and interpreted.

The systems tracts and depositional environments of 34 crinoid - bearing localities were interpreted within this well defined cyclic framework. From these interpretations, meaningful comparisons can be made between paleoecological samples from the same systems tracts of different cycles, between different systems tracts of the same cycle, and between systems tracts and cycles from different tectono-stratigraphic regions.

Figure 2.1) Model Kansas - type cyclothem (after Heckel, 1977).

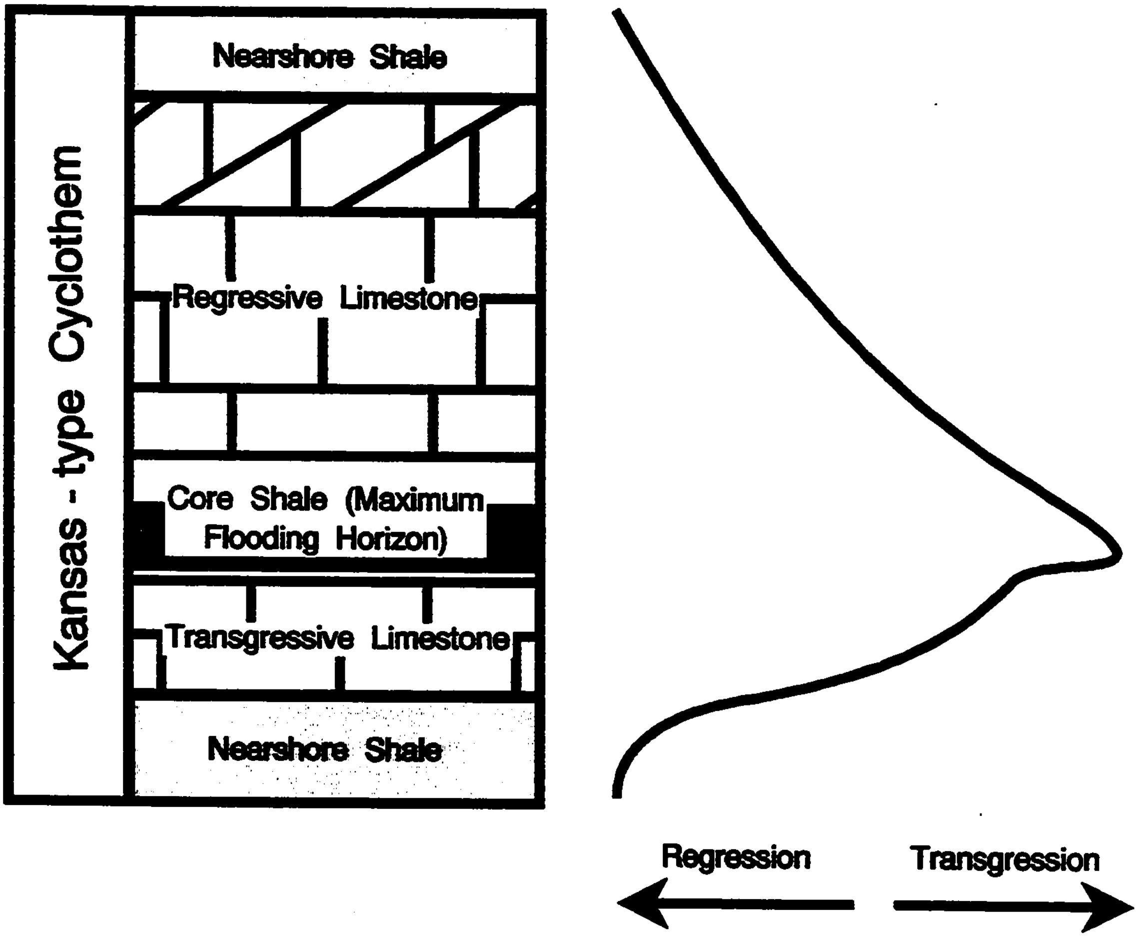

Kansas - type Cyclothem
Nearshore Shale
Regressive Limestone
Core Shale (Maximum Flooding Horizon)
Transgressive Limestone
Nearshore Shale
Regression
Transgression

Figure 2.2) Stratigraphic subdivisions of the Lansing Group in its type region of northeastern Kansas and northward into Nebraska.

Kansas River Valley, Kansas / Platte River Valley, Nebraska

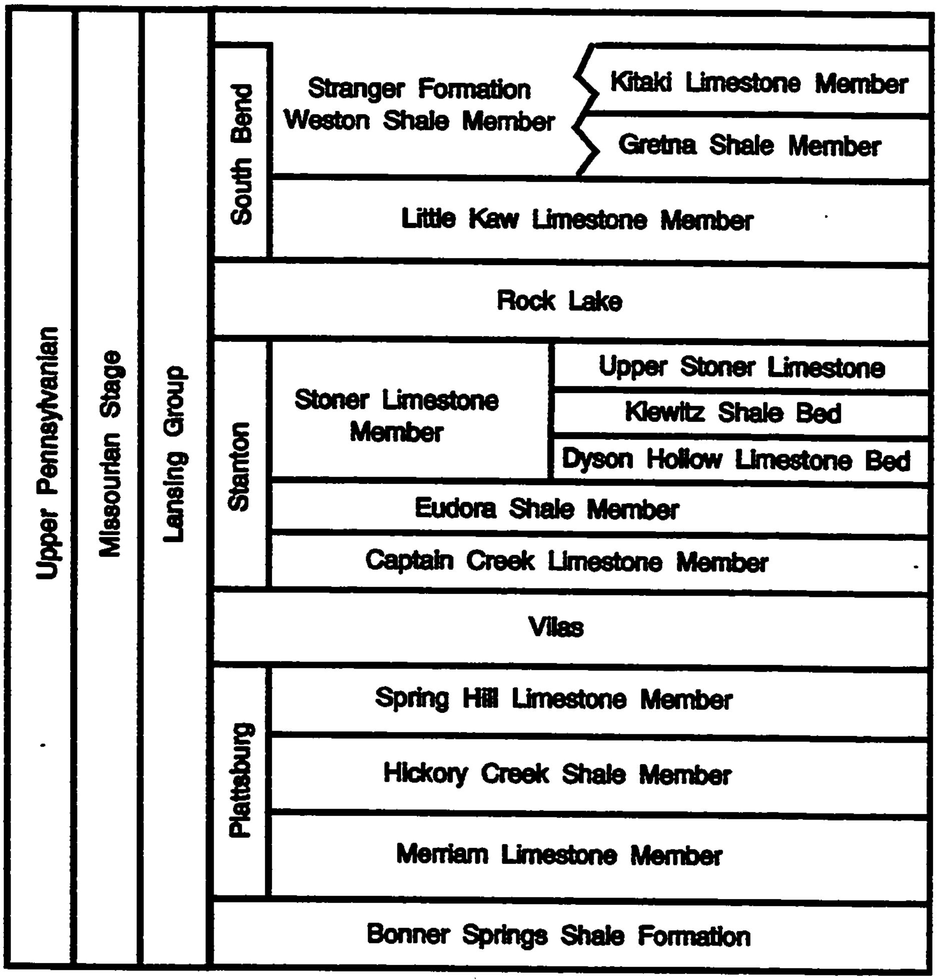


Figure 2.3) Standard section and sea - level curve for the Lansing Group in northeastern Kansas. Bonner Springs Formation is silty nearshore shale with paleosol developed at top (Enos et al., 1989). Local tidal channels cut through Bonner Springs and are filled by transgressive units of the Merriam Limestone (Enos and Hermann, 1989). Hickory Creek Shale is dark gray with dysaerobic fauna in local lows but is typically an intermediate depth gray core shale. Regressive Spring Hill Limestone grades into overlying silty shales and sandstones of the Vilas Formation. Fossiliferous upper Vilas and Captain Creek Limestone are transgressive systems of overlying maximum flooding Eudora Shale; a deep, black, major cycle core shale. Regressive Stoner Limestone has an exposure surface developed at its top north of Kansas City. Overlying Rock Lake Shale indicates increased accommodation space and siliciclastic input during early transgression. Transgression accelerated during Little Kaw deposition and culminated in basal Weston Shale (Gretna Shale equivalent) deposition of intermediate core shale, dysaerobic facies.

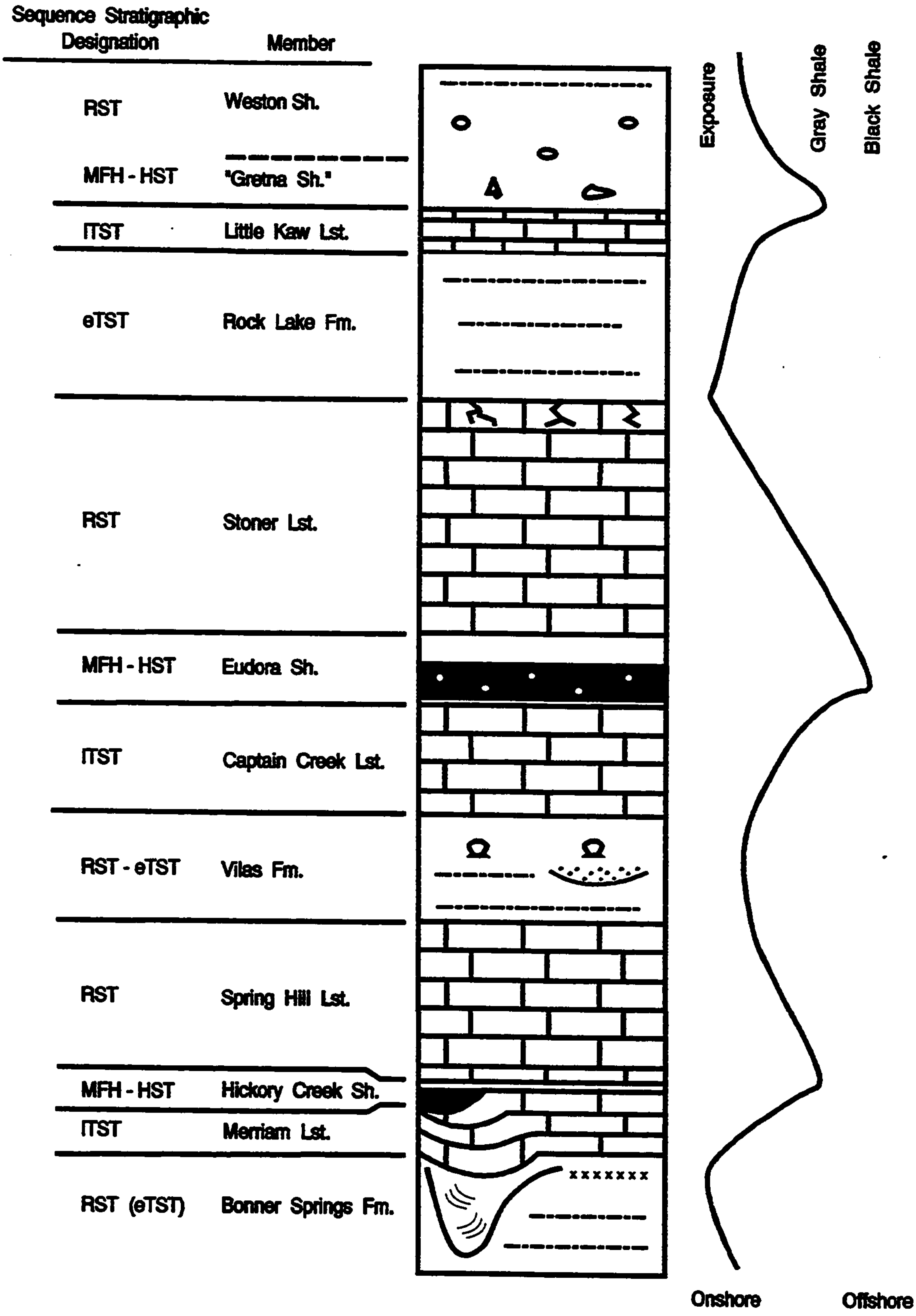

Sequence Stratigraphic Designation
Member
RST
Weston Sh.
MFH - HST
"Gretna Sh."
ITST
Little Kaw Lst.
eTST
Rock Lake Fm.
RST
Stoner Lst.
MFH - HST
Eudora Sh.
ITST
Captain Creek Lst.
RST - eTST
Vilas Fm.
RST
Spring Hill Lst.
MFH - HST
Hickory Creek Sh.
ITST
Merriam Lst.
RST (eTST)
Bonner Springs Fm.
xxxxxxx
Exposure
Gray Shale
Black Shale
Onshore
Offshore

Figure 2.4) Paleogeography of the midcontinent during the Missourian. Collisional tectonics in southern Oklahoma uplifted Wichita - Arbuckle - Ouachita Mountians and produced foreland basins to the north. Subsidence rates decreased steadily northward into the North American craton. A northern carbonate - dominated shelf region and a southern terrigenous basin region are recognized by the vast difference in cyclothem motif produced by these different tectonic regimes. Dominant sources of siliciclastics are from the east in the northern midcontinent and from the south in the southernmost basin area. Other structures which influenced sedimentation include the Chautauqua Arch, Bourbon Arch, Nemaha Arch, and Forest City Basin. Numerous local structures and sedimentological buildups also influenced cyclothem deposition.

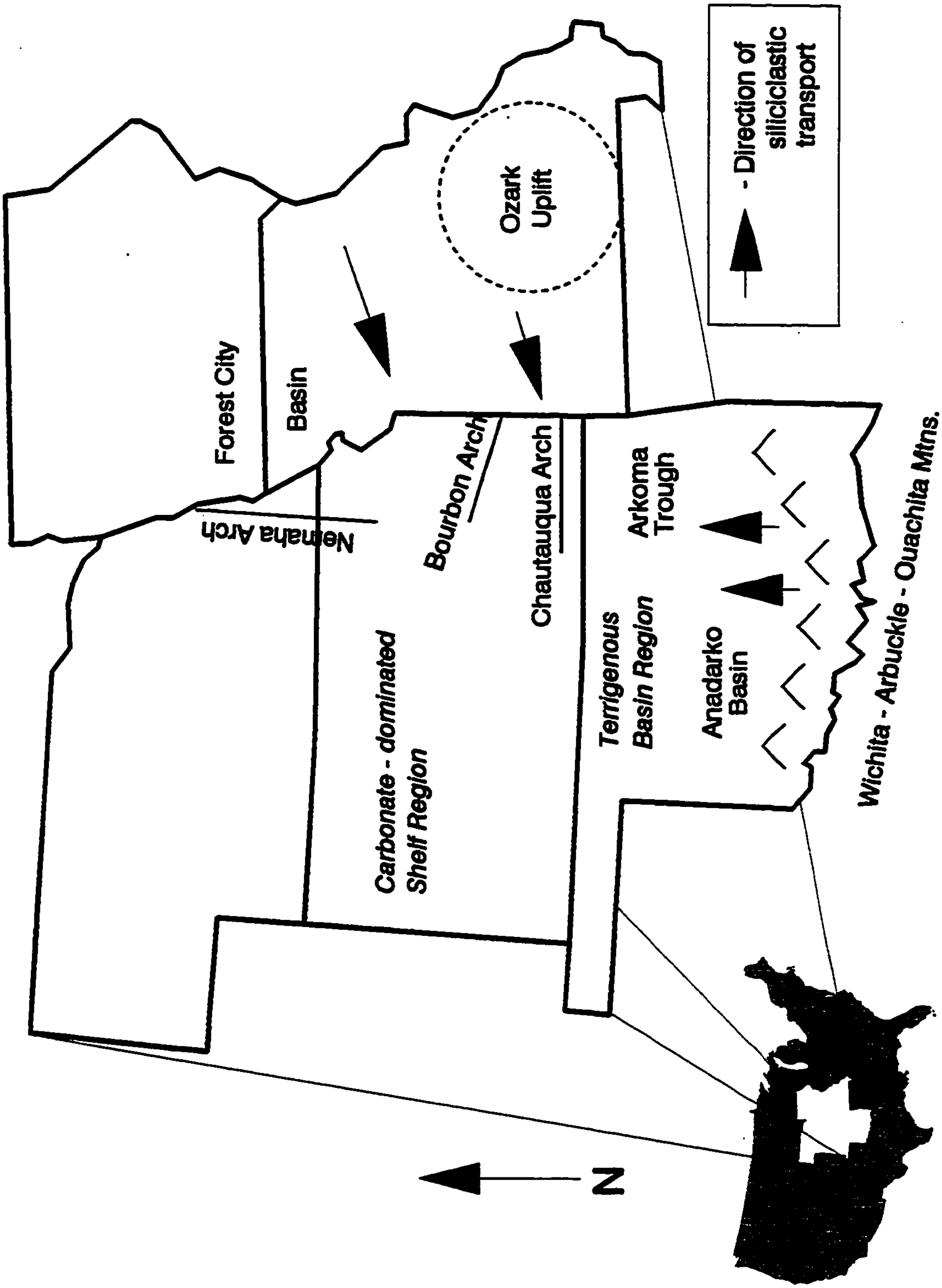

Forest City
Basin
Ozark
Uplift
Nemaha Arch
Bourbon Arch
Chautauqua Arch
Carbonate - dominated
Shelf Region
Terrigenous
Basin Region
Arkoma
Trough
Anadarko
Basin
Wichita - Arbuckle - Ouachita Mtns.
- Direction of
siliciclastic
transport
N

Figure 2.5) Study area and line of sections in midcontinent North America. Consistent differences in siliciclastic input and subsidence rates allows subdivision of the two major tectono - stratigraphic regions into four facies belts (Heckel, 1980). The Northern Shoreward, Open Marine, and Algal Mound Facies Belts constitute the carbonate shelf region while the Terrigenous Detrital Facies Belt basically defines the terrigenous basin region. Numbers correspond to standard sections of interregional cross sections of Figs. 2.6 and 2.7.

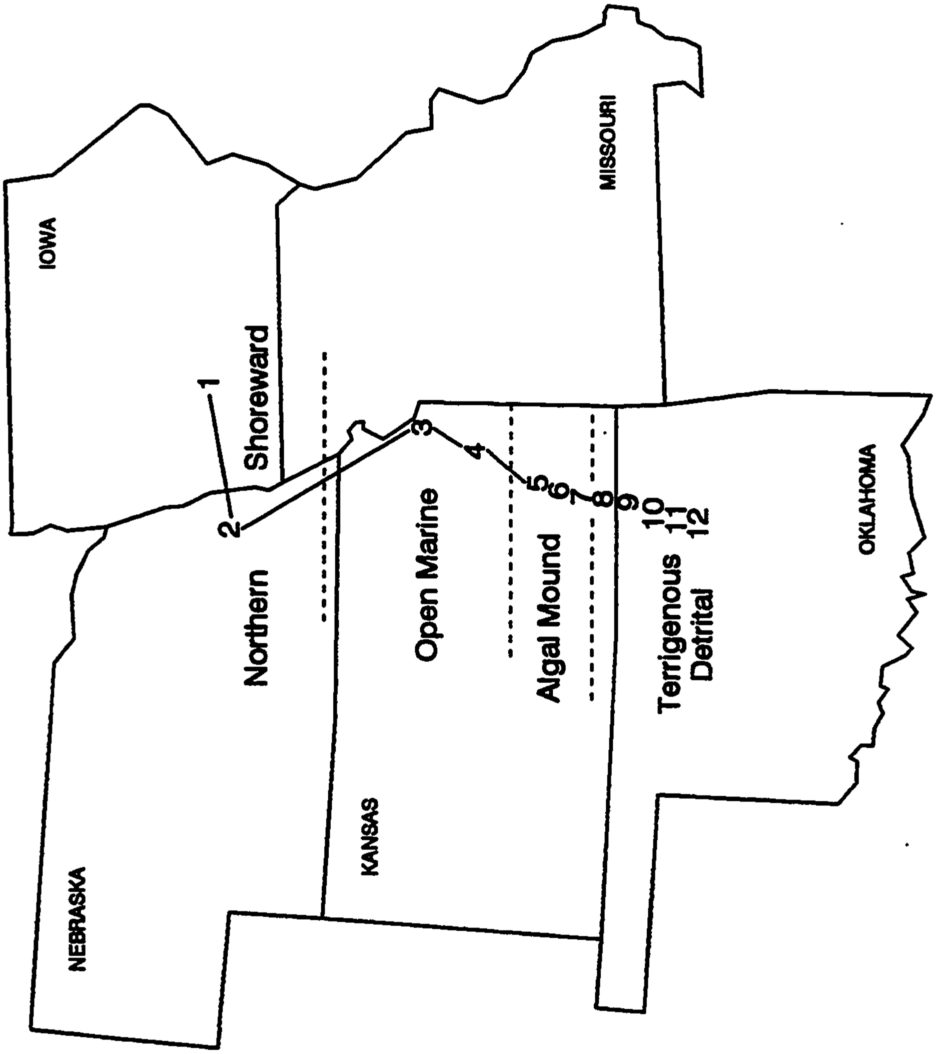
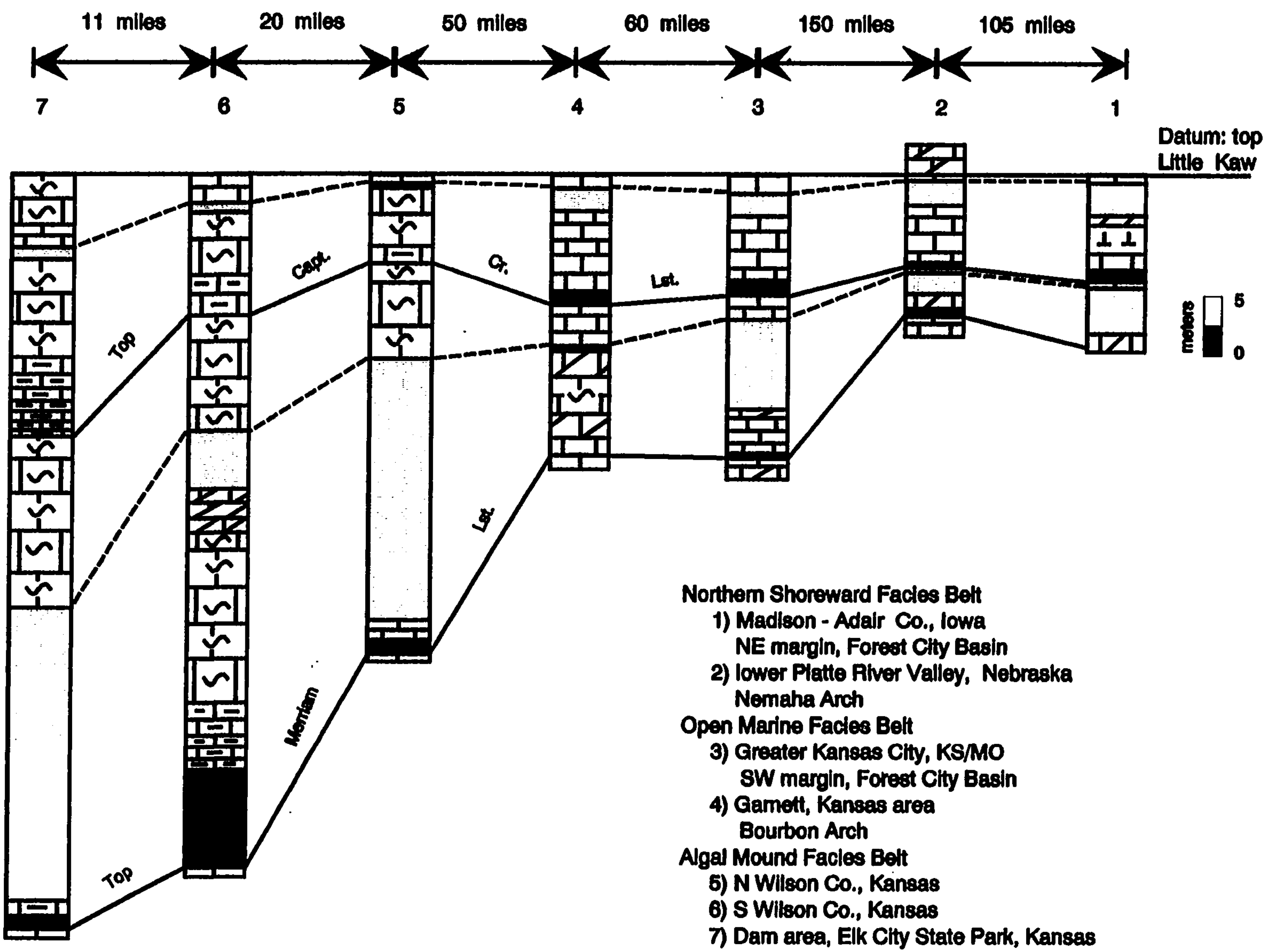

IOWA
MISSOURI
NEBRASKA
KANSAS
OKLAHOMA
Shoreward
Northern
Open Marine
Algal Mound
Terrigenous
Detrital
1
2
3
4
5
6
7
8
9
10
11
12

Figure 2.6) Regional cross section of the Lansing Group across the carbonate shelf. Legend for lithologies found in List of Symbols. Solid lines of correlation are along the tops of the transgressive systems tracts as these provide the most consistent and persistent surface of correlation. Dashed lines are the "sequence boundaries" at the base of the flooding units. Section 1 modified from Heckel (1992), sections 5 - 7 modified from Harbaugh et al. (1965) and Heckel (1978). See text for explanation

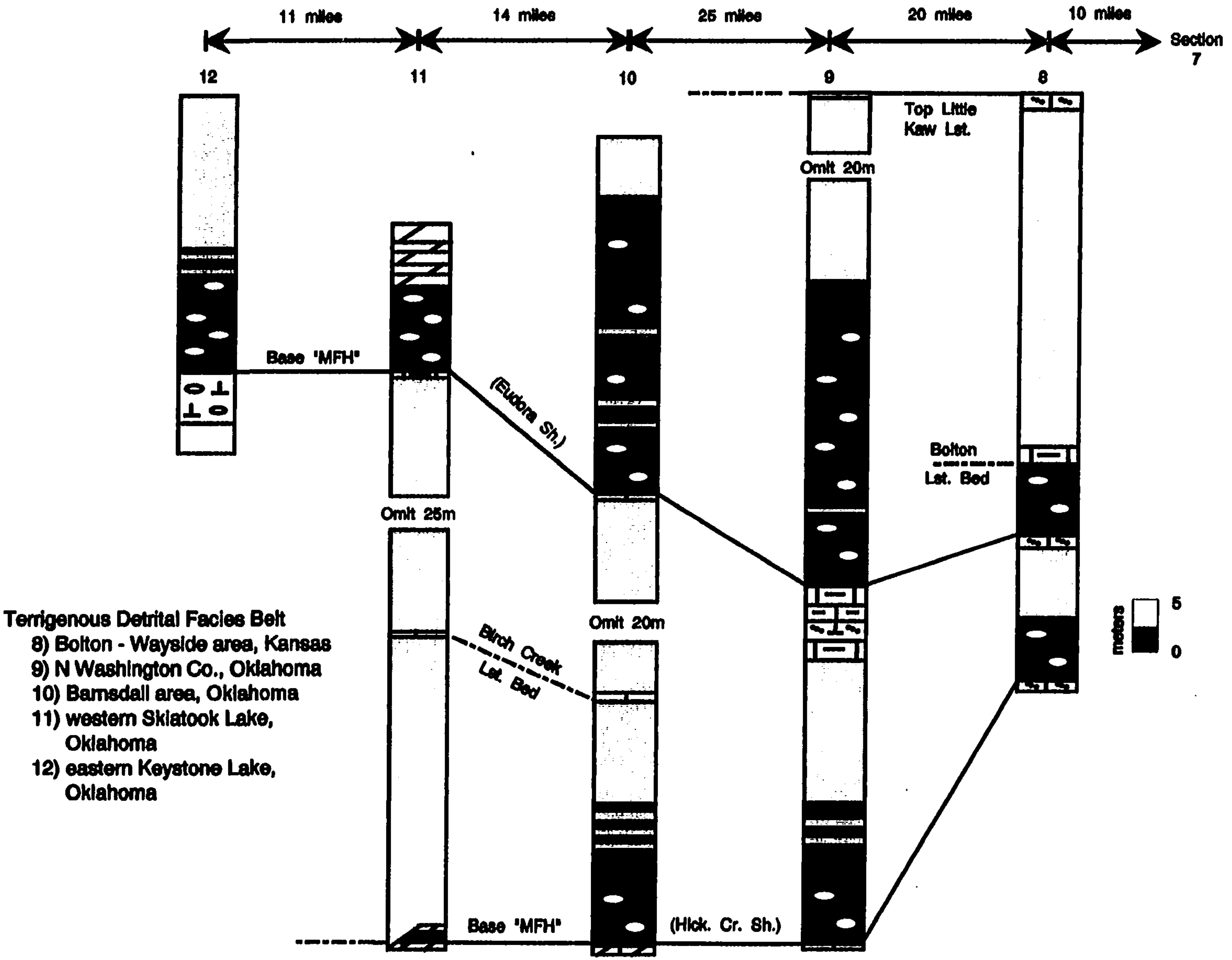


Northern Shoreward Facies Belt
1) Madison - Adair Co., Iowa
NE margin, Forest City Basin
2) lower Platte River Valley, Nebraska
Nemaha Arch

Open Marine Facies Belt
3) Greater Kansas City, KS/MO
SW margin, Forest City Basin
4) Garnett, Kansas area
Bourbon Arch

Algal Mound Facies Belt
5) N Wilson Co., Kansas
6) S Wilson Co., Kansas
7) Dam area, Elk City State Park, Kansas

Figure 2.7) Regional cross section of the Lansing Group across the terrigenous basin region. Correlations are along base of maximum flooding horizons (top of TST). Datum for sections 8 and 9 is top Little Kaw. South of Little Kaw pinch out, datum for sections 10 and 11 is base of Hickory Creek equivalent maximum flooding horizon. South of Hickory Creek pinch out datum for section 12 is base of Eudora equivalent maximum flooding horizon. Section 8 modified after Heckel, (1975a). Sections 9 - 11 modified after Heckel (written comm.). See text for explanation.



Terrigenous Detrital Facies Belt
8) Bolton - Wayside area, Kansas
9) N Washington Co., Oklahoma
10) Barnsdall area, Oklahoma
11) western Skiatook Lake, Oklahoma
12) eastern Keystone Lake, Oklahoma

Figure 2.8) Model basinal cyclothem (after Boardman et al., 1984; Bennison, 1985). Base of transgressive system may include highly bioturbated siltstones and shales overlying rippled and cross bedded top of underlying cycle. A thin, often ferruginous, skeletal packstone with epifaunal suspension feeding fauna indicates shutdown of terrigenous sedimentation during rapid rise in sea - level. This condensed carbonate interval can be overlain by gray, limonite concretion - bearing shale with a dysaerobic molluscan fauna or, if associated with a major transgression, black, fissile, phosphatic shale indicating oxygen depleted conditions during maximum transgression (MFH). Highstand facies may begin to expand because of equilibration and ensuing progradation of siliciclastic depositional systems back into the basin. Through regression, these dysaerobic shales grade into aerobic shales with normal, epifaunal suspension feeders. However, sedimentation rates may increase exponentially as forced regression and siliciclastic progradation fill the basin, precluding the establishment of a filter feeding epifauna. These regressive clastics include hummocky cross laminated siltstone and fine sandstones, planar and lenticular bedded medium sands, symmetrical ripple bedded siltstones, and massive, medium grained sandstones with soft sediment deformation structures.

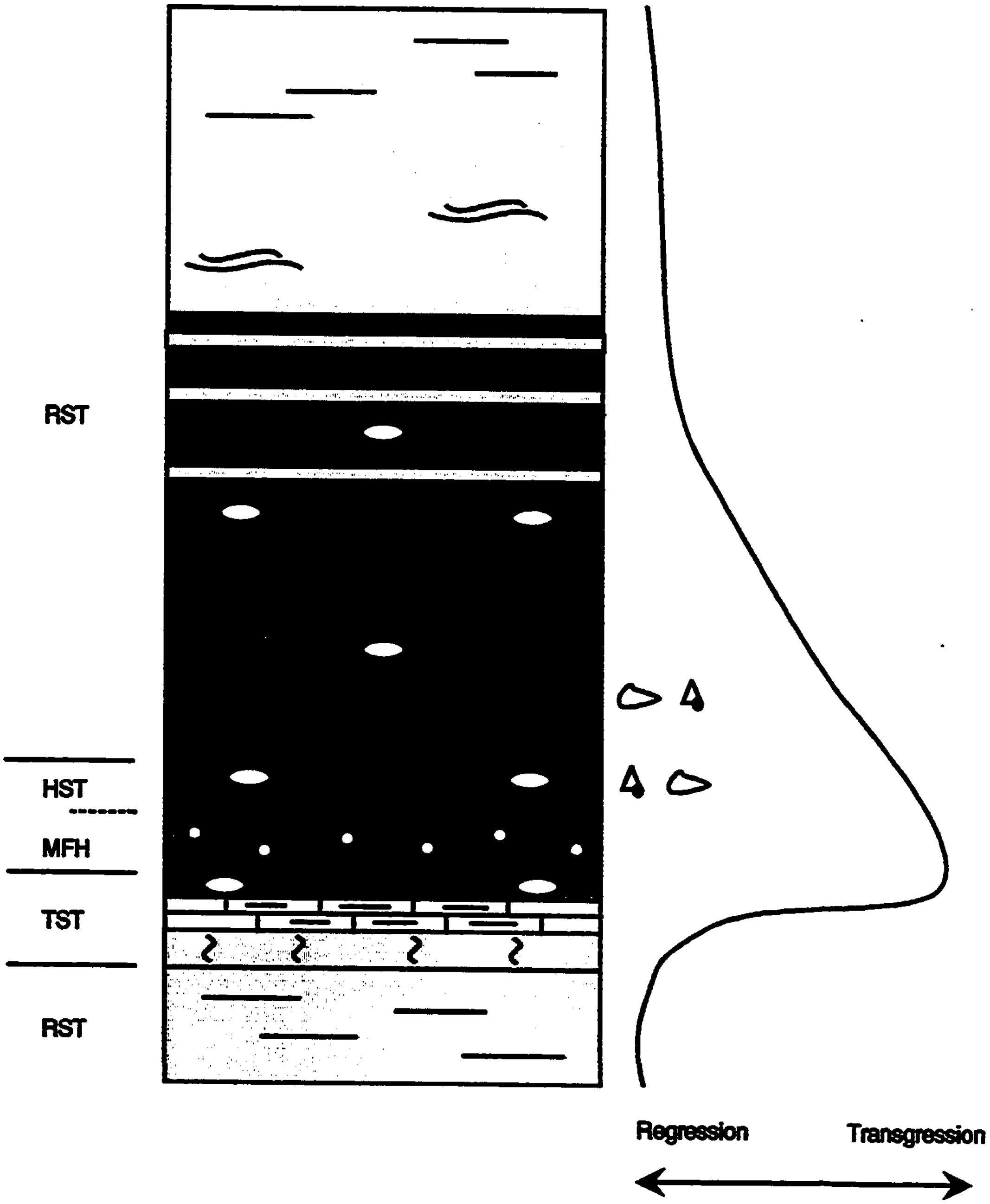

RST
HST
MFH
TST
RST
Regression
Transgression

Figure 2.9) Oklahoma formation equivalents to the Lansing Group. Plattsburg cyclothem is equivalent to upper marine cycle in the Wann Formation. Stanton cyclothem is equivalent to marine cycle of the Barnsdall Formation. South Bend cyclothem is equivalent to a marine zone in the Tallant Formation. Oklahoma formation boundaries do not correspond to cycle tops or bottoms. For example, base of Barnsdall formation is the top of the Birch Creek Limestone. However, type Birch Creek is a small limestone lentil within the regressive systems tract of the underlying upper Wann Formation. Thus, there is a substantial thickness of sandstones and variegated shales included within the basal Barnsdall Formation that are considered equivalent to the upper Vilas Formation.

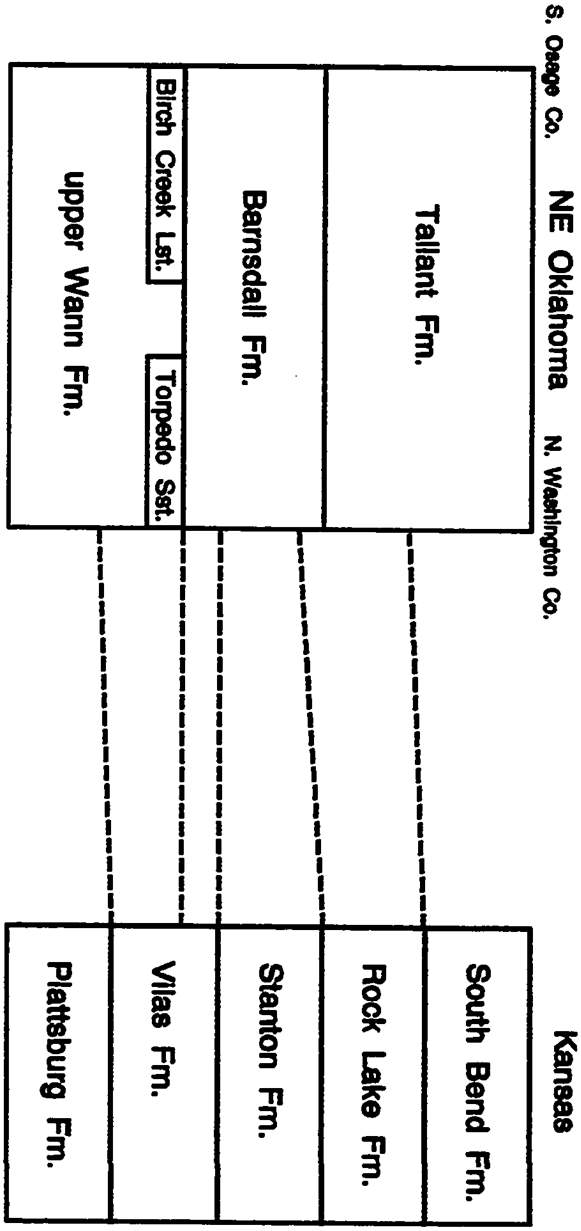

S. Osage Co.
NE Oklahoma
N. Washington Co.
Tallant Fm.
Barnsdall Fm.
Birch Creek Lst.
Torpedo Sst.
upper Wann Fm.
Kansas
South Bend Fm.
Rock Lake Fm.
Stanton Fm.
Vilas Fm.
Plattsburg Fm.

Figure 2.10) Cross section of the South Bend Formation in southern Montgomery County, Kansas. * denotes location of principle crinoid samples; (#) denotes section used for constructing interregional cross section. Aggradational shelf margin bank of transgressive systems tract (Little Kaw Limestone) thins basinward into condensed, sponge rich wackestone. This sponge wackestone facies begins to shale out basinward toward the southern clastic sources. See text for discussion.

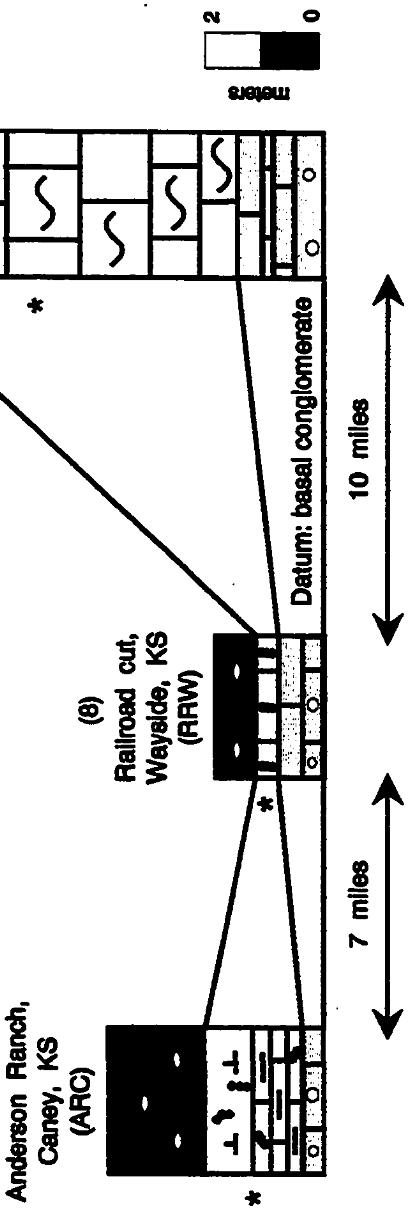

(7)
Elk River Quarry
(ERQ)
(8)
Railroad cut,
Wayside, KS
(RRW)
Anderson Ranch,
Caney, KS
(ARC)
Datum: basal conglomerate
10 miles
7 miles
meters
2
0
*
*
*

Figure 2.11) Shelf margin to basin transition of the lower Lansing Group in southern Montgomery County, Kansas (modified from Harbaugh et al., 1965; Heckel, 1975). * denotes location of principle crinoid sample; (#) denotes section used in interregional cross sections. Note thinning of transgressive systems tract of Stanton Formation from aggradational shelf margin bank to condensed, sponge - rich wackestone in basin. This is very similar to the shelf to basin transition in the Little Kaw Limestone of the South Bend Formation. Also note the development of transgressive oolite at Tyro, Kansas. Highstand facies of the Stanton Formation returns to black, phosphatic facies in the southern basin compared to thin gray shale and whole fossil, skeletal grainstones over the transgressive mound. Regressive systems tracts of the Stanton proceed from carbonate algal bank on the shelf margin to thick shale sequence in the basin to the south. See text for discussion.

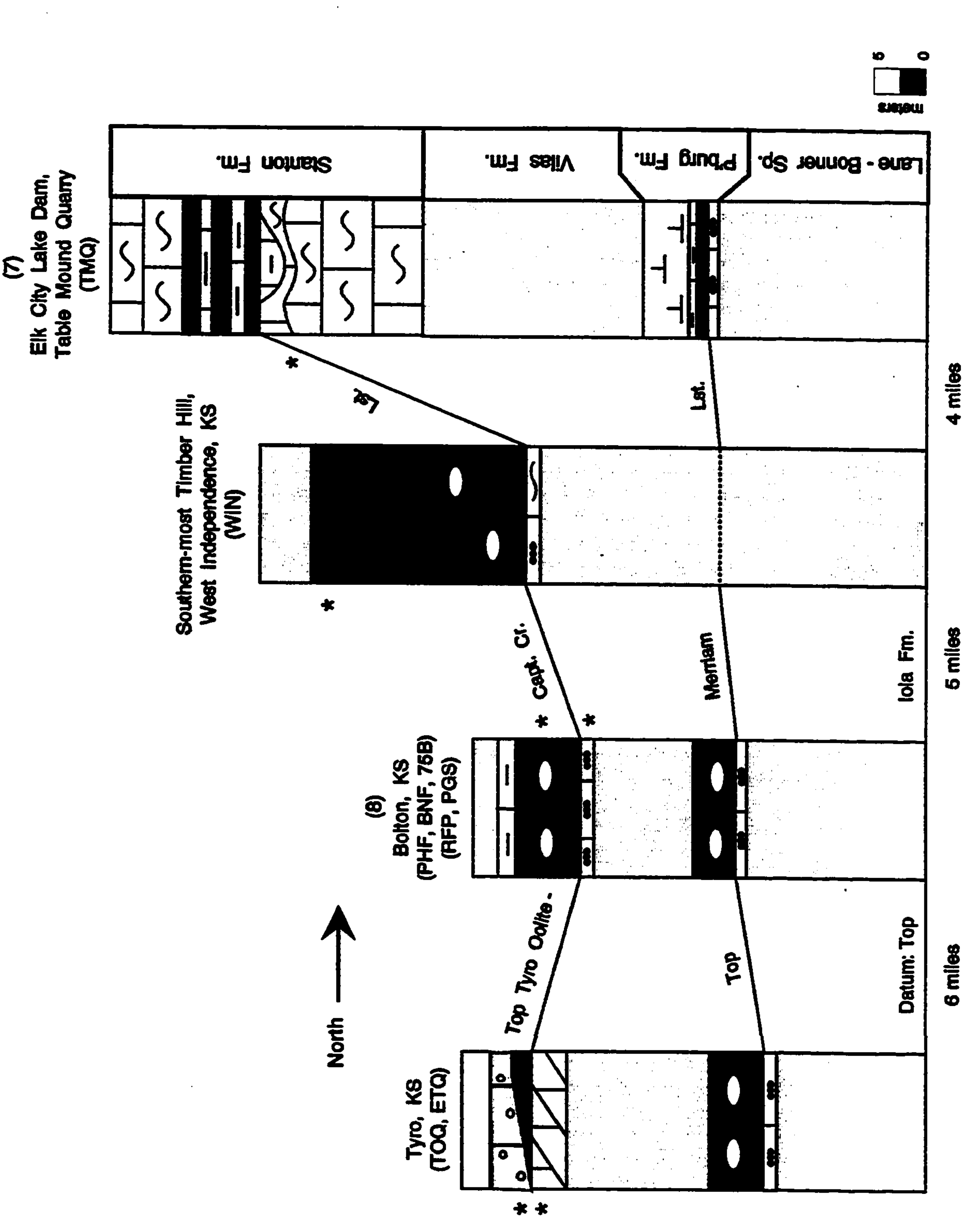

(7)
Elk City Lake Dam,
Table Mound Quarry
(TMQ)
Southern-most Timber Hill,
West Independence, KS
(WIN)
(8)
Bolton, KS
(PHF, BNF, 75B)
(RFP, PGS)
Tyro, KS
(TOQ, ETQ)
North
Stanton Fm.
Vilas Fm.
P'burg Fm.
Lane - Bonner Sp.
Lst.
Capt. Cr.
Top Tyro Oolite -
Lst.
Merriam
Top
Iola Fm.
Datum: Top
4 miles
5 miles
6 miles
meters
5
0
*
*
* *
* *

Figure 2.12) Schematic representation of the Stanton Formation transgressive systems tract transition and facies development from shelf margin to basin. Thick, aggradational carbonate bank is developed over southern margin of late regressive shelf margin clastic wedge of previous cycle. As both units thin basinward, bank facies are replaced by thin, sponge-rich wackestones. This facies is developed behind a structurally - controlled topographic rise to the south, the Chautauqua Arch. Here, the transgressive systems tract developed an oolite shoal, dissipating wave and current energy and establishing an offshore embayment behind it. This embayment was the site of the sponge wackestone.

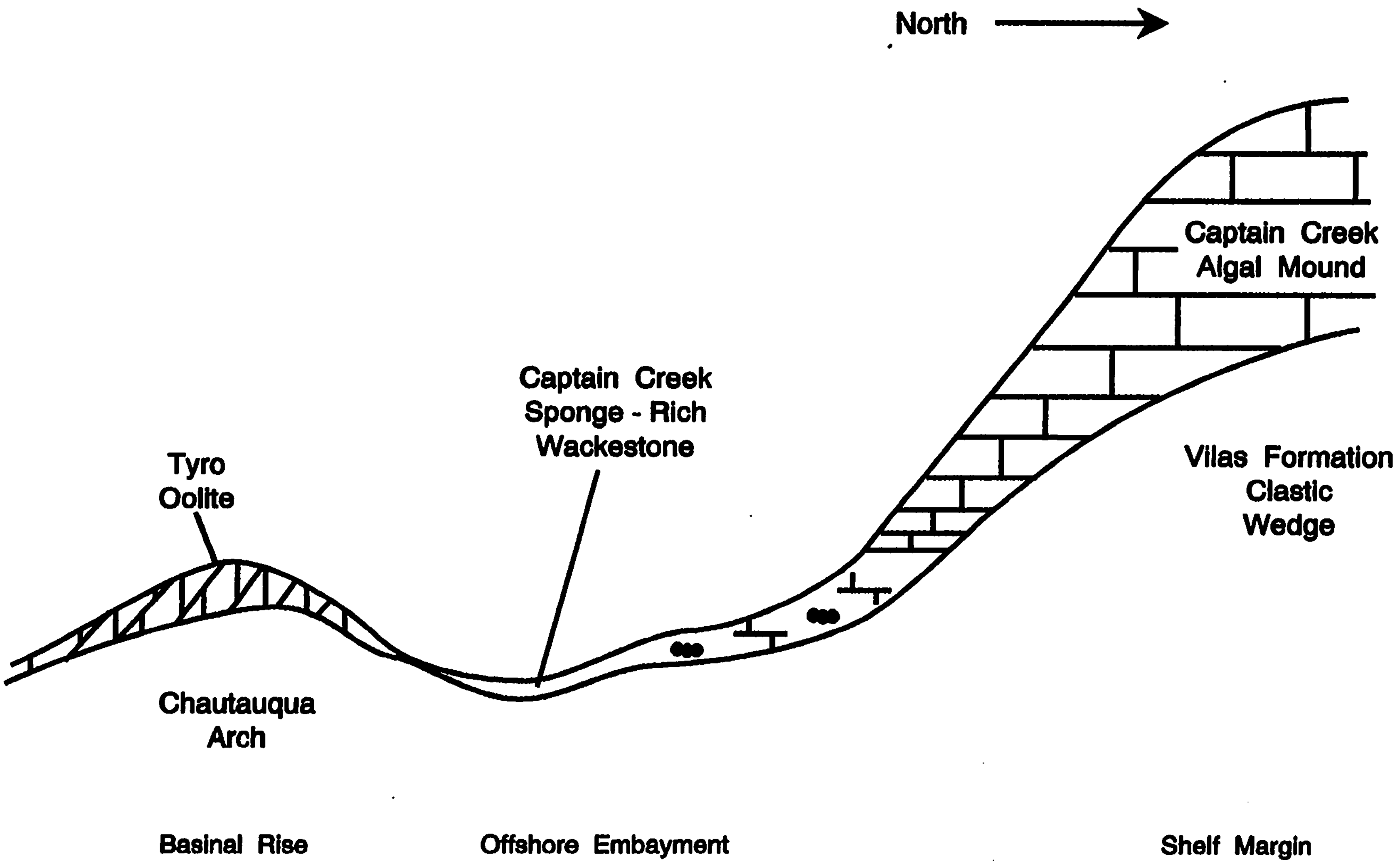

North
Captain Creek Algal Mound
Captain Creek Sponge - Rich Wackestone
Tyro Oolite
Vilas Formation Clastic Wedge
Chautauqua Arch
Basinal Rise
Offshore Embayment
Shelf Margin

Figure 2.13) Local north - south structural cross section through the Stanton equivalent Barnsdall Formation near Copan, Oklahoma. * denotes principal crinoid sample, + denotes location of ancillary crinoid collections. Dip from Twin Mound to Water Tower Knoll approximates regional dip. Dip increases significantly from Water Tower Knoll to Copan Hill, indicating draping of this cycle over a structural or sedimentological feature. The transition of a regressive carbonate atop this feature to sandstones in the low indicates these dips reflect original relief with siliciclastics diverted around the high.

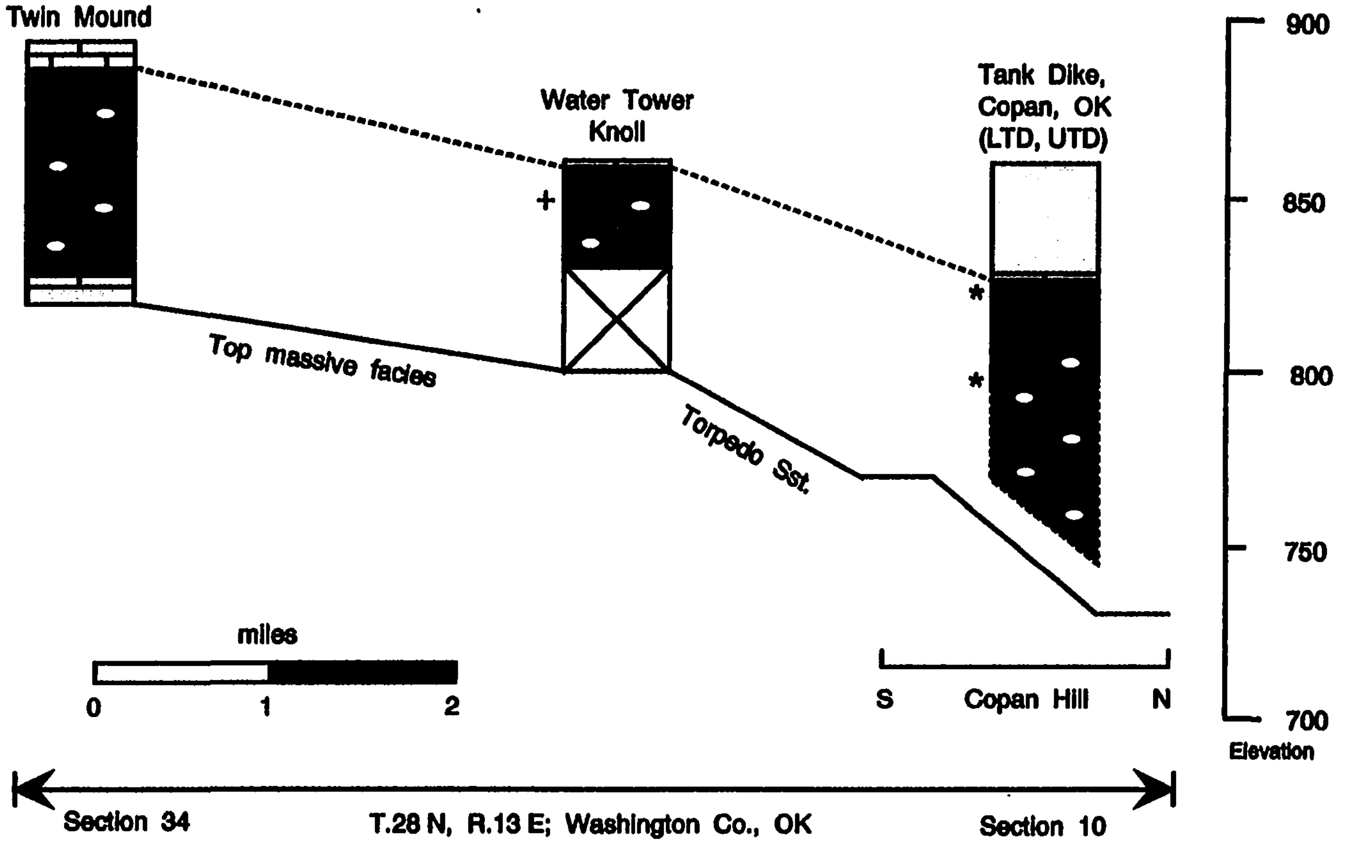

Twin Mound
Water Tower Knoll
Tank Dike, Copan, OK (LTD, UTD)
+
*
*
Top massive facies
Torpedo Sst.
900
850
800
750
700
Elevation
miles
0
1
2
S
Copan Hill
N
Section 34
T.28 N, R.13 E; Washington Co., OK
Section 10

Figure 2.14) Local structural cross section through the Stanton equivalent Barnsdall Formation from Copan Lake in the north to Bartlesville in the south. * denotes principal crinoid samples, + denotes ancillary crinoids collections. In the Copan Lake area to north these units crop out unusually far west and displays sedimentary features indicating active flexure during deposition of this cycle (see text). Anomalous south dip to Bar - Dew Lake area is adjustment to "normal" regional dip. This cycle rises dramatically over the Backius Anticline and displays a facies change from black to gray maximum flooding shale and a pronounced thinning of the fossiliferous marine regressive shales over this feature. These facies changes strongly indicate that this structure was active during deposition of this cycle.

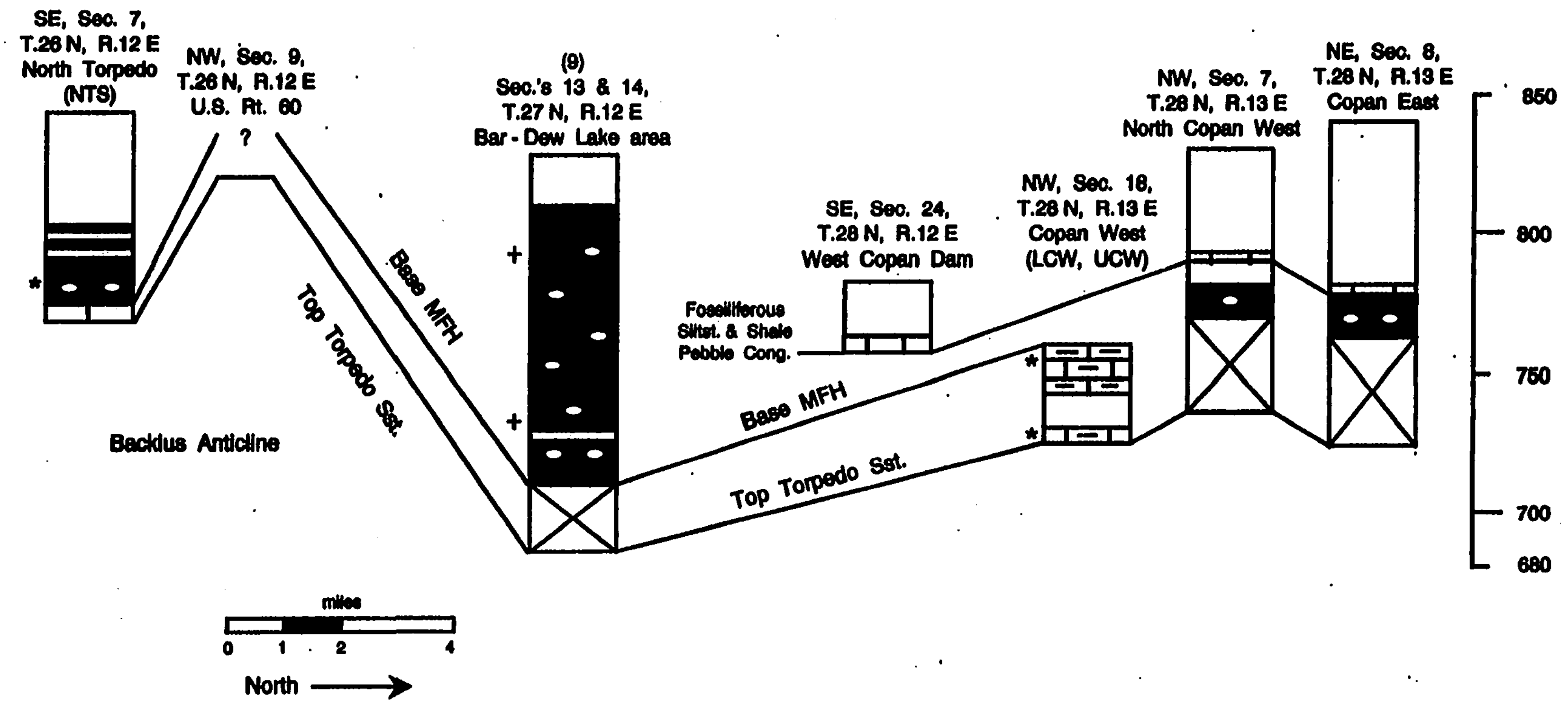

SE, Sec. 7,
T.26 N, R.12 E
North Torpedo
(NTS)
NW, Sec. 9,
T.26 N, R.12 E
U.S. Rt. 60
?
(9)
Sec.'s 13 & 14,
T.27 N, R.12 E
Bar - Dew Lake area
SE, Sec. 24,
T.28 N, R.12 E
West Copan Dam
NW, Sec. 18,
T.28 N, R.13 E
Copan West
(LCW, UCW)
NW, Sec. 7,
T.28 N, R.13 E
North Copan West
NE, Sec. 8,
T.28 N, R.13 E
Copan East
Fossiliferous
Siltst. & Shale
Pebble Cong.
Base MFH
Top Torpedo Sst.
Base MFH
Top Torpedo Sst.
Backlus Anticline
850
800
750
700
680
miles
0
1
2
4
North

Figure 2.15) Cross section through the Plattsburg cyclothem from Altoona in the north to Elk City State Park in the south (modified from Harbaugh et al., 1965; Heckel, 1978). * denotes principal crinoid samples; (#) denotes sections used to construct interregional cross sections. See text for explanation.

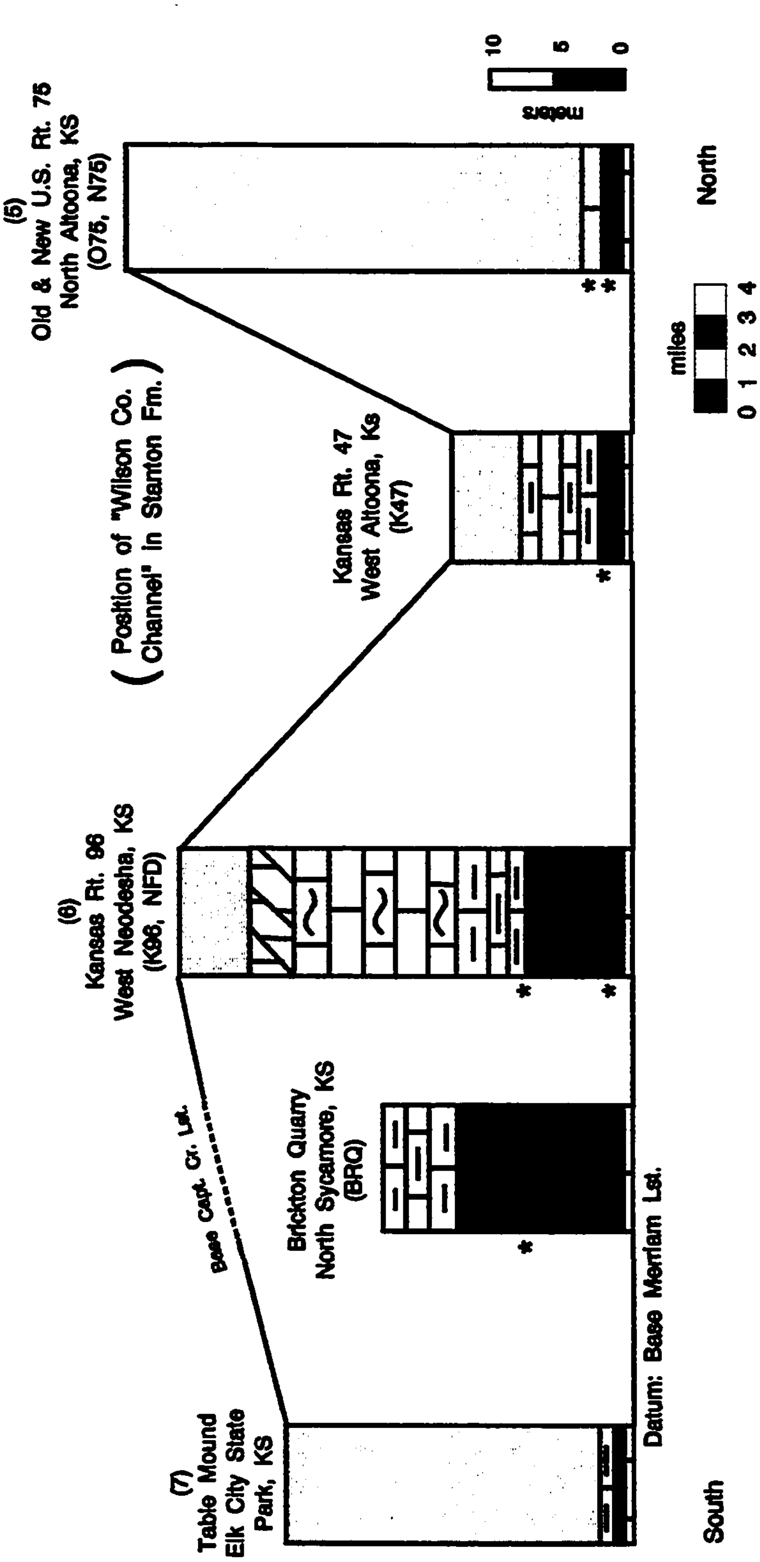
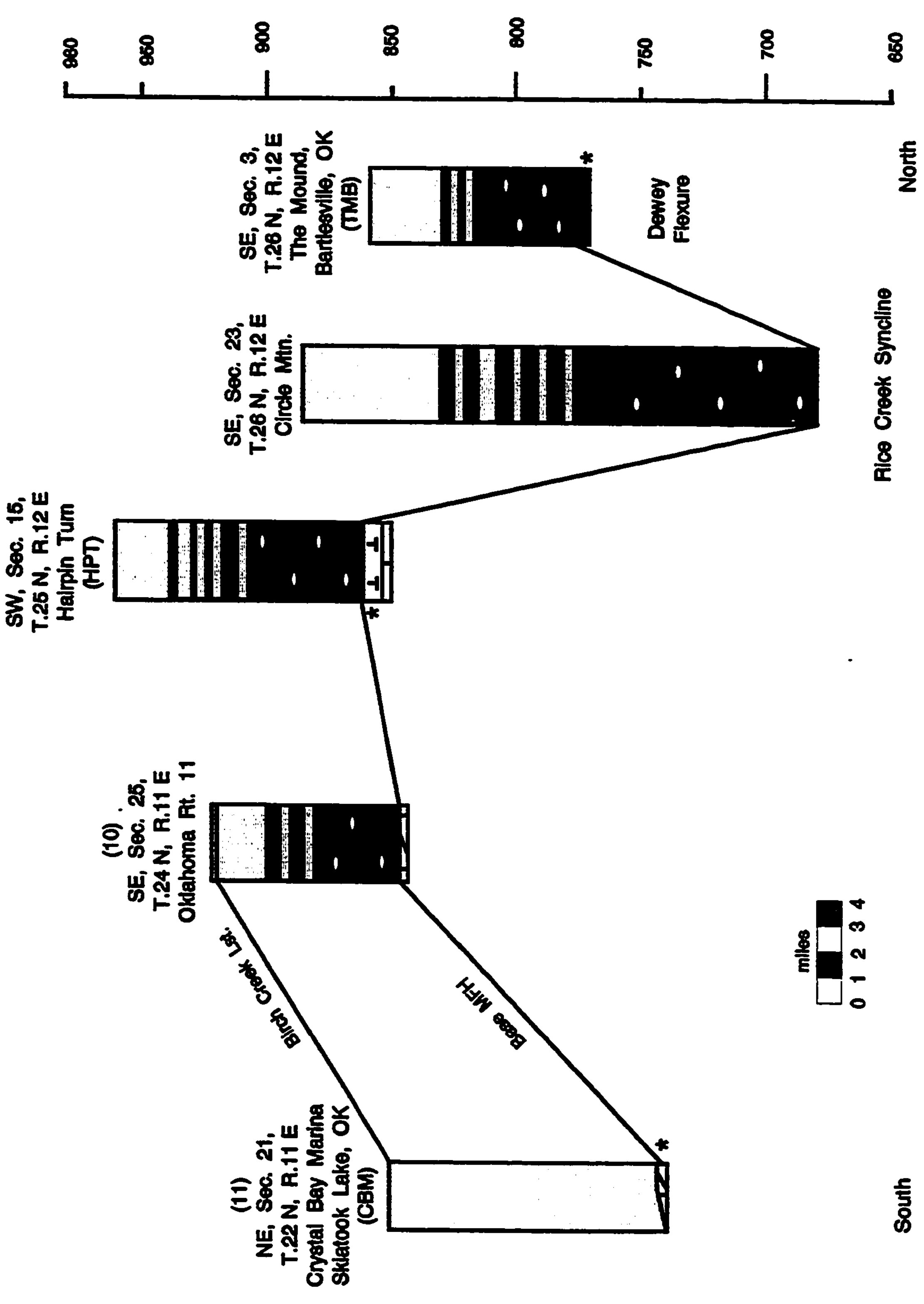

(5)
Old & New U.S. Rt. 75
North Altoona, KS
(O75, N75)
(Position of "Wilson Co. Channel" in Stanton Fm.)
Kansas Rt. 47
West Altoona, Ks
(K47)
(6)
Kansas Rt. 96
West Neodesha, KS
(K96, NFD)
Base Capt. Cr. Lst.
Brickton Quarry
North Sycamore, KS
(BRQ)
(7)
Table Mound
Elk City State
Park, KS
Datum: Base Merriam Lst.
South
North
miles
0 1 2 3 4
meters
10
5
0
*

Figure 2.16) Local structural cross section through the Plattsburg equivalent upper Wann Formation from Bartlesville in the north to Skiatook Lake to the south. * denotes principle crinoid localities; (#) denotes sections used to construct interregional cross sections. See text for explanation.


(11)
NE, Sec. 21,
T.22 N, R.11 E
Crystal Bay Marina
Skiatook Lake, OK
(CBM)
(10)
SE, Sec. 25,
T.24 N, R.11 E
Oklahoma Rt. 11
SW, Sec. 15,
T.25 N, R.12 E
Hairpin Turn
(HPT)
SE, Sec. 23,
T.26 N, R.12 E
Circle Mtn.
SE, Sec. 3,
T.26 N, R.12 E
The Mound,
Bartlesville, OK
(TMB)
Birch Creek Ls.
Base MFH
Rice Creek Syncline
Dewey
Flexure
South
North
miles
0 1 2 3 4
960
950
900
850
800
750
700
650
*
T

CHAPTER 3

PART 1

THE APPLICATION OF FILTRATION THEORY TO CRINOID ECOLOGY AND PALEOECOLOGY.

Introduction

Virtually all organisms are somehow influenced by the flow of the fluid medium in which they live, be it air or water (Vogel, 1981). Although easily taken for granted, it would be difficult to underestimate the importance of ambient flow conditions on the ecology of aquatic benthic organisms (Nowell and Jumars, 1984). The nature of the flow associated with these organisms can control dispersal and recruitment (Jumars and Nowell, 1984), generate mechanical stresses organisms must endure (Koehl, 1984; Denny, 1988), mediate respiration (Nixon et al., 1971; LaBarbera, 1982), and of particular importance to this study, determine the availability of food resources and the efficiency with which food particles can be captured by passive suspension feeders (Rubenstein and Koehl, 1977; LaBarbera, 1984).

All suspension feeders possess some type of filtering structure by which they acquire food particles. LaBarbera (1984) divided the feeding process into four stages: 1) transport of water past the filter, 2) particle capture, 3) particle transport to the mouth, 4) ingestion. The third and fourth steps can be thought of as biological processes in that different groups utilize different means of accomplishing this process, e.g., ciliary transport in a food groove, rasping of the filter elements over the mouth. The second step is dominantly a micro-scale hydrodynamic process and is thus more universal: at the level of individual particles and filter elements, different modes of "aerosol" filtration affect capture, regardless of biology (LaBarbera, 1984). Suspension feeders can be divided into two major groups which differ only in the first step; *passive* suspension feeders rely solely on external currents to bring food particles to the filtering structure, in contrast to *active* suspension feeders which must expend energy to pump fluid and particles past the filter (LaBarbera, 1984; Baumiller, 1990).

Passive suspension feeders' complete reliance on external flow makes them particularly sensitive to ambient flow conditions within a habitat (Baumiller, 1990). Modern crinoids, as passive suspension feeders, appear to be strongly affected by both microenvironmental and broader, habitat-wide flow regimes and can alter their posture and filtration fans in response to changing flow conditions (Meyer, 1973, 1982a; LaTouche, 1978; Byrne and Fontaine, 1981; Baumiller et al., 1991). Significantly, the distribution of different crinoid taxa is intimately related to basic structural differences in filtration fan morphology and differences in local flow regimes (Meyer, 1973, 1979; Macurda and Meyer, 1983; Messing and Llewellyn, 1991). Models based on the relationship of basic crinoid morphotypes to the energy regime of the depositional environment have been used successfully to interpret the distribution of Middle Mississippian crinoids of the midcontinent United States (Kammer and Ausich, 1987).

Before the significance of crinoid distribution patterns within the Lansing Group can be assessed, the mechanics of filtration feeding and the relationships between crinoid morphology and environmental conditions need to be established. Once this fundamental framework is in place, Late Paleozoic crinoids can be subdivided into functional groups, or guilds, based on morphological traits that are significant in their feeding ecology. The consistency of the onshore - offshore distribution of these guilds within the Lansing Group to filtration theory would demonstrate the importance feeding mechanics has in controlling crinoid ecology. If guilds are randomly distributed along the environmental gradient, then some other mechanism needs to be sought to interpret crinoid distribution patterns.

Filtration Theory and Crinoids

The hydrodynamics of the filtering process can be roughly broken down into two levels: 1) the behavior of individual particles and filter elements; and 2) the behavior of the entire filtering structure and fluid stream. The former is encompassed by aerosol filtration theory, the latter relates filter morphology and ambient flow conditions and thus describes the fluid flux (the volume of fluid passing through the entire filter; Baumiller, 1990).

Aerosol Filtration. Sieving, or the capture of particles larger than the gaps of a filter, is not the only means by which particles can be captured and, indeed, may not even be prevalent (Fig. 3.1; LaBarbera, 1984). Aerosol filtration mechanisms cannot only capture these large particles but, more importantly, can capture particles smaller than the mesh size of the filter (Rubenstein and Koehl, 1977; LaBarbera, 1984). The process of aerosol filtration involves four important parameters: 1) capture of small particles (<1 cm in size), 2) capturing particles with low settling velocities (neutrally buoyant), 3) flow regimes dominated by viscous forces (low Reynolds numbers), 4) particles adhering to the filter on contact. These parameters will be discussed below and put into the context of crinoid feeding.

As a rather firm generalization, filter feeding occurs at extremely small sizes, both in terms of the individual filter element and particles captured (Vogel, 1981; LaBarbera, 1984). Crinoids are no exception in that they can capture and ingest particles only up to 0.5 mm in maximum dimension (LaTouche and West, 1980; Meyer, 1982b). However, podial manipulation may allow alignment of the particle parallel to the length of the food groove making the secondary long axis more significant. In this case particles are generally less than 0.15 mm in width (Liddell, 1982). In either case, particle size is indeed small and conforms to the first parameter set out above. Additionally, most captured particles are various phytoplankton and zooplankton as well as varying amounts of organic detritus and sediment (Latouche and West, 1980; Meyer, 1982b; Liddell, 1982), most of which is rather neutrally buoyant, conforming to the second parameter listed above.

The Reynolds number (Re) is an index of flow regime, calculated as the ratio of inertial forces to viscous forces (Vogel, 1981). Three factors affect Re: kinematic viscosity, flow rate, and length of an object along the axis parallel to flow (Vogel, 1981). For the sake of this discussion, the viscosity is constant because all observations are within sea water. Thus, flow rate and object size determine Re; for rapid flow and/or large objects, fluid stream lines shear past one another, velocity gradients are steep, and turbulence prevails; Re is high. In contrast, for low flow rates and/or small objects, stream lines are uniform and do not shear, velocity gradients are mild and flow is orderly; Re is low (Vogel, 1981).

Labarbera (1984) provides a "rough rule of thumb" for figuring Re of objects in sea water: 100 times the length of the object (in cm) times the flow rate (in cm/sec). With this estimate, one can get a general sense of the magnitude of the flow regime experienced by the filtering element. For crinoids the tube feet are the operational units of particle capture and the diameter of an individual tube foot typically hovers around 0.05 mm (Meyer, 1979, 1982b; Liddell, 1982). Crinoids experience a wide range of flow conditions, but for this discussion we are interested in the maximum potential flow regime a feeding crinoid would experience at the tube feet. As current flow approaches 50 cm/sec., even robust comatulids begin to curtail feeding and seek refuge; by 75 cm/sec. feeding has effectively ceased (Meyer, 1973; LaTouche, 1978).

Using these numbers, Re would rarely exceed 25, and, more typically, would be from 1 to 10. At the lower range of Re, streamlines remain attached to the tube foot; there is no flow separation (Fig. 3.2). In the upper range flow separates from the back of the tube foot and two small counter-current eddies develop on the leeward side; however flow is still uniform and non-turbulent (Fig. 3.2; Vogel, 1981; LaBarbera, 1984). In any case these low Reynolds numbers indicate that the situation is dominated by viscous forces and flow around the tube feet is smooth, satisfying the third parameter of aerosol filtration theory listed earlier.

Finally, crinoids are armed with mucous glands within papillae on the tube feet which are activated when particles brush past (Meyer, 1982a; Byrne and Fontaine, 1983). In this way crinoids are "sticky filters" (Meyer, 1982b) where particles adhere to the tube feet and are subsequently transported and ingested. This fulfills the fourth parameter listed earlier and confirms that aerosol filtration mechanisms may be responsible and significant in the capture of particles for crinoids.

Aerosol filtration can be accomplished by four separate mechanisms (Fig. 3.1; Rubenstein and Koehl, 1977; LaBarbera, 1984). Direct interception occurs when a particle, fully entrained in flow, comes within one particle radius or less to the filter fiber and is captured. Inertial impaction takes place when a particle, either with fairly substantial mass or travelling within swift flow, crosses flow lines as flow diverges around the filter fiber and impacts the fiber by its own inertia. Gravitative deposition also involves the particle cross-cutting stream lines but in this instance under the force of gravity. Motile particle, or diffusive, capture is essentially the capture of randomly moving particles (relative to ambient flow), be they either actively mobile organisms or diffusive particles.

These mechanisms differ in their effectiveness of particle capture and are dependent on flow velocity, fiber (i.e. tube foot) volume and filter density, and particle size. For example, at a given particle size and concentration, increasing fiber volume will compress stream lines as flow diverges around the fiber, drawing particles to within the critical distance for direct interception (Fig. 3.3). This also increases flow rates via a pressure drop at the fiber, which, in turn, increases the frequency and inertia of passing particles. This increase in flow at the fiber not only increases the likelihood of direct interception, but also of inertial impaction (Rubenstein and Koehl, 1977). One drawback is that by increasing individual filter fiber volume, neighboring fibers reduce the filter gaps, thereby reducing the volume of fluid passing through the filter. Therefore, increasing ambient flow conditions will drive more fluid through the filter, compensating for this volume reduction and maintaining these capture processes. In contrast, at high flow rates motile particles would not be in the vicinity of the filter fiber long enough to allow random movement to bring it within critical capture distances. Thus, direct interception and inertial impaction are most effective with dense filters at high flow rates while motile particle capture is less effective at these high flow rates.

LaBarbera (1984) points out that most suspension feeding situations involve biological particles very close to the density of water. This, added to the fact that Reynolds numbers are low, dictates that inertial forces are low and direct interception may predominate; LaBarbera (1978) calculated that direct interception was two orders of magnitude more important than inertial impaction in aerosol filtration experiments with the brittle star *Ophiopholis aculeata*.

The efficiency of motile particle capture is, as stated above, inversely proportional to flow rate (Rubenstein and Koehl, 1977). In order to reduce flow rates around the filter fiber, fiber volume needs to decrease to reduce the pressure drop over the fiber (Fig. 3.3). Additionally, the interaction of neighboring fibers to increase flow rates also needs to be reduced, so the spacing between fibers should be increased. Thus, motile particle capture is most effective with open filters in slow flow regimes. One added thought is that although the definition of motile particle capture states that the motion of the particle is random relative to uniform flow, one could contend that the randomness of motion is more critical to the filter than to flow. Thus, multidirectional flow may impart a "random" motion to particles relative to the filter, thereby enhancing motile particle capture.

The next step is to see if the particles actually captured by crinoids and various crinoid filtration fan morphologies conform to predictions of aerosol filtration theory. A significant digression here involves the experimental test by LaBarbera (1978) on the suspension feeding of the brittle star *Ophiopholis aculeata*. This echinoderm, like crinoids, uses mucous-coated tube feet to capture particles. LaBarbera presented the brittle stars with control particles smaller than the spacing of the tube feet. Capture rates were significant and demonstrated that some form of aerosol filtration was responsible for the capture of the particles. He further demonstrated that direct interception was responsible for the capture of particles and that capture efficiency greatly increased using charged particles.

Size frequency data of crinoid gut contents presented by Rutman and Fishelson (1969), Meyer (1979, 1982b), LaTouche and West (1980), and Liddell (1982) clearly show that the vast majority of captured particles are smaller than the spacing between the tube feet, a pattern similar to that shown by LaBarbera (1978). Thus, sieving is not a meaningful means of food acquisition for crinoids and that the dominant mode is aerosol filtration.

Meyer (1973, 1979) has demonstrated that different species of comatulid crinoids have fundamentally different filtration fan morphologies and that these different morphologies are strongly correlated to the flow conditions of their respective reef microhabitats. Specifically, crinoids with closely spaced, short tube feet and planar pinnule arrays produce a dense - mesh filtration fan and feed on exposed reef positions within generally higher energy, uni-directional currents (Pinnules are small side branches of the arms which themselves do not branch - they possess a food groove and bear the tube feet). Inversely, crinoids with widely spaced, long tube feet and pinnules alternately disposed at 90 degrees produce an open mesh filtration fan and feed within the reef framework from lower energy, multidirectional currents. Meyer (1979) argued that the different fan types were well suited to exploiting food resources in their respective habitats by utilizing different modes of aerosol filtration. He stated that crinoids having a dense - mesh fan utilize direct interception in high energy environments and crinoids having more open - mesh fans utilize motile particle capture in settings of multidirectional flow.

Thus, aerosol filtration theory has excellent explanatory capabilities by coupling crinoid morphology with feeding styles and environmental conditions. However, processes at the level of aerosol filtration also have implications for the fluid dynamic behavior of the filtration system as a whole.

Filter Structure and Fluid Flux. Baumiller (1990) provided an excellent experimental and analytical study of the relationships between filter density, flow regime, and metabolic energy budgets of crinoids. This study provides the basis for the following discussion.

A filter placed within an unconstrained fluid stream will act as a partial barrier to flow. Thus, some proportion of the fluid passes through the filter while the rest of the fluid is diverted around the filter. That proportion of fluid passing through the filter is the fluid flux and depends on the ambient flow velocity of the fluid stream and the resistance of the filter to flow. Resistance is principally determined by the size and spacing of the filter fibers (the filter's density) and reflects the volume reduction of flow, as discussed previously concerning direct interception. At any given ambient flow velocity, denser filters provide more resistance to flow, causing velocities to decrease in front of the filter, which in turn reduces flux, or the volume of fluid passing through the filter.

It follows intuitively that if a filter were infinitely dense, it would be a solid plate and no fluid could pass through. To turn this around, as flow velocities decrease, the amount of flow passing through a given filter will also decrease until no fluid passes through the filter. Thus, the denser mesh the filtration fan, the more rapid the flow needs to be to drive fluid through the filter (Fig. 3.4a).

Thus, for different filter densities there are corresponding velocities below which fluids cannot be effectively sampled for food particles and the crinoid slips into an energy deficit (metabolic energy output exceeds energy input). The flow velocity at which a crinoid with a given filter density becomes functionally opaque to flow is the Minimum Velocity Threshold (MinVT)(Fig. 3.4; Baumiller, 1990). The MinVT for dense mesh crinoids will be higher than open mesh crinoids because of their increased resistance to flow (Fig. 3.4b). MinVT is also affected by the concentration of nutrients in the water mass; high concentrations of food particles will allow dense mesh crinoids to survive in lower flow environments than would be possible at "normal" concentrations.

The relationship between flux, filter density, and ambient flow velocities can also be viewed from the other extreme. Dense mesh crinoids in rapid ambient flow conditions will be able to retard flow sufficiently to allow particles to be captured and adhere to the tube feet and be transported down the ambulacral groove. Because flow can pass relatively unimpeded through their filtration fan, open mesh crinoids will not be able to sample and retain food particles effectively. This upper flow velocity limit to effective filtration is the Maximum Velocity Threshold (MaxVT)(Fig. 3.4;Baumiller, 1990). Thus, the MaxVT will be lower for open mesh crinoids than for dense mesh forms (Fig. 3.4b).

Aerosol filtration mechanisms complement the MinVT and MaxVT parameters detailed above. For instance, the MinVT for dense mesh crinoids simply implies that as flow slows, feeding efficiency deteriorates because of insufficient fluid flux. This is obviously related to direct interception, as it has been shown to be most effective for dense mesh crinoids in rapid unidirectional flow, which complements MinVT. Likewise, the concept of MaxVT implies that as flow rates increase, feeding efficiencies for open mesh crinoids decrease. Again, motile particle capture has been shown to be most effective for open mesh crinoids in slow, multidirectional flow regimes, complementing MaxVT.

There is no implied sharp break between any of these phenomena and crinoids may utilize any feeding mechanism given certain morphological and environmental constraints. From this it can be surmised that different crinoid species, given key differences in filtration fan morphology, will be optimal filters in different flow regimes - a spectrum of fan morphologies optimizing filtration along an energy gradient (Fig. 3.4b). Likewise, crinoids with similar filtration fans should have the same basic filtration limitations and should be found in similar environmental settings.

The processes of crinoid passive suspension feeding discussed in the preceding sections are based on the mechanics of how objects behave in fluids; there are no specific taxonomic parameters to these models. Because of this, these filtration models can be applied not only to other groups of suspension feeders (see Rubenstein and Koehl, 1977 and LaBarbera, 1984) but also to fossil crinoids. The only assumption is that fossil crinoids used their arms to form filtration fans as modern crinoids do.

Application to Fossil Crinoids. Late Osagean (Middle Mississippian) crinoids from the east-central United States have been the subject of paleoecological analyses which have utilized filtration theory to explain crinoid distribution patterns (Ausich, 1980; Kammer, 1985; Kammer and Ausich, 1987). These studies show that crinoids with dense mesh filtration fans (pinnule-bearing) are most abundant and characteristic in high energy settings. Specifically, poteriocrine inadunates dominate coarse clastic settings whereas monobathrid camerates dominate carbonate sand environments. Both of these taxa are inferred to have mostly used direct interception for particle capture. By contrast, crinoids with open mesh filtration fans (non-pinnulate) are dominant in low energy settings, specifically siliciclastic mudstones. These crinoids are inferred to have used motile particle capture for filtration feeding.

An important point to be made here is that the open mesh crinoids, the disparid and cyathocrine inadunates and flexibles, occur in some abundance in high energy facies, but are dominant in the low energy environments "by default" because the dense mesh forms do not range into these environments (Kammer and Ausich, 1987). Thus, the low energy mudstones host a refractory assemblage of generalist, open mesh species while the dense mesh forms can be considered high energy specialists.

One of the predictions of the model presented by Baumiller (1990) is that open mesh crinoids should be more generalized in their distribution than dense mesh forms. The rationale for this scenario is that low energy microhabitats, either produced by rough bottom topography or baffling by other organisms, can be found in high energy settings while higher energy microhabitats are unlikely to be found in dominantly low energy settings. Thus, open mesh forms can be more widely distributed across environmental gradients while dense mesh forms are restricted to higher energy settings. This theoretically predicted pattern of ubiquity, or morphology-based predictions of generalist versus specialist taxa, is empirically supported by the distribution patterns of Mississippian crinoids described by Kammer and Ausich (1987).

Body Size and Crinoids

A significant observation made by Meyer (1973, 1982) and LaTouche (1978) demonstrates that large, robust crinoids inhabit high energy environments while small, less robust crinoids live in lower energy settings. They make a reasonable interpretation that robust crinoids need a heavy framework to maintain their filtration fan and feeding position during high energy conditions. In contrast, low energy crinoids do not need to invest in a large support structure. Additionally, fully cryptic species are adapted to life within the smaller spaces of the reef framework.

Some other implications of body size differences and environmental preferences between crinoids involve metabolic energy demands and predation. Although unit mass metabolic energy rates are higher for small organisms versus large, absolute energy demands are higher for larger organisms (Peters, 1983). Additionally, crinoids that inhabit exposed, high energy settings invest more in skeletal defenses and/or experience significantly higher rates of sub-lethal predation versus crinoids in cryptic, low energy settings (Meyer, 1985, 1988; Schneider, 1988). From these points one can infer that crinoids in exposed, high energy settings, having large mass and investing resources in body armor or repair from predation, are resource exploitive and have adopted a high yield/high risk strategy; resources may be abundant and functionally easy to obtain but at the price of high energy expenditures and increased predation-induced mortality. Inversely, crinoids in low energy and cryptic habitats, with low body mass, are energy conservative; resources may be scarcer or more difficult to obtain, increasing stress by approaching the MinVT, but energy expenditures and predation risks are correspondingly lower.

Late Paleozoic Crinoid Guilds

A 'guild' is a "group of species that exploit the same class of environmental resources in a similar way" (Root, in Simberloff and Dayan, 1991). It is clear that crinoids have divergent arm morphologies and use different methods in different settings to acquire food particles. An assumption can be made, based upon the previous discussions, that crinoids with similar arm morphologies and body sizes are utilizing resources in a similar way and this therefore provides the definition of crinoid guilds.

This definition for guilds might be considered merely criteria for distinguishing functional groups. This narrow functional view would be followed if one considers guilds only as "arenas of intense competition", highlighting the interaction of species which are utilizing the same resources (Simberloff and Dayan, 1991). However, another view of guilds is one in which members are molded by adaptation to the same resources or environmental conditions, deemphasizing the competition between guild members (Root, in Simberloff and Dayan, 1991). Indeed, it has been suggested that autecological pressures can over - ride synecological interactions to produce convergence between competing guild members (Vadas, 1990). For crinoids, it seems doubtful that one species of crinoid can capture enough of the dispersed food particles in a well - mixed water mass to make it a limiting resource. Thus, competition between guild members for food may be minimal. Also, given the sensitivity of arm morphology to ambient energy conditions in food capture, crinoid guilds are here viewed as groups of crinoids which are coincidently adapted, via arm morphology and body size, to similar environmental conditions independently of competitive interactions between members.

For this study, seven crinoid guilds have been identified and are presented in Table 1. These seven guilds are subdivided between six pinnulate guilds and a non - pinnulate guild. Pinnulate crinoids have small side branches, which themselves do not branch, emanating from alternate sides of successive arm plates (brachials)(Fig. 3.5, *1-5*). Non - pinnulate crinoids have no such side branches or have ramulate side branches that are spaced between every other brachial (Fig. 3.5, *6-8*).

The pinnulate guilds are distinguished by the combination of arm branching pattern, geometry of the individual brachials, and body size (Table 1).

Two major arm branching motifs are recognized: crinoids that have more than a single arm bifurcation per ray, resulting in greater than ten arms (Fig. 3.5, *1,2,4*; 3.6, *1*) and crinoids that have only one or no arm bifurcations per ray, producing crinoids with ten arms or less. (Fig. 3.5, *3,5*; 3.6, *2,3,4*). Two major types of brachials are recognized: uniserial and biserial. Biserial brachials do not extend across the width of the arm so that successive arm plates alternate up the sides of the arm (Fig. 3.5, *1,3*). Uniserial brachials extend across the entire width of the arm (Fig. 3.5, *2,4,5*). The cutoff between large versus small body size is at approximately 8 mm of dorsal cup width. Thus, small species typically have dorsal cups smaller than 8 mm while large species typically have cups larger than 8 mm. Taken together, these guilds define a spectrum of fan densities and body sizes.

Implications for Biofacies Analysis

Baumiller (1990) points out that the flow velocity requirements of different crinoid species is a first order ecological parameter and that crinoids cannot alter their distributional limits beyond these velocity thresholds.

Given the importance that energy conditions have in controlling crinoid ecology, predictions of filtration theory state that: 1) nearshore and/or high energy settings should contain crinoid assemblages dominated by large, dense fan guilds, 2) progressively more offshore assemblages should be dominated by smaller, more open fan guilds, 3) diversities should be highest in the relatively high energy settings where both energy specialists and generalists co-occur; diversities should drop offshore as the assemblages are dominated by energy generalists.

CHAPTER 3

PART 2

DEFINITION, DISTRIBUTION, AND PERSISTENCE OF CRINOID BIOFACIES IN UPPER PENNSYLVANIAN CYCLES OF MIDCONTINENT NORTH AMERICA.

Introduction

Using a rigorous statistical procedure, Johnson (1962) identified several Pennsylvanian fossil assemblages in which the species were significantly correlated in their distribution. He referred to these Pennsylvanian "interspecific associations" as "life - assemblages" (communities), recognizing that these suites of species consistently co-occurred in particular lithologies throughout these cyclothems. His concept of quantitatively - defined species associations as communities is clearly what earlier authors had in mind in delineating faunal zones within Pennsylvanian cyclothems (Elias, 1937; Moore, 1964). He regarded these communities as groups of basically independent species with similar responses to prevailing physical environmental conditions (Johnson, 1964; 1972).

This concept of communities as coincident occurrences of basically independent species led to the idea that community boundaries should be defuse across environmental gradients (see Springer and Miller, 1990). If species continue to respond to repeated environmental changes in the same way, there is no reason why a point along the gradient would not host the same suite of species. In this way paleocommunities recur between cycles even though the species are not "locked" into an integrated unit (Hoffman, 1979; Miller, 1990a,b).

However, if conditions do not recur or if environmental variables are not correlated through time, then recurrent species associations may not be possible. The alternation of glacial - interglacial climates during the Quaternary did not involve the coordinated latitudinal expansion and contraction of temperature and precipitation belts. Rather, these meteorological variables changed independently in response to orbital forcing (Huntley and Webb, 1989). Species responded independently to these fluctuating conditions, dependent upon the environmental variables to which they were most sensitive. Because of the uniqueness of orbitally - forced climate phases, the entire global climatic milieu changed. Thus, in many instances, successive glacial or interglacial paleocommunities have no analog to any previous interglacial or glacial paleocommunities, respectively (Coope, 1979; Huntley and Webb, 1989; Bennett,1990). However, the recurrence of paleocommunities within specific phases of several cycles reflects the return of these unique conditions within the glacio - eustatic/climatic cycle.

As noted in Chapter 1, midcontinent cyclothems are aerially divisible into facies belts in which cycles develop unique vertical sequences of lithologies and biotas. However, despite these lateral facies variations, all depositional systems reflect coordinated changes in bathymetry related to glacio - eustatic sea - level change. Boardman et al. (1984) and Boardman and Malinky (1985) demonstrated that spatial variations in vertical sequences of paleocommunities were controlled by local environmental conditions, particularly siliciclastic input. However, all of these vertical sequences are linked by temporal environmental changes forced by glacio - eustatic sea level change. Similarly, Brett et al. (1986, 1990) also showed that Middle Devonian sequences and paleocommunities are strongly influenced by local facies development, but that the dominant control over all local facies sequences was basin wide sea level change. Thus, global sea level change was a first order control on paleocommunity and facies development, which was modified by local, second order controls. Crinoids in Lansing Group cyclothems should be distributed along energy gradients dictated by this complex interplay of global and local processes.

The goals of this section are 1) to determine if crinoid taxa are structured into recurrent paleocommunites, or biofacies, within cyclothems; 2) to test the consistency of filtration theory with the environmental distribution of guilds within the cyclothems; 3) to assess the persistence of the biofacies among depositional environments between cyclothems.

Methods and Procedures

Taphonomic Assumptions. The only assumptions concerning the occurrence of individuals and species within a sample are that: 1) each sample represents populations which experienced the same environmental conditions through a limited period of time and 2) individuals are sampled (both taphonomically and during collection) such that the relative abundances of species in the sample are proportional to their relative abundances in that environment during life. These points are elucidated below.

The "same environment" of the first point simply implies that there has been no gross mixing of depth zones or depositional environments through time. As Bambach and Bennington (1992) point out, the standing biomass at any instant, the seasonal variations in population density, and degree of patchiness will be lost through even moderate levels of time averaging. However, changes in depositional regime and concomitant biotic responses are correlated sufficiently to be reflected in the rock record except under conditions of extreme sedimentological condensation (see Kidwell, 1991a,b).

With respect to the second point, systematic taphonomic biases can substantially alter the original composition of the paleocommunity. The muscular and ligamentary articulation of the multiplated skeletons of all echinoderms leads to rapid disarticulation of these organisms (Lewis, 1980; Meyer and Meyer, 1986). Even given this universally rapid rate of disarticulation, styles and rates of disintegration among subtaxa of major groups are significantly different (see Greenstein, 1991; Meyer et al., 1989). Lane and Webster (1980) note that any paleoecological study that does not utilize fragmentary crinoid remains when assessing faunal composition and diversity is seriously flawed by grossly underestimating crinoid contributions to the paleocommunity. Although their emphasis is on the role crinoids play in the structure of whole paleocommunities, their point is even more germane for analyses of crinoid distribution patterns.

Although crinoidal remains may be abundant at any sample locality, articulated specimens may be rare. Utilizing fragmentary remains expands the potential sampling base and allows more meaningful comparisons between a spectrum of facies. Additionally, as pointed out by Meyer et al. (1989), various crinoid morphotypes may be more prone to disarticulation than others, regardless of taphonomic setting. It was observed during the course of this study that, although the isolated plates of some taxa were relatively common, their articulated remains were rarely, if ever, encountered. This systematic preservational bias mandated that disarticulated remains be used to assess the composition and diversity of crinoids at the various sampling localities.

Thus, collected samples do not necessarily represent "communities", but rather the biotic composition of a depositional facies during a limited period of time. Individual samples are paleocommunities, or fossil assemblages, or any of a number of terms used to describe mildly time-averaged, multispecies samples from a well defined depositional setting. However, groups of these paleocommunities can show some degree of similarity to each other. Groups of samples with similar biotic composition are here referred to as biofacies to limit any connotations to single, *in situ* biotic communities.

Derivation of Samples. Specimens, both articulated and fragmentary, used in this study were derived from two sources: field sampling and museum collections. Field sampling involved surface collecting from exposures with good stratigraphic control. If there were any questions as to the exact position of the crinoid-bearing horizon at the outcrop or in the overall stratigraphic framework, that sample was not used. Additionally, localities that had not previously been bulk-sampled for museum collections were so sampled if possible. This involved either sweeping limestone residues or excavating shale samples. Samples weighed between 5 and 10 kilograms and were either oven dried, soaked in light kerosene, and washed through a 500 micron sieve or simply washed with water through the sieve. Samples were then picked with the assistance of a low magnification jeweler's visor or binocular microscope and specimens separated into their respective taxa and counted.

Museums often contain "stratigraphic collections", which range from well curated collections of specimens from single localities and horizons to material that was never cataloged and broken up into the systematic collections. Quite often these collections include loose plates and/or washed bulk samples. If the museum locality and stratigraphic data could be verified in the field, these samples were used. Most of these samples still had to be separated into taxonomic groups and then counted. Museums from which collections were used include the University of Cincinnati Geology Museum (UCGM), Springer Collection of the National Museum of Natural History (NMNH), the University of Iowa Geology Museum(SUI), the University of Nebraska State Museum (UNSM), and collections at Bartlesville Wesleyan College (BWC).

Specimen Counts. All disarticulated remains can be confidently identified to the familial level, while many generic identifications can be made simply because their families are monogeneric during the Late Pennsylvanian. In any event, the criteria used for counting individuals within each taxa are as follows: 1) articulated crowns, dorsal cups, or portions of cups which include a unique element (e.g. infrabasal circlet or anal series) are counted as one individual; 2) disarticulated unique elements (plates of which an individual of that taxa would possess only one, e.g. fused infrabasal cone of *Paragazzisocrinus* or any of the plates comprising the anal series of cromyocrinids) are counted as one individual; 3) diagnostic radials and primibrachials were counted in multiples of five (e.g. the first five plates equals one individual, six to ten plates two individuals, eleven to fifteen plates three individuals, etc.). For this study 11,465 *individuals* from 27 different "families" were tallied between 34 samples.

Quantitative Methods. The data were subjected to a variety of numerical analyses to help elucidate underlying structure to the distribution of crinoids. These included measures of diversity and equitability, as well as multivariate statistical analyses.

All of the multivariate analyses utilize some measure of similarity between pairs of samples and variables (taxa). For this study angular measures of similarity were used. These "coefficients of proportional similarity" only measure the angular separation of sample vectors in variable space (Imbrie and Purdy, 1962). Thus, while two samples may vary greatly in the number of individuals within different variables, if the proportion of individuals within the variables is the same between samples, then their vectors differ only in magnitude and therefore have no angular separation. Cosine transformation of this angle of separation (θ), yields a similarity coefficient of one, or exact similarity. As the angle of separation between samples increases, the $\cos\theta$ measure of similarity drops. This technique can ameliorate some of the problems associated with drastic differences in sample size while still retaining the quantitative fidelity of the samples that would be lost by using rank or presence - absence measures of similarity.

The multivariate techniques used in this study assisted in defining biofacies and also helped in assessing whether these units are discretely or gradationally distributed along environmental gradients. As alluded to previously, different paleocommunity models make different predictions about how species are distributed among environments. The tracking model predicts that species distribution patterns should be highly coordinated and that boundaries between species associations (paleocommunities) should be sharp. Thus, paleocommunites should be discrete subdivisions of species along an environmental gradient. Inversely, the independent response model predicts that species are independently distributed according to their own ecological tolerances. Thus, paleocommunities should be gradational transitions of species abundance peaks distributed along environmental gradients (see Springer and Bambach, 1985; Springer and Miller, 1990).

Cluster analysis is a classification technique that divides objects into groups, or clusters (Kovach, 1988). Agglomerative, hierarchical clustering begins by tying together samples or variables that have the highest pair-wise similarity scores. Other objects, either individual samples/variables or previously tied clusters, are clustered together at successively lower levels of similarity until the entire data set is tied together at low similarity levels. This hierarchical clustering is most effectively presented as a dendrogram with branch points corresponding to levels of similarity (Kovach, 1988). For this study, clustering was performed using the "unweighted pair group method with arithmetic averaging" (UPGMA) run on a FORTRAN program written by J. Sepkoski and J. Sharry and later modified for microcomputer by A. Miller.

Q - mode analyses cluster samples based upon the similarity of their taxonomic (variable) composition. R - mode analyses cluster variables (taxa) based upon the similarity of their distribution among samples. These two analyses can be combined into a "two-way" cluster diagram in which the abundances of the different taxa are presented to highlight the structure of the R-mode and Q-mode clusters (Springer and Bambach, 1985; Miller, 1988). Two-way cluster diagrams also allow the meaningful ordering of clusters by cross referencing opposing clusters and abundance patterns.

While cluster analysis can be instrumental in identifying groups of samples as biofacies or groups of species as paleocommunities, the technique itself imposes a character upon the data which may not actually exist (Springer and Bambach, 1985; Springer and Miller, 1990). A sample may be forced into a cluster due to linkage to a single similar sample included in that cluster, yet it may bear a greater gross similarity to samples in another cluster (Warhauser and Smosna, 1981). This may be especially true for unique samples or transitional samples that have a similar proportion of one or two ubiquitous taxa yet share few others. Additionally, clustering averages successive clusters of samples and variables, producing discontinuities in the data which may not be real. Thus, other techniques may be useful in helping to elaborate upon and/or clarify patterns identified through clustering and to bring out the potential intergradation of objects.

A minimum spanning tree (MST) is a nearest neighbor plot that connects objects that have the greatest similarity (distance [1 - similarity] between objects is minimized), links all objects to at least one other object, and minimizes the sum of the distances between all objects (Warhauser and Smosna, 1981; Bjerstedt, 1988). For this study, MST's were generated using NTSYS - pc version 1.50 written by Rohlf (1989). This procedure produces a point-by-point path through the original data matrix, thereby eliminating algorithm-induced distortion to the relationships between objects (Warhauser and Smosna, 1981). The main axis, or trunk, of the tree is determined by the longest chain of linked objects, with objects at opposite ends of the tree being least similar (Bjerstedt, 1988). However, only the distances between directly linked objects have any significance and the distance between multiple objects is not additive (Bjerstedt, 1988). Thus, while the MST may be invaluable for identifying misclassified objects in cluster analysis and depicting the intergradation between clusters (Warhauser and Smosna, 1981; Bjerstedt, 1988), it cannot show the spatial similarities among objects simultaneously.

Ecological data are represented as objects within sample or variable space. For example, samples can be identified as points defined by the abundance of one taxon versus another. These two variables are easily conceptualized as axes defining a two - dimensional variable space. However, as species are continually added, the number of dimensions defining the position of samples becomes geometrically intractable and discerning patterns becomes virtually impossible. The role of ordination in ecological analysis is to reduce the dimensionality of this sample or taxonomic hyperspace while maintaining the relationships between these objects as faithfully as possible (Gauch, 1982). The primary goal of this procedure is to produce a scatter plot of samples or taxa in which similar objects are close together while dissimilar objects are far apart.

Unlike cluster analysis, ordination simply attempts to locate samples or taxa within ordination space rather than assigning membership into a group, although if the data are indeed organized into discrete groups, this would be reflected in the ordination plot (Springer and Bambach, 1985). In this way ordination is useful in graphically representing continuous variation among samples or taxa (Bjerstedt, 1988). It is more comprehensive than MST in that ordinations can simultaneously assess the relationships between all objects rather than simply constructing a chain of nearest neighbors. Two types of ordination techniques were utilized in this study.

Non - metric multidimensional scaling (MDS) was used to generate two - dimensional ordination scatter plots. This technique proved to be superior to metric techniques in producing interpretable ordinations. First, non - uniform changes in diversity and in species composition distorted metric ordinations, producing clumped plots that were difficult to resolve. MDS proved to be less sensitive to these irregularities. Second, metric distances among samples or taxa were not regarded as being intrinsically meaningful, relaxing the linear assumption of object relationships to a more generalized assumption of monotonicity between objects (simple rank order decrease in object similarities as ordination distances increase). Third, metric ordination techniques did not resolve a significant proportion of the data variability in two dimensions whereas MDS did, although this is accompanied by a certain level of distortion, called stress, which will be described below.

For this study, MDS was executed using SYSTAT version 3 (1986). MDS begins with a matrix of dissimilarity scores (1 - similarity coefficients) and assumes that there is a simple, monotonically increasing relationship between interobject dissimilarity scores and interobject ordination distances; the algorithm only uses the rank order of the interobject dissimilarity scores and not their magnitude (Fasham, 1977). With the objects ordered according to their rank dissimilarity, the algorithm generates an initial configuration of the objects and places them in Euclidean space. If the dissimilarity scores and initial ordination distances are plotted against each other, ideally a monotonically increasing curve should be produced (Fasham, 1977; Gnanadesikan, 1977). This is seldom the case and a best fit curve is constructed through the actual scatter diagram and the divergence of this curve from ideal is a measure of stress (Fasham, 1977; Gnanadesikan, 1977). The algorithm then reorganizes the ordination distances to reduce stress. This iterative process is continued until the reduction in stress between iterations is negligible or stress is reduced to zero. Different levels of stress have been given informal "goodness of fit" terms, ranging from perfect (.00) to poor (>.40), to succinctly convey how severely the original dissimilarity matrix has been distorted (Rohlf, 1989).

Plotting the MST directly on the MDS ordination can help identify the nature of the distortions in the MDS by linking objects that are far apart on the ordination (Rohlf, 1989). The MST can also identify the major gradient upon which the data may be organized by the plot of objects along the main axis of the MST (Bjerstedt, 1988).

Factor analysis is a multivariate technique that was used in this study but not in generating ordination plots. The goal of factor analysis is to reduce the variation of a data set down to a few linear combinations of composite samples and variables whose variability is more easily recognized and explained (Sepkoski, 1981). In Q - mode analysis, each sample is decomposed into a mixture of a few, uncorrelated, idealized composite samples, or factors. Each actual sample is related to each factor by a loading, which is basically the square root of the proportion of the factor contributed to the sample (Sepkoski, 1981). The idealized variable composition of each factor is indicated by the factor scores, which measures the relative importance of each variable (taxon) to that factor (Sepkoski, 1981). Thus, if a group of actual samples have high loadings for a factor, then they closely resemble that idealized sample. Taxa which have high factor scores for that factor dominate the structure of that idealized sample and therefore contribute more to the structure of the actual samples than other taxa.

The factor analysis algorithm used for this study was CABFAC, a FORTRAN program written by J. Klovan, modified by J. Sepkoski, and updated for microcomputer by A. Miller. During the course of computing these factors, the first factors often attempt to represent the average of the entire fauna, giving high factor loadings to all samples and high factor scores to a few important, but completely uncorrelated taxa. Aside from producing confusing results, this violates two important objectives of the analysis: 1) for each factor, only a subset of the samples should have high loadings; 2) each sample should have a high loading on only a limited number of factors. To alleviate this problem, a "varimax rotation" rotates the principal vectors in sample space, segregating the samples onto different factors and maximizing the variability of each factor.

Several measures of "diversity" were used to characterize the biofacies identified by the various multivariate analyses. Simple "species" richness, *S*, was employed but has obvious drawbacks when sample sizes are not comparable; small samples yield small *S*.

Although the number of taxa within an assemblage is quite important, most of the samples and biofacies were observed to have the same number of species, yet differ greatly in the distribution of individuals among taxa. Thus, measures of dominance and evenness were needed to characterize the diversity structure of the biofacies more accurately. The Shannon - Wiener index, *H*, is a measure of dominance diversity. Large values of *H* indicate that individuals are rather equally distributed among the various taxa whereas small values indicate that the assemblage is dominated by a few taxa (Peet, 1974; Dodd and Stanton, 1981).

One drawback to *H* is that it is dependent upon *S*, which was observed to vary with sample size (Dodd and Stanton, 1981). To overcome this problem a measure of evenness, *E*, was employed. This measure calculates the ratio of observed *H* to the value of *H* for that sample if all species were exactly equally abundant (Dodd and Stanton, 1981). *E* is then a measure of how closely the observed *H* is to the ideal maximum possible *H* (*H*max) for that sample; high *E* approaches maximum possible evenness, low E indicates reduced evenness.

Definition of Crinoid Biofacies within the Stanton Cyclothem

As noted in Chapter 2, the Stanton Cyclothem is the middle, major cycle of the Lansing Group. Because of its variety of facies and large number of samples (20), it was singled out for investigating crinoid distribution within a Late Paleozoic cycle. The stratigraphic and depositional settings of all crinoid-bearing localities were presented in Chapter 2.

Results: Distribution of Taxa. Table 2 presents the crinoid taxa recovered from the Stanton Formation and their assignments to the seven crinoid guilds. Over 8,600 individual crinoids representing 27 "genera" were examined (Appendix 2). A two - way cluster analysis of the Stanton crinoid data is displayed in figure 3.7. The twenty samples are grouped into five Q - mode clusters which are henceforth recognized as biofacies. Biofacies 1 is generally characterized by the presence of taxa from R - mode cluster 1, more specifically by the abundance of taxon 1 (ampelocrinids), taxon 2 (*Stellarocrinus*), taxon 6 (pirasocrinids), taxon 10 (*Delocrinus*), and taxon 11 (*Graffhamicrinus*). Biofacies 2 contains many different taxa, but is most abundant in taxon 20 (*Erisocrinus*) and taxon 23 (*Apographiocrinus*), as well as *Delocrinus* and pirasocrinids. Biofacies 3 is clearly defined by the abundance of *Apographiocrinus* and taxon 22 (*Cibolocrinus*), as well as *Erisocrinus*, *Delocrinus*, and taxon 25 (*Kallimorphocrinus*). Biofacies 4 is easily differentiated as a distinct group based upon the abundance of taxon 26 (*Exocrinus*) and *Apographiocrinus*. Biofacies 5 is basically monospecific, dominated by taxon 27 (*Paragazzisocrinus tarri*). While biofacies 3, 4, and 5 can be readily identified, biofacies 1 and 2 are more difficult to immediately recognize.

An MST of the samples and biofacies helped to elucidate clusters (Fig. 3.8). Sample TMQK (G) is readily assigned to biofacies 2 because of its single link to sample WLQK (I), a member of biofacies 2. The abundance of *Ulocrinus* (taxon 14) makes this sample unique and forced an inappropriate clustering with biofacies 1. The MST clearly shows the outlier status of this sample by plotting it at the end of a branch off the main trunk. The interpretation of sample PRQN (F) is more subtle. *Delocrinus* (taxon 10) is the most abundant taxon in this sample, as it is in sample LKCK (E). The high abundance of this ubiquitous taxon and the presence of taxa from R - mode cluster 1 in both sample F and Biofacies 1 has forged a strong link between the two. However, the abundance of *Apographiocrinus* (taxon 23) and *Erisocrinus* (taxon 20) in sample F is clearly more characteristic of biofacies 2. This is brought out by the MST, which shows a link between sample F and sample TOQK (K), a member of biofacies 3 which is rich in both *Apographiocrinus* and *Delocrinus*. Thus, for this analysis, sample F is included in biofacies 2, clearly acknowledging its transitional nature between biofacies 1 and 2.

The MST also verifies the ordering of the biofacies in the Q - mode cluster dendrogram (Fig. 3.7, 3.8). Samples of biofacies 1 are linked sequentially along the main axis of the tree. Biofacies 2 follows but is obviously strongly interlinked with members of biofacies 3. Biofacies 4 is linked to both biofacies 3 and 5 along the main axis. Thus, the assignment of biofacies numbers in sequential order along the Q - mode dendrogram is consistent with the ordering of samples and biofacies along the trunk of the MST and this ordering is regarded as indicating a significant structuring of crinoids along some ecological gradient.

To refine the assignment of samples to biofacies and to achieve a more concise understanding of the way different taxa are structuring these biofacies, factor analysis was performed. Figures 3.9 through 3.13 plot the factor loadings for each sample along the Q - mode clusters. Together, these five factors account for more than 83% of the variance of the data set. While a few samples from various biofacies may have high factor loadings for more than one factor, it is clear that each biofacies as a whole corresponds rather strongly to one of the five plotted factors. The noise may be an indication of the gradational nature of these biofacies and the inappropriate ordering of samples *within* clusters. However, the systematic association of cluster-defined biofacies and factors clearly indicates that both multivariate techniques, with all of their associated idiosyncracies, are picking out a clear signal in the distribution of these crinoids.

A review of the stratigraphic positions and depositional settings of each of the samples reveals that they are basically ordered along a depth gradient. Biofacies 1 samples include: 1) SLWO and BCQO, which are from early transgressive deposits from the southern shelf area of Oklahoma; 2) LKCK, which is from an elevated shelf position deposited during mid-transgression; 3) UTDO and WINK, which are from late regressive deposits within the southern basin. All of these samples were exposed to shallow, higher energy conditions.

Biofacies 2 samples include: 1) PRQN from an early regressive ramp setting in the northern shoreward facies belt; 2) TMQK and WLQK are from mid/late transgressive and highstand/early regressive, respectively, shelf margin algal mound-associated facies; 3) NTSO from an elevated basin position deposited during early regression; 4) LCWO from an early transgressive basinal setting. These samples represent a range of "mid - depth" settings indicative of moderate energy conditions.

Biofacies 3 samples include: 1) PHFK, 75BK, BNFK are all from mid/late transgressive basinal facies deposited within an offshore embayment; 2) TOQK from a late transgressive setting atop a elevated basin rise; 3) UCWO from a late transgressive facies within the basin; 4) UKCK from transitional latest transgressive - highstand settings atop an elevated shelf feature. All of these samples are from transgressive settings indicative of offshore, low energy conditions.

Biofacies 4 is composed of two samples from the southern basin associated with the transition from either transgressive to dysaerobic highstand deposits (ETQK) or from dysaerobic highstand to aerobic regressive facies (LTDO).

Samples from biofacies 5 (RFPK, PGSK) are associated with basinal highstand, dysaerobic molluscan faunas.

Thus far, all multivariate analyses indicate that, while each biofacies has a distinct character, transitions between some biofacies are gradational. MDS ordination was performed to elucidate the intergradational nature of the samples (Fig. 3.14). The final stress of this plot was .129, which is considered a "good" fit to the original similarity matrix (Rohlf, 1989). The samples are connected by the MST to illustrate the distortion that is present and to illustrate the gradient upon which the samples are distributed. Sample G again plots with samples from biofacies 1, yet is connected to members of biofacies 2. This folding over of branches of the MST is an indication of distortion in collapsing the multidimensional space onto two dimensions.

The MDS - MST plot of the original samples (Fig. 3.14) and the distribution of the corresponding biofacies (Fig. 3.15) clearly shows the grouping of samples into biofacies and the transition from one biofacies to the next. The distribution of the samples and biofacies in this ordination space and the trajectory of the trunk of the MST also demonstrate that the distribution of the crinoids are responding to two important environmental parameters related to depth. Biofacies 1, 2 and 3 are all basically dispersed along dimension 1 and confined to a narrow zone along dimension 2. However, biofacies 4 and 5 are trailing into negative values of dimension 2. These biofacies are associated with oxygen - stressed conditions of highstand deposits. Thus, the distribution of crinoids alone not only orders samples along a generalized depth gradient, but differentiates an energy gradient and an oxygen gradient. Thus, dimension 1 represent an energy gradient from high energy to low energy facies and dimension 2 represents an oxygen gradient from aerobic to dysaerobic facies.

Results: Distribution of Guilds. To this point, all multivariate analyses and biofacies identifications have been based upon the taxonomic composition of the samples, rather than the guild composition. Thus, while systematic patterns to the distribution of crinoids may produce distinct biofacies tied to particular environments, this may be occurring completely independent of morphology and feeding ecology. To assess the congruence of taxonomic and morphological distribution patterns, the relative abundance of each guild was determined for each sample and these abundances contoured upon the taxonomically - defined MDS environmental surface. If there is little correlation between taxonomic and morphologic distribution patterns, the contour diagrams should be very irregular with few interpretable trends across the surface. However, if there is a relationship, a recognizable abundance peak with fairly regular slopes should be identifiable. Additionally, if patterns are consistent with filtration theory, then different guilds should be most abundant within particular fields of the environmental surface.

The results of this procedure are presented in figures 3.16 through 3.19. These diagrams clearly shown that there is a correlation between taxonomically

- defined biofacies and morphotype guilds. One member of guild 4, *Paragazzisocrinus*, was excluded and plotted individually because of its unique morphology and correspondingly unique distribution pattern. The large calyx, pinnulate guilds (1 - 4) are most abundant in the higher energy fields of the environmental plots (Fig. 3.16, 3.17). The small calyx, pinnulate guilds and the non - pinnulate guild are most abundant in the lower energy fields of the environmental plots (Fig. 3.18, 3.19). The small calyx, pinnulate guild 5 and the stemless member of guild 4, *Paragazzisocrinus*, are most abundant, and indeed restricted, to the dysaerobic fields of the environmental plots (Fig. 3.18, 3.19).

The different fields of the environmental plots have been shown to correspond to different biofacies (Fig. 3.15). Thus, the distribution of guilds between samples can be summarized as the guild composition of biofacies (Fig. 3.20). This clearly shows that the shallow, high energy biofacies 1 is dominated by large calyx, pinnulate guilds 1 - 4 with minimal contributions from guilds 5 - 7. The "mid - depth" biofacies 2 has reduced contributions from guilds 1 - 4 which is compensated by contributions from guilds 6 and 7. Offshore, low energy biofacies 3 is dominated by non - pinnulate guild 7 and the small calyx, pinnulate guild 6. Offshore, transitional dysaerobic biofacies 4 is dominated by small calyx, pinnulate guilds 5 and 6. Offshore, dysaerobic mollusk - associated biofacies 5 is basically a monospecific crinoid assemblage dominated by *Paragazzisocrinus*.

While the distribution of guilds between biofacies displays a clear change in dominance of one morphotype for another along an onshore - offshore gradient, it also suggests that different biofacies were able to harbor a wider variety of guilds than others. The taxonomic structure of the biofacies was analyzed to assess whether this guild diversity pattern is translated into taxonomic diversity differences between biofacies (Table 3). Not surprisingly, the taxonomic "diversity" (equitability) of the biofacies mirrors the guild composition of the biofacies: equitable diversity structure for the shallower biofacies 1 and 2 with a change to progressively more dominance offshore in biofacies 3, 4 and 5 (Table 3).

Summary. A variety of multivariate statistical analyses reveal that the twenty crinoid samples from the Stanton cyclothem are members of five basic crinoid biofacies. These biofacies are not randomly distributed within the facies mosaic of the Stanton cyclothem, but rather are controlled by position within transgressive, highstand, or regressive systems tracts, regional paleogeographic position, and local topography. These, in turn, control the local hydrographic energy regime, which is considered paramount in crinoid ecology (Baumiller, 1990).

Biofacies 1 is found in early transgressive, late regressive, and/or elevated shelf and basinal settings disposed to shallow, higher energy conditions. It is characterized by the abundant co-occurrence of *Delocrinus*, pirasocrinids, ampelocrinids, *Stellarocrinus*, and cromyocrinids as well as the presence of other taxa included in R - mode cluster 1 of figure 3.7. These are generally dense fan, large calyx crinoids included in guilds 1 - 4.

Biofacies 2 encompasses a variety of "mid - depth" settings ranging from early regressive shelf, mid/late transgressive shelf, and early transgressive basinal settings. It contains abundant *Erisocrinus* as well as other taxa included in R - mode cluster 2. Other important taxa of biofacies 2 include pirasocrinids and *Apographiocrinus*. Thus, the crinoids of biofacies 2 represent a wide variety of guilds; high diversity is characteristic of this biofacies.

Biofacies 3 is diagnostic of mid/late transgressive basinal or transitional late transgressive - highstand shelf settings indicative of offshore, low energy conditions. It is dominated by crinoids from guilds 7 and 6, specifically the non - pinnulate *Cibolocrinus* and the small calyx, open pinnulate *Apographiocrinus*. Other crinoids of R - mode cluster 3, as well as *Delocrinus* and *Erisocrinus* of guild 2, also contribute to biofacies 3.

Biofacies 4 represents mildly dysaerobic basinal deposits associated with the transition from aerobic to dysaerobic highstand facies. It is dominated by the small calyx, pinnulate crinoids *Exocrinus* and *Apographiocrinus* of guilds 5 and 6.

Biofacies 5 is intimately associated with basinal, highstand dysaerobic molluscan faunas. It is basically a monospecific assemblage of *Paragazzisocrinus*, a unique, stemless member of guild 4.

Most of these biofacies are not discrete entities which are repeated with absolute fidelity between samples of a biofacies, with the exception of biofacies 5. Rather, biofacies are characterized by the *abundance* within a set of samples of a select group of taxa which are not abundant, but may still be present, in other samples. As the abundance peaks of different taxa shift from sample to sample, biofacies membership of the samples also shifts. This "distinct yet gradational" definition of biofacies is very much the same pattern observed by Springer and Miller (1990) for paleocommunity transitions along environmental gradients of both sub - fossil marine mollusk assemblages and Ordovician invertebrate assemblages.

The distribution of crinoid guilds and the composition of crinoid biofacies within the Stanton Formation is basically consistent with the distributional hypotheses set forth by filtration theory: large crinoids with dense mesh filtration fans are most abundant in high energy facies while small crinoids with open mesh filtration fans are dominant in low energy facies. Additionally, high and moderate energy biofacies harbor a more equitable diversity of crinoids than low energy offshore biofacies. However, exceptions and additional observations require some amendments to the simple hypotheses posed above. For example, open fan crinoids are not the most wide-spread taxa, as predicted by filtration theory. In relation to this, the low diversity offshore biofacies is not composed of "refractory generalists", but is instead composed of taxa that are unique to this biofacies. Indeed, the taxa which have the most wide spread and abundant distribution are two dense fan crinoids of guild 2, *Delocrinus* and *Erisocrinus*; this also contradicts filtration theory. These issues will be addressed after an analysis of the entire Lansing Group to assess the consistency and pervasiveness of these patterns.

The Persistence of Crinoid Biofacies between Cycles of the Lansing Group

Review of Chapter 2 shows that the Stanton cyclothem is bracketed by the two other cyclothems of the Lansing Group; the South Bend cyclothem above and the Plattsburg cyclothem below. Fourteen samples from these two intermediate cyclothems were added to the 20 samples of the Stanton cyclothem and their stratigraphic position and depositional settings are discussed in Chapter 2.

All three cycles were investigated to assess whether the five crinoid biofacies identified in the Stanton cyclothem were recognizable as repeated, persistent units. The hypotheses that, from cycle to cycle, if different combinations and abundances of crinoids were developed within the same facies (because of the vagaries of dispersal, recruitment, colonization, different rates of sea - level change, etc.) then different biofacies would be identified from cycle to cycle. This would produce a high resolution ecostratigraphic framework for the Lansing Group because cycles could be diagnosed by the unique biofacies developed within them. Multivariate statistics would delineate unique faunal signatures for each cyclothem. Alternatively, if the Stanton biofacies are persistent units, either from integration and tracking or free access to the entire crinoid species pool during the development of biofacies in each cycle, then multivariate analyses would not permit discrimination of environments among cyclothems.

Results. Taxa identified from the Lansing Group, their guild assignments, and designations for the multivariate analyses are presented in Table 4. A two - way cluster analysis of the 34 sample by 27 taxa data set shows that the five sample clusters identified in the Stanton are still recognized within the pooled data set of the Lansing Group (Fig. 3.21). Examination of the biofacies assignments of samples within the different cyclothems also shows that these additional samples are completely integrated into Stanton biofacies 1 - 3 (Table 5). The isolation of biofacies 4 and 5 could be considered an ecostratigraphic signature of the Stanton cyclothem as these biofacies were not identified within the sample sets of the South Bend and Plattsburg used for statistical analyses. However, ancillary collections from these cyclothems have produced rare specimens of *Paragazzisocrinus*, indicating the sporadic development of biofacies 5. This is consistent with stratigraphic interpretations of these two cyclothems as intermediate cycles which only locally developed oxygen - stressed facies during maximum flooding.

Plotting all abundance data, including trace percentages, points out the lack of meaningful presence - absence distribution patterns to distinguish biofacies 1 through 4 and underscores the importance of utilizing abundance data in biofacies analysis. Again, while the clusters do not seem to have discrete boundaries, the biofacies are rather clearly defined by the shifting abundance of selected taxa. While some crinoid taxa have been reassigned to different clusters, the dominant distinction of five taxonomic associations is also consistent with that observed for the Stanton cyclothem (Fig. 3.21).

R - mode MDS ordination of the taxa reveals interesting patterns in their associations. Members of R - mode clusters 1 and 2, which define biofacies 1 and 2, display a gradational distribution in ordination space (Fig. 3.22). This indicates that their segregation into two clusters may be an artifact of clustering and their abundance distribution between biofacies highly gradational. R -

mode cluster 3, defining biofacies 3, forms a distinct, although diffuse, group in ordination space. This would indicate that these taxa form a loosely related, but distinct, association whose coordinated abundance patterns define biofacies 3. R - mode groups 4 and 5 are clearly separated from other groups and each other and show the unique influence these taxa have in defining biofacies 4 and 5.

Although this R - mode ordination is based on the similar distribution patterns of individual taxa between samples, a significant observation emerges when the guild assignments are plotted in place of the individual taxonomic designations (Fig. 3.23). Groups 1 and 2 are composed entirely of large calyx, pinnulate crinoids of guilds 1 - 4, while group 3 is composed entirely of small calyx, pinnulate and non - pinnulate guilds 5 - 7. The unique taxonomic groups 4 and 5 are composed of the small calyx, pinnulate *Exocrinus* of guild 5 and the stemless guild 4 member *Paragazzisocrinus*, respectively. This pattern clearly indicates that repeated taxonomic associations reflect a higher level of coordination between similar functional groups (guilds) that tend to have correlated distributions among facies.

Q - mode MDS ordination and sample linkage by MST reveals a pattern quite similar to that of the Stanton cyclothem (Fig. 3.24). The main trunk of the MST runs from sample A to sample h with the biofacies arranged successively along the main axis. Superimposing cluster - defined biofacies boundaries on this ordination indicate that these biofacies, while rather diffuse within their fields, are more distinctly separated from one another compared to the Stanton ordination, with little intergradation of samples in ordination space (Fig. 3.25). This is interesting in that one might intuitively suspect that, with additional samples, the ordination would become more distorted because of increased sampling noise. Instead, stress levels are actually lower compared to the smaller data set of the Stanton ordination and also remains faithful to the cluster boundaries. The implication is that, with additional samples, the noise and idiosyncracies of a smaller data set from a single depositional cycle are dampened and the ordination is identifying the "cores" of variable, but distinct, crinoid associations that were repeated through the Lansing Group.

As suggested by the Stanton ordination, the distribution of crinoid taxa between samples faithfully arranges the samples into an environmental surface with a hydrographic energy gradient along the first dimension (horizontal axis) and an oxygen gradient along the second dimension (vertical axis).

To help elucidate the relationships between samples and biofacies and to clarify the taxonomic structure of the biofacies, a factor analysis was performed. These five factors accounted for over 81% of the variation in this data set. Each of the five factors has a loading peak on one of the biofacies

(Table 6). This is confirmed by the high mean factor loadings for each biofacies on one of the factors. Although the order of the taxa with the highest factor scores vary from that seen for the Stanton cyclothem factor analysis, the factor loadings and biofacies are still dominantly controlled by the same taxa.

Factor one accounted for almost 25% of the variation in this data set. The highest average factor loadings are from biofacies 3. These high factor loadings slowly decline towards high energy and dysaerobic biofacies 1 and 5, respectively. This factor is dominantly controlled by members of guild 6 (*Apographiocrinus*, graphiocrinids) and members of guild 7 (*Cibolocrinus, Kallimorphocrinus*). There is also a fairly strong contribution from *Delocrinus*, a member of guild 2. The consistency of this pattern with that of the Stanton Formation underscores the importance of guilds 6 and 7 in characterizing biofacies 3 throughout the Lansing Group cyclothems.

Factor two accounted for 23% of the variation in this data set. The highest average factor loadings are of samples from biofacies 1. These high loadings decline gradually towards biofacies 5. Like the Stanton Formation, this factor is dominantly controlled by members of guilds 1 through 4, with the strongest contribution from *Delocrinus* of guild 2.

Factor three accounted for over 20% of the variation in this data set.

The high negative loadings and scores of this factor are probably an artifact of the algorithm maintaining orthogonality between the different factors. The "highest" average loading are of members of biofacies 2. Loadings decline rather uniformly away from this biofacies.. This factor is overwhelmingly controlled by *Erisocrinus*, a member of guild 2. Compared to the Stanton Formation factor analysis, this biofacies seems to the most taxonomically volatile of the five biofacies, although the dominant role played by *Erisocrinus* in defining this biofacies is only strengthened by analysis of the entire Lansing Group.

Factor four accounted for almost 6% of the variation in this data set. The highest loadings reflects the basically monotypic biofacies 5, dominated by *Paragazzisocrinus tarri*.

Factor five accounted for over 8% of the variation in this data set. The highest average loadings are for samples form biofacies 4. This factor is controlled not only by a positive correlation to *Apographiocrinus* and *Exocrinus* of guilds 6 and 5, respectively, but also by a negative correlation to *Delocrinus* and *Cibolocrinus*. Thus, biofacies 4 is defined not only by the abundance of *Apographiocrinus* and *Exocrinus* but also by the absence of *Cibolocrinus* and *Delocrinus*, two taxa which are abundant in biofacies 1 through 3.

To this point, little attention has been paid to the distribution of crinoid guilds between samples and taxonomically - defined biofacies of the Lansing Group. As might be suspected from the consistency of biofacies and taxonomic associations between the Stanton cyclothem and Lansing Group, the gross patterns of guild abundance peaks are similar to the Stanton patterns (Fig. 3.26, 3.27). However, the surface topography of guilds 1 through 4 is more irregular, particularly guilds 1 and 3 (Fig. 3.26). This indicates some incongruence between the taxonomic composition of some of the samples, their biofacies designations, and their guild composition. The area of irregular topography is between fields of biofacies 1 and 2. These biofacies are characterized by the abundance of taxa which compose R - mode clusters 1 and 2, all members of guilds 1 - 4; they were already shown to be diffusely interrelated by R - mode ordination. The implication is that members of these guilds are only loosely confined to either of these biofacies and different samples have varying compositions of these guilds.

Guilds 5, 6 and 7 are still confined to small, well - defined areas corresponding to biofacies 3 and 4 (Fig. 3.27). This confirms that these guilds are strongly restricted to these offshore biofacies throughout the cycles of the Lansing Group.

The guild composition of the taxonomically - defined biofacies of the

Lansing Group is summarized in figure 3.28. This distribution of guilds is virtually identical to that shown by the biofacies of the Stanton cyclothem alone (Fig. 3.20). The distribution of guilds within the Plattsburg and South Bend cyclothems also strongly resembles the overall pattern within the Lansing Group (Fig. 3.29, 3.30). This persistence of biofacies guild structure along onshore - offshore gradients of Lansing Group cyclothems may reflect a fundamental level of organization of these biofacies, providing a framework within which individual taxa are assembled into "paleocommunities".

As might be expected from the guild distribution patterns, the diversity of the biofacies also mirrors that observed for the Stanton cyclothem (Table 7). Although biofacies 1, 2, and 3 have basically the same number of taxa, biofacies 1 and 2 have the more equitable distribution compared to biofacies 3, 4, and 5.

While many of the samples from biofacies 1 are from high energy and nearshore settings, they seem to represent unstressed, fully marine conditions, indicated by the fairly high diversity of this biofacies. Although the diversity of individual samples varies greatly within this facies, a subset of samples from more stressful marine environments was sought to assess the shoreward continuation of the diversity trend.

The Liberty Memorial Shale Formation (Lane Shale of past usage) is a nearshore shale unit within the Kansas City Group that lies two cycles below the Plattsburg Formation. This unit caps the Iola cyclothem in northeastern Kansas and is dominantly a silty shale with numerous micaceous siltstone stringers and abundant macerated plant material (Watney et al., 1989). Marine fossils, particularly bellerophontid gastropods, bivalves, and crinoids, are rather abundant at the base of this unit as it rests upon the top of the underlying Raytown Limestone, the regressive carbonate of the Iola Formation. This fauna represents the transition from open marine carbonate deposition to rapidly deposited deltaic shales and silts.

The taxonomic composition of this horizon is very similar to biofacies 1 (Table 7). However, the species richness and equitability of this fauna clearly shows the stressful influence of the oncoming prodeltaic wedge. This nearshore reduction in diversity helps to define a symmetrical onshore-offshore diversity pattern for Late Pennsylvanian crinoids: low diversities at nearshore and offshore extremes and the highest levels of diversity at "mid - depth".

Summary and Discussion. Crinoids from the three cyclothems of the Lansing Group are clearly not randomly distributed in space and time. Consistent associations of crinoids are recognized from samples within single cycles and are repeated between the three cyclothems. These crinoid associations are found within specific depositional settings controlled by phase of transgression and regression, regional paleogeographic position and local topography. Thus, these crinoid associations define repeated biofacies within the facies mosaic of Upper Pennsylvanian cyclothems.

Biofacies 1 is characterized by the dominance of *Delocrinus* with co-occurring pirasocrinids, ampelocrinids, *Stellarocrinus*, and cromyocrinids, as well as other crinoids of the generally dense fan, large calyx guilds 1 - 4. Biofacies 2 is dominated by the abundance of *Erisocrinus* with stenopecrinids, *Apographiocrinus*, and a uniquely wide variety of other crinoid taxa from virtually all guilds. Biofacies 3 is dominated by crinoids from guilds 6 and 7, especially the small calyx, open pinnulate *Apographiocrinus* and the non - pinnulate *Cibolocrinus*. Other important crinoids include *Delocrinus* and *Erisocrinus* of guild 2. Biofacies 4 is dominated by the small calyx, pinnulate crinoids *Exocrinus* and *Apographiocrinus* of guilds 5 and 6. Biofacies 5 is basically a monospecific assemblage of *Paragazzisocrinus*, a unique, stemless member of guild 4.

While the biofacies have been defined on the basis of their taxonomic make-up, utilizing the relationship between morphology and environment provides a more generally applicable system for future work. To convey this meaningful relationship, the biofacies are renamed according to their dominant guild structure:

The Dense Fan Biofacies (1) is found in early transgressive, late regressive, and/or elevated shelf and basinal settings disposed to shallow, higher energy conditions.

The High Guild Diversity Biofacies (2) encompasses a variety of "mid - depth" settings ranging from early regressive shelf, mid/late transgressive shelf, and early transgressive basinal settings.

The Open Fan Biofacies (3) is diagnostic of mid/late transgressive basinal or transitional late transgressive - highstand shelf settings indicative of offshore, low energy conditions.

The Small Calyx, Pinnulate Biofacies (4) is found in mildly dysaerobic basinal deposits associated with the transition from dysaerobic to aerobic highstand facies. Boardman et al. (1984) recognized the association of *Exocrinus* with dysaerobic conditions. However this biofacies was not observed to be intimately associated with a dysaerobic molluscan fauna.

The *Paragazzisocrinus*-Mature Molluscan Biofacies (5) is intimately associated with basinal, highstand dysaerobic molluscan faunas as identified by Boardman et al. (1984). This consistent association was demonstrated not only with the two samples used in the quantitative analysis, but also from ancillary collections made from all three cyclothems of the Lansing Group.

The shift in dominance from dense fan guilds to open fan guilds along an onshore - offshore gradient mirrors patterns observed by Kammer (1985) and Kammer and Ausich (1987) for Mississippian crinoids. Thus, the distribution of dominant guilds between biofacies is consistent with previous paleoecological studies, which suggest that large, dense fan crinoids are best adapted for filtration in high energy settings while smaller, open fan crinoids are best adapted for filtration in low energy settings.

One interesting observation to come from guild analysis is the consistency of guild structure within biofacies from cycle to cycle. Review of the guild and taxonomic make up of each biofacies from each cyclothem (Appendices 1 - 3) indicates that while there is some taxonomic volatility from cycle to cycle in the form of rank reorganizations and epiboles, the general proportions of the dominant guilds and their rank abundance within their biofacies remains consistent throughout the Lansing Group. This probably reflects a dominant control imposed by morphology and environment. In other words, crinoid taxa can only dominate in environments in which their filtration fan is reasonably adapted; while taxa fluctuate from cycle to cycle, members of the dominant guilds still control the structure of the biofacies. In paleoecological analysis, this cycle-to-cycle taxonomic volatility may be ameliorated by examination of pooled samples, which dampens this variation and allows the overall character of the biofacies to emerge.

Taxonomic and guild diversity patterns also reflect the interaction of morphology and environment. The moderate to high taxonomic diversities of the nearshore facies reflect the diversity of the few large calyx, dense fan guilds that dominate these environments rather than the contribution of taxa from a variety of guilds.

In the mid-depth environments, the overlapping ranges of characteristically nearshore and offshore taxa, together with taxa restricted to this biofacies, produced the high diversity. Thus, conditions must have been sufficiently energetic to allow the establishment of dense fan crinoids but not so much as to preclude the proliferation of small, open fan forms. The high diversity of mid - depth paleocommunities is a pervasive phenomenon in the Paleozoic (Sepkoski, 1988).

Diversity decreases rather dramatically offshore and reflects the stress experienced by crinoids in environments of low energy, oxygen depletion, and potentially diminished food supply and cooler temperatures. The dominance of small, open fan forms and the concomitant reduction in diversity offshore is reminiscent of the "refractory assemblages" of Mississippian offshore settings observed by Kammer and Ausich (1987). However, this pattern is not the product of simple winnowing of stenotopic nearshore taxa progressively offshore, as is predicted by filtration theory. There is an actual replacement of numerous characteristically nearshore taxa for fewer characteristically offshore taxa from onshore to offshore. This replacement is clearly demonstrated by the taxonomic and guild distinctness of the offshore biofacies, as shown by multivariate analyses.

That open fan taxa are not ubiquitous across all biofacies contradicts predictions of filtration theory and studies of fossil crinoids. Mississippian non-pinnulate crinoid genera, such as *Synbathocrinus*, *Cyathocrinites*, *Halysiocrinus*, and various flexibles, are widespread across a range of facies from the Middle Mississippian of the east-central United States (Kammer and Ausich, 1987) and are considered typical of energy-generalist morphologies (Baumiller, 1990). Inversely, non-pinnulate genera from the midcontinent Upper Pennsylvanian are found almost exclusively in the lowest energy, oxygenated facies. *Apographiocrinus*, a small, open fan pinnulate crinoid, is abundant in offshore and mid - depth facies, but accounts for only a trivial percentage of any nearshore samples (Fig. 3.21, taxon 20). The large, open fan pinnulate members of guild 4, principally ampelocrinids and cymbiocrinids, are actually diagnostic of the Dense Fan Biofacies and are restricted to nearshore settings (Figs. 3.17, 3.26). Thus, individual taxa of Pennsylvanian open fan crinoids were environmental specialists compared to the wide distribution of individual open fan taxa of the Mississippian.

The only crinoids composing a non - trivial percentage of any samples within the Dense Fan, High Guild Diversity, and Open Fan biofacies, are *Delocrinus* and *Erisocrinus* of the large calyx, dense fan guild 2 (Fig. 3.21, taxa 10 and 15, respectively). Not only are these crinoids environmentally widespread, but they are also diagnostic taxa of the Dense Fan and Diverse Guilds biofacies. That these characteristically nearshore and mid - depth crinoids, with their dense filtration fans, should range rather abundantly into the offshore Open Fan Biofacies is a strong contradiction to filtration theory. The answer to this paradox may lie within the structure of the arms themselves.

The arms of pinnulate poteriocrine crinoids, particularly *Delocrinus* and the ampelocrinid *Aesiocrinus*, are recognized as having prominent muscular articulations between brachials (Lane and Burke, 1976; Lane and Macurda, 1975). This arm musculature should have allowed a variety of feeding postures to be assumed, dependent upon prevailing flow conditions, much like modern comatulids (Meyer, 1982a). These dense fan crinoids may have been able to achieve an open fan by manipulating the position of the arms and pinnules during feeding. However, this excursion into hostile habitats was not without effect, and both *Delocrinus subhemisphericus* and *Erisocrinus typus* also display systematic ecophenotypic variation correlated with depth. This variation in *D. subhemisphericus* is an outcome of feeding stress and altered growth patterns.

The dysaerobic Small, Pinnulate and *Paragazzisocrinus* biofacies are both dominated by taxa which are basically endemic to these facies. If the onset of density stratification and dysaerobic conditions was accompanied by a thermocline (Heckel, 1991b), then these crinoids may be responding to a sharp temperature transition as well as oxygen and energy conditions, although the oxygen conditions are what appear to be best reflected in the sediment and fauna (Boardman et al., 1984). Modern stalked crinoids are very sensitive to elevated temperatures (Baumiller et al., 1991), indicating that they are specifically adapted to the cool thermal regimes of the deep ocean. *Exocrinus* and *Paragazzisocrinus* may also have been thermally adapted to cooler, deep environments rather than depleted oxygen conditions *per se*.

Paragazzisocrinus was not only unique in its distribution and isolation from virtually any other passive filters feeders, but also in its stemless morphology (Fig. 3.6, *4*). Recovery of specimens *in situ* and published reports

(Ettensohn, 1980) clearly indicate that this crinoid lived on the bottom with its infrabasal cone inserted into the substrate. This semi-infaunal lifestyle, in very clay-rich marine mud, and association with a host of gastropods and infaunal bivalves (Boardman et al., 1984), contradicts assertions of Byers and Miller (1990) that an active infauna in a muddy substrate should generate sufficient turbidity to drive crinoids from these environments, e.g. generate teiring. Latouche and West (1980) indicated that the large amount of detritus in the diet of the modern comatulid *Antedon bifida* may contain sufficient bacterial overgrowth to supply a substantial proportion of the nutrition needed by this crinoid. Thus, *Paragazzisocrinus* may actually have been adapted to feeding from turbid bottom waters contrary to the predictions of Byers and Miller (1990). The well-developed muscular articulations of this crinoid would not only provide flexibility in feeding postures, but also would provide mobility (Ettensohn, 1980) - a useful trait if dislodged by the active molluscan fauna.

Biofacies and Cyclicity. The theme repeated throughout this discussion is that crinoids were not randomly distributed across the sea - floor but, rather, were tied by morphology and feeding mechanics to specific depositional environments. Many taxa were coincidently adapted to the same environmental conditions and this shared ecological preference produced repeated species association whenever these conditions prevailed. The result is that distinct biofacies can be identified and correlated to particular depositional settings.

While these biofacies are confidently identified using multivariate techniques, individual taxa within these biofacies may vary in the latitude of their ecological tolerances. This independent response along environmental gradients makes the identification of discrete boundaries somewhat problematic, except for the dysaerobic biofacies. As noted by Springer and Miller (1990), this distinct yet gradational character makes it difficult to assess whether these taxa are simply responding independently to environmental changes or if the distinct associations, repeated in time and space, represent fairly integrated packages which track environmental zones.

Other observations shed some light onto this quandary. It is not unusual for biofacies to be omitted from vertical sequences within densely sampled areas of the study. For example, the transgressive Captain Creek Limestone sample LKCK of the Dense Fan Biofacies is immediately overlain by sample UKCK of the Open Fan Biofacies with no intervening Diverse Guilds Biofacies present. Likewise, the regressive Barnsdall Formation sample LTDO of the Small Pinnulate Dysaerobic Biofacies is overlain by sample UTDO of the Dense Fan Biofacies with apparently no other intervening biofacies. These are just two of many examples in which the vertical sequence from one biofacies to another is consistent with deepening or shallowing, yet the perfect sequential development of biofacies is not found. This is an indication that biofacies are not tracking depth zones along the sea - floor, but rather that individual biofacies are distributed according to local environmental conditions within the framework of changing sea level. However, this does not disprove the existence of integrated biofacies units, as discontinuities, rapid facies changes, and simple faunal bypass of these local features may also have produced these patterns.

However, if, among several cycles, a biofacies is consistently present somewhere within the entire facies mosaic of one hemicycle yet is entirely absent from the other, then this asymmetry in biofacies development would strongly suggest that "what comes in is *not* what goes out" and that biofacies are not tracking sea level. Not only would this indicate that taxa are not structured into integrated units, but also that environmental conditions must have been unique to one hemicycle compared to the other in order to bring together independently responding taxa into unique biofacies.

This indeed seems to be the case for the Open Fan Biofacies. This is the best represented biofacies, both in numbers of individuals and samples, in the Lansing Group (Table 7). Even with this abundance, it is consistently found associated with mid to latest transgressive systems tracts, particularly within the southern basin; it has yet to be identified in any depositional setting of any regressive systems tract. This strongly suggests that a suite of environmental factors came together during late transgression that simply did not recur during the subsequent regression. These unique conditions in turn brought together a suite of open fan crinoids which would not co-occur again during regression.

As noted earlier, the Open Fan Biofacies is strongly controlled by the abundance of non-pinnulate crinoids, particularly by the flexible *Cibolocrinus* and the disparid *Kallimorphocrinus*. While these taxa are very abundant in samples from this biofacies, they are very rare or absent in all other biofacies. Thus, conditions during transgression were conducive to the expansion and explosive population growth of these non-pinnulate forms.

As noted in the previous chapter, transgression is accompanied by many other environmental changes, including the avulsion of siliciclastics, increases in productivity, potential changes in runoff and subsequent water mass structure, and temperature regimes to name a few. While these factors certainly influence the biota, the abundance of these crinoids and the structure of this biofacies strongly suggest acute low energy conditions during mid to late transgression from sluggish bottom currents and/or the reduced influence of storm - generated waves. However, the association of sponges, brachiopods, bryozoa, and other marine invertebrates with these crinoids indicates that conditions were not stagnant to the point of oxygen depletion. It is clear that the dynamics of transgression and regression, and their influence upon Late Paleozoic marine biofacies, need to be investigated further.

The asymmetric distribution of biofacies within Lansing Group cyclothems is quite similar to biofacies patterns noted for Quaternary climate cycles (Coope, 1979; Huntley and Webb, 1989). This fragmentation and reassembly of "communities" discounts hypotheses that organisms become coadapted to their interactions and that these integrated units persist for long intervals of time (Morris, 1992; Schopf, 1992). This is not to discount the importance of species interactions when they do co-occur, but rather the influence this interaction has on biofacies persistence.

In retrospect, it may be more interesting that, given the vagaries of population, community, and environmental dynamics, recurrent associations of taxa are recognized at all.

CHAPTER 3

PART 3

FILTRATION THEORY AND CRINOID PALEOAUTECOLOGY: ONSHORE - OFFSHORE STRESS RESPONSE OF *DELOCRINUS SUBHEMISPHERICUS* IN THE STANTON FORMATION.

Introduction

As extensively discussed in the previous part, consistent co - variation in the abundance patterns of crinoids along the onshore - offshore gradient defines crinoid biofacies. Filtration theory was able to predict the distribution of crinoids based upon the density of the crinoid filtration fan and the prevailing energy conditions of the depositional environment. The inferred mechanism controlling these abundance patterns is filtering efficiency and nutrient intake, which in turn controls fitness. Thus, crinoids which inhabit environments approaching their MinVT or MaxVT are susceptible to periodic extinctions and sporadic recolonization and should only be able to maintain patchy and/or low - density populations. This resource intake/fitness mechanism has been quantitatively, or synecologically, demonstrated by the shifting dominance of crinoid taxa of different crinoid guilds along the onshore - offshore energy gradient. However, the qualitative, or autecological, affects of this mechanism has not.

The focus of this part is to investigate the stress response of a species as it approaches its minimum velocity threshold. However, analysis of the stress response provides more insight than simply how abundance patterns are generated. Understanding how a species behaves over its entire environmental range can provide significant clues as to how the species responds to various ecological pressures and its long - term evolutionary history.

As noted earlier, *Delocrinus subhemisphericus* is one of the most environmentally wide - spread and abundant crinoids in the Lansing Group. Additionally, the abundance of articulated specimens from different environmental settings of the Stanton Formation and its size - independent indicators of maturity, crucial for growth rate determinations, make this species ideal for this analysis.

Stress. In biology, and paleobiology as well, stress is a liberally used term with a wide range of meanings (Grime, 1989). Although various authors may invoke different meanings for stress, definitions of stress at the organismal and population level converge around a few central points. It is considered an external force, either physical or biotic, that reduces resource intake, growth rate, fecundity, survival probability or in some other way injures or constrains an organism as to reduce its Neo-Darwinian fitness (Calow, 1989; Grime, 1989; Parsons, 1991). The range of factors inducing organismal stress can range from daily variations in weather to catastrophic volcanism and bolide impacts. In addition to their magnitude, stresses can also vary in their frequency, being either temporary and acute "pulse" disturbances or long-term, chronic "press" stresses (Underwood, 1989).

Stresses experienced by individuals during their life span can be extended through time as stress regimes experienced by individuals throughout the history of populations in a particular environment, which in turn affects the history of the lineage. Thus, what happens at the individual level can be seen as proceeding up the ecological - evolutionary hierarchy: stress-induced variation in individual fecundity and survival controls the structure and viability of populations in different environments, influences the dispersion of populations within a region, and delimits the species' biogeographic boundaries. Temporal expansion and contraction of stress regimes, the magnitude and frequency of the stresses, and the ability of individuals and populations to cope with these stresses determines the ultimate fate of species or clades. Two well documented examples include: 1) the relationship between onshore-offshore stress gradients, dispersal ability/geographic range, and species longevity in benthic marine mollusks (Jackson, 1974; Jablonski, 1980; Jablonski and Valentine, 1981); and 2) the relationship between ecology, speciation and extinction histories, and the expansion, contraction, fragmentation, and migration of species ranges in response to Neogene climatic forcing (Coope, 1979; Huntley and Webb, 1989; Vrba, 1987). These examples serve to underscore the importance of understanding species' ecology, environmental tolerance, and response to stress, to generate potential hypotheses and models concerning evolutionary dynamics.

Framework for Stress Analysis

Although there are many ways in which organisms and populations can respond to different stresses, this study focuses on two: variations in morphology and life-history.

Morphology. Morphological responses to stress can be either genetically-based polymorphisms triggered by some environmental cue (developmental conversion) or phenotypic variation passively responding to environmental conditions (phenotypic modulation) (Smith-Gill, 1983; Stearns, 1982). Conversion can be thought of as alternative pathways of development resulting in morphs of discretely different phenotypes. Extended differentiation and modification to the alternative polymorphisms could potentially lead to speciation (West-Eberhard, 1989). Modulation acts more as a rheostat, changing the rate of development with the results being an intergrading range of morphologies. Environmentally-induced changes in the rate and timing of development can be described in terms of heterochrony (McKinney and McNamara, 1991) and the resulting morphs as heterochronic ecophenotypes (Holterhoff, 1992). Although modulation may simply result from the organism's inability to buffer external influences during development, lasting changes to the developmental sequence and other (i.e. life-history) adaptations may produce significant divergence between populations leading to heterochronic speciation (McKinney, 1986).

An obvious stress affecting growth rate is nutrient availability. Analyses of modern mollusks and echinoids show that individuals grow more rapidly and attain a larger adult size in environments with abundant, high quality food versus more resource limited environments (Cerrato, 1980; Seed, 1980; Stanton et al., 1979; Vadas, 1977). Indeed, an upper size limit can be imposed on individuals in resource - stressed environments (Sebens, 1982; Seed, 1980). This transformation of environmental variation into phenotypic variation is the reaction norm (Stearns, 1992). The relationship between growth rates, life history properties, and reaction norms will be discussed more fully in the following section.

Life History. Stearns and Koella (1986) and Stearns (1992) address the plasticity of life history traits, specifically how these traits vary to maximize fitness in the face of stresses inducing reduced growth rates. Several key points and assumptions need to be made here. They consider fitness as *r*, the population growth parameter of the Euler-Lotka equation; optimal life histories maximize *r* in any given environment. Additionally, a change in growth rate not only affects morphology via phenotypic modulation, it is also assumed to be a cue to the organism of the demographic environment to be expected, specifically environmentally - induced adult and juvenile mortality patterns. It is also assumed that fecundity and offspring quality (intrinsic juvenile survival potential) are strongly controlled by parental size and/or age at maturity; the larger and/or older the adults, the greater the fecundity and offspring survival, given equal growth rates. This is balanced by the advantages of short generation time, which increases the potential population growth rate and minimizes extrinsic juvenile mortality before first reproduction. Stearns (1992) points out that changes in age (and correlated size) at maturity and juvenile survival have particularly large impacts on fitness across a variety of life history types.

Stearns and Koella (1986) calculated optimal ages and sizes at maturity across a range of growth rates and other life history parameters. By plotting these points on an age versus size diagram, they were able to delineate optimized reaction norms, which represent the phenotypic expression of size and age at maturity given environmentally induced variations in growth rates.

The results of their analytical study are summarized in table 8.

Synthesis. The response of species along a stress gradient predicts that organisms in resource - rich environments enjoy rapid growth, attain a large adult size (accelerated ecophenotypes), mature early, have high fecundities, and experience lower mortality rates. Conversely, in resource - poor environments, or in settings in which organisms are otherwise prohibited from effective nutrient intake, individuals experience reduced growth rates (neotenic ecophenotypes), attain a smaller adult size, have reduced fecundity, and delay maturity. McKinney and McNamara (1991) state that the response to stress should be a reduction in growth and a delay in reproduction. Stearns and Koella (1986) cite several examples of this phenomenon; Vadas (1977) also demonstrated this response pattern in the echinoid *Strongylocentrotus*.

Thus, species are able to maintain viable, albeit struggling, populations in marginal habitats by adjusting life history traits in response to extrinsic stresses of reduced growth and increased mortality - a microevolutionary response to prevailing local conditions. Implicit in this description is that a species can have its growth attenuated and can adjust its life history parameters. If size, age at maturity, or developmental sequence are highly constrained, environmentally - induced modulations would not be possible. A high degree of variability for a species as a whole, in response to variable environmental conditions, could allow for habitat expansion and may itself be adaptive and therefore under selection (Caswell, 1983; McKinney and McNamara, 1991).

Intraspecific variability attributed to environmental forcing is abundantly documented in the fossil record (Alexander, 1974, 1975; Spencer, 1978,1988; Stanton et al., 1979; Ettensohn, 1980; Cisne et al., 1980, 1982; Pachut and Anstey, 1979; Pachut, 1989; Pachut and Cuffey, 1991; Johnson, 1981; Hickey, 1987; Speyer and Brett, 1988; Titus, 1989). The challenge is to isolate elements of the stress gradient and relating these to specific stress responses in the fossil record. Amplifying Stearns' (1992) comments, we need to disentangle what specific environmental parameters are fluctuating or are producing the most stress in a given setting and how these factors are affecting the organisms at hand before we can interpret phenotypic differences between populations.

Depositional Settings

This study attempts to relate differences between two paleontological populations of *Delocrinus subhemisphericus* to the onshore - offshore energy gradient of the Stanton Formation. The offshore population is from the pooled samples PHFK, BNFK, and 75BK from the upper portion of the Captain Creek Limestone west and southwest of Bolton, Montgomery County, Kansas (Fig.

2.5; 2.7, section 8). These samples lie within two kilometers of each other and are all from the same horizon and lithology and were clearly deposited during the same interval in the same environment. As covered in Chapter 2, these pooled samples, or collective Bolton locality, are in the northernmost portion of the southern basinal facies and lie within a depression between the shelf edge to the north and a rise on the Chautauqua Arch to the south (Fig. 2.11; 2.12; Heckel, 1975; Bennison, in prep.).

The intervening depression could best be considered an offshore, protected embayment and harbored a distinctive sponge - dominated fauna in a dense wackestone - packstone to boundstone (Fig. 3.31; Heckel, 1975). This locality is typical of the Open Fan Biofacies and is dominated by *Apographiogrinus typicalis* and *Cibolocrinus conicus* (Fig. 3.7; Appendix 2). As covered extensively in the previous part, this biofacies is diagnostic of very low energy conditions. Although flow appears to have been minimal, oxygen - stressed conditions did not develop as this unit does not contain a dysaerobic molluscan fauna (Boardman et al., 1984)

The basinal Captain Creek carbonate complex is immediately overlain by phosphatic black shale of the Eudora Member (Fig. 3.31; Heckel, 1975) indicating that these units were finally drowned by continued transgression and submerged below a pycnocline. (Heckel, 1977; 1991b). Thus, paleogeographic, stratigraphic, and faunal data indicate that the Captain Creek *D. subhemisphericus* population at Bolton lived in a deepening upward unit, basinward of the shelf edge break, in a protected embayment experiencing exceptionally low energy conditions with a low diversity crinoid fauna and therefore exposed to chronic press stress associated with these restricted conditions.

The nearshore population is from the Kiewitz Shale Bed of the Stoner Limestone Member of locality PRQN (Fig. 2.5; 2.6, section 2). The depositional setting of the Kiewitz bed is discussed in Chapter 2; a detailed section is provided in figure 3.32. The Kiewitz carries a diverse fauna, including productid patches in life position and fusulinids. It is overlain by an argillaceous fusulinid packstone representing an offshore shoal of the basal upper Stoner. Thus, the Kiewitz was deposited in an open marine, foreshoal setting.

The crinoid fauna, as discussed early in this chapter, supports this interpretation as it is characterized by dense-fan crinoids with an important contribution of open fan forms, indicative of the Diverse Guilds Biofacies (Fig. 3.7; Appendix 2). Thus, the Louisville population of *D. subhemisphericus* from the Kiewitz Shale lived in a shallowing - upward unit, high on the shelf, in a moderate energy setting with a high diversity fauna and although exposed to occasional pulse stresses (storms), experienced little chronic press stress.

Ontogeny and Feeding Paleoecology of *D. subhemisphericus*

Ontogeny. A brief taxonomic note is required before description of the ontogeny of *D. subhemisphericus.* The specimens here regarded as juvenile *Delocrinus* would historically be assigned to the genus *Endelocrinus.* Indeed, the developmental stages considered here correspond to different species concepts of *Endelocrinus.* This is not the first instance in which the validity of *Endelocrinus*, and its relationship to *Delocrinus*, has been questioned. Strimple (1950, 1977) has remarked on the potential juvenile - adult relationship between these genera and stated (1950) that:

> "It could be that many forms, now being considered as *Endelocrinus*, are in reality the young of *Delocrinus*...(however) it appears practical to recognize and use the genus *Endelocrinus* unless, or until, it is proven to be congeneric with *Delocrinus.*"

Although a complete taxonomic revision of *Endelocrinus* is beyond the scope of this paper, preliminary results stemming from ongoing research are enlightening.

The stratigraphic range of *Endelocrinus* not only coincides with that of *Delocrinus*, but all members of the family. Virtually every locality that produces delocrinids also produces *Endelocrinus.* At any single locality, individuals of *Endelocrinus* are invariably smaller than individuals of delocrinids.

Progressively larger individuals of *Endelocrinus* are progressively more convergent upon coeval delocrinids. The precise temporal overlap of *Endelocrinus* with all members of the "Catacrinidae", the consistent co - occurrence, consistent size differences and patterns of progressive convergence strongly suggest that *Endelocrinus* is not only the juvenile of *Delocrinus*, but also represents the juvenile stages of all members of the family.

There are many morphological features of *Delocrinus* that change during its ontogeny in addition to the obvious increase in body size. Some of these other characters can be used as size - independent indicators of maturity. Two important changes include the distal to proximal transition from uniserial to biserial arm plates, or brachials and a decrease in the height-to-width ratio of the primibrachials. Unfortunately, articulated crowns are rare, so for this study changes in the dorsal cup were used to assess maturity. Although these dorsal cup modifications form a continuum, three growth intervals can be rather easily recognized. An early juvenile stage (J1) is characterized by pronounced convexity, or tumidity, of the calyx plates and well developed dimples at B-B-R, B-R-R, and B-R-x plate triple junctions (Fig. 3.33, *1 - 3*). A late juvenile stage (J2) is characterized by suppression of plate tumidity but the retention of mild dimples, particularly at B-R-R and B-R-x plate junctions (Fig. 3.33, *4 - 6*). The mature stage (A) is characterized by smooth suturing of the entire dorsal cup

(Fig. 3.33, *7 - 8*). These three growth stages were used to assess the proportion of juvenile versus mature individuals preserved within each population so that size variation could be interpreted in light of, and independently of, juvenile mortality patterns.

Feeding Paleoecology. The importance of filtration fan morphology to crinoid autecology has been extensively covered in the previous sections. To briefly reiterate, dense mesh filtration fans are more efficient filters at higher flow conditions while open mesh fans are more optimal filters at lower flow velocities. Baumiller (1990) demonstrated that dense mesh crinoids will fall into an energy deficit at higher minimum flow velocities than open fan forms. Thus, dense fan forms should be most abundant and generally restricted to higher flow regime environments.

All mature delocrinids have a filtration fan composed of ten biserial, pinnulate arms (Fig. 3.34). This combination generates a dense mesh filtration fan and one would anticipate that *D. subhemisphericus* is best adapted for higher energy conditions. This was borne out in the previous part as *Delocrinus* is indeed the most abundant crinoid in the nearshore Dense Fan Biofacies of the Lansing Group. The corollary to this is that *D. subhemisphericus* should not be able to effectively feed in slower flow regimes. Populations in offshore, low flow habitats should have experienced stress brought on by the reduction in filtering efficiency. Thus, the hypothesis is that for *D. subhemisphericus*, stress increases *offshore*, and that any stress responses should be more pronounced in offshore populations. For this study, evidence of stress should be more pronounced in the basinal, transgressive Bolton population compared to the regressive, shoreward Louisville population.

Materials and Methods

As stated earlier in this chapter, samples for this study were examined from surface collections, bulk samples, and museum collections.

Like the biofacies analysis, these samples do not represent true "snapshot" populations; however they do represent an amalgamation, or time averaged assemblage, of populations that experienced the same environmental conditions through a limited period of time (see Richards and Bambach, 1975; Bambach and Bennington, 1992); there is no evidence that these horizons represent condensed intervals with the attendant mixture of facies (Kidwell, 1991a,b). The assumption is that the environment culled individuals from the populations such that, through time, the thanatocoenoses reflect the mortality and growth patterns imposed by that environment. Thus, if a particular set of environmental conditions imposes high juvenile mortality upon a series of populations, it is here assumed that the fossil sample will contain a large proportion of juveniles. Potential taphonomic problems associated with this assumption will be addressed explicitly in a later section. Likewise, if these same conditions cause a phenotypic response in this species, this phenotype is what will be preserved in the sample. Through the remainder of this paper, "population" refers to this type of paleontological population.

A single measure of body size was desired to simplify comparisons between populations. For this study the posterior - anterior width of the cup was used because thecal volume is clearly controlled by this parameter (fig. 3.34). Material collected during this study and specimens from the University of Nebraska State Museum were measured to the nearest 0.1 mm using vernier dial calipers. The relative maturity of each cup was noted and placed within one of the three maturity classes. Some depositional environments may preferentially disarticulate certain body types over others (Meyer et al., 1989). To assess any taphonomic biases in juvenile or adult cup preservation between localities, the width of isolated radial plates was also measured, as cup width is dictated by radial width (Fig. 3.34). From these data, various size - and maturity - based analyses were performed to characterize the two populations and facilitate their comparison. Ninety - five percent confidence intervals were calculated using the t-distribution to determine significant size differences between populations.

Results

Size frequency - maturity histograms for the two localities are presented in figure 3.35a. Both samples are normally distributed and are not qualitatively different from each other. This is also shown in the cumulative size frequency plot (Fig. 3.35b). The character of the two curves are similar, although larger individuals are lost more abruptly from the Bolton population than the Louisville population. Quantitatively, the two populations are quite different from each other. The mean and median size of the Bolton population is 4 mm smaller than that for the Louisville population, which is statistically significant at $\propto=.05$ level (Fig. 3.36a). The smallest preserved individuals are 2 mm smaller at Bolton than Louisville. In contrast, the largest individuals are 9 mm larger at Louisville than Bolton.

The populations also differ substantially in the frequency of the relative maturity groups (Fig. 3.36b). The Bolton population has a much higher proportion of juveniles, specifically the late juvenile group (J2), than does the Louisville population, which is dominated by adults.

The mean, 95% confidence interval, and maximum sizes for each maturity group were also calculated and are plotted in figure 3.37a. Although there is some overlap of the early juvenile groups between the two populations, the late juvenile and adult groups are significantly different at α=0.05 among the two populations. The differences are even more pronounced by comparing the maximum sizes attained by each group between populations; the Louisville population contains mature individuals up to 9 mm larger than the Bolton population. In contrast, the smallest adults are 3 mm smaller from the Bolton population than from the Louisville population (Fig. 3.35).

The size differences among successive growth stages are significant for the Louisville population while there is not significant differentiation among successive groups in the Bolton population (Fig. 3.37a). A growth rate plot, connecting mean and maximum sizes of growth stages, can be used to summarize these data (Fig. 3.37b). This plot shows that each Bolton growth stage is smaller than the corresponding Louisville growth stage and the rate of size increase is lower for the Bolton population than that of the Louisville population. Comparing maximum sizes shows an even more pronounced differentiation in growth rates between the two populations.

Discussion

Size Biases. A number of different factors, including current sorting, dissolution, compaction, selective predation, and sampling failure, can alter the population so that the sample no longer reflects a meaningful size frequency distribution (Richards and Bambach, 1975; Cadee, 1988; Bailey, 1990; Cate and Evans, 1992). The strata from which these populations were derived are very poorly sorted, have *in situ* components (sponge-algal-foram boundstones and productid patches), and the occurrence of articulated crinoids indicate that little current transport and sorting of skeletal material occurred at either locale. Very minute crinoid pinnular and arm ossicles have been recovered from both localities, indicating that smaller high-Mg skeletal elements were not selectively dissolved from the samples.

Biostratinomic processes, burial compaction, and sampling problems could all have contributed to biases in articulated specimens. To determine whether there were any taphonomic biases producing size - selective disarticulation between populations, the mean, 95% confidence intervals, and maximum sizes of isolated radial plates were calculated and plotted (Fig. 3.38). Although the relative growth stage of isolated radials cannot be ascertained, the size differences of the disarticulated material mirrors the size differences of the articulated populations at each locality (Fig. 3.36a), suggesting that no biases exist.

One perplexing problem is the lack of any individuals from the 1 and 2 mm size classes (Fig. 3.35). A review of the literature shows that no endelocrinids have been described from this size range and that, in fact, the minute 3 and 4 mm size classes documented here from Bolton represent the smallest (en)delocrinids yet reported. The sampling procedure should have picked up these size classes if they were present. Even if small body size mortality rates were high, the exponential decline in survivorship should still show up as a right - skewed distribution with the mode in the smallest size classes that are represented in the samples.

Two not entirely unrelated explanations may be responsible for this absence. One involves very rapid growth through the "cystidean" and very early juvenile stages - rapid enough such that random processes do not effectively sample (kill) these individuals and add them to the sample. Stanton *et al.* (1979) invoked rapid juvenile growth rates to explain the absence of small size classes in their sample of *Dendraster excentricus*. Brower (1974) has commented that modern comatulids have highly variable growth rates and that the phase between the "microcrinoid" (cystidean) - early pentacrinid stage and early adult stage can be a period of very rapid growth. The other explanation involves preservation potential: for the very small, young individuals that are killed, thecal plates are not well sutured and quickly disarticulate upon death. Indeed, rapid growth may preclude rigid suturing of the calyx. It is concluded here that rapid very early juvenile growth for all delocrinids precludes their recovery from size classes much smaller than 3 mm in cup width.

The Stress Response. It is clear that the hypothesis that *D. subhemisphericus* experienced stress offshore at the Bolton locality compared to the onshore Louisville locality is supported by the data. Significant size differences of growth stages and differences in the rate of size increase among populations shows that growth rates were reduced offshore. This is consistent with observations noted earlier for mussels and echinoids. The smaller adult sizes in the Bolton sample compared to the Louisville sample indicate that the entire developmental sequence was completed within a narrower size range, producing a population of "stunted" individuals. Indeed, the abnormally small juveniles and the size overlap of growth stages in the Bolton sample and the significant size differences among maturity classes of the Louisville sample may reflect dampening of the potentially rapid growth of the very early juvenile stage at Bolton.

As discussed earlier, the environment not only reduces growth rates, but can also impose an upper size limit beyond which individuals are not viable. These size based mortality patterns can be tied to energy consumption, in that larger individuals have higher absolute energy requirements than smaller individuals (Peters, 1983). Thus, mortality will be more intense in smaller size classes, truncating the larger size classes; this pattern will naturally include a high proportion of juveniles. This appears to be the case for the Bolton sample: there is a rapid drop in abundance above the 11 mm size class and no individuals are larger than 16 mm (Fig. 3.35). Likewise, 72% of the Bolton thanatocoenosis is composed of juveniles whereas only 32% of the Louisville sample are juveniles (Fig. 3.36b).

Thus, although some individuals at Bolton successfully survived the reduction in growth and reached maturity, most did not. The largest early juveniles from the two populations are the same size and the size differences increase with each successive growth stage (Fig. 3.37). This may be an indication that while there was some plasticity within the population, most individuals exhibited a growth trajectory to a predetermined size and experienced high juvenile mortalities. While some individuals of *D. subhemisphericus* displayed ecophenotypic heterochrony, development for many was not completely free to adapt to local conditions. If this population were entirely successful in adapting to this environment, developmental telescoping should have permitted the full attainment of maturity at even smaller sizes, and reduced juvenile mortality. Such radical changes in the developmental program of this species, if accompanied by allometric changes, would have produced morphological changes tantamount to speciation and produced a depth - related heterochronocline (McKinney and McNamara, 1991).

The implication of these patterns (decreased growth and increased juvenile mortality) for life histories of the Bolton population is that maturity was delayed (age of first reproduction) so as to increase individual fecundity to maintain *r* (Stearns, 1992; Stearns and Koella, 1986). By contrast, increased growth rates at Louisville should have caused a gain in fecundity, which should have shortened the time to maturity, maximizing *r* (Stearns, 1992; Stearns and Koella, 1986). While it is impossible to measure the fecundity or compare the absolute timing of maturation events of fossils, persistent differences in life histories between populations should produce differences in the preserved assemblages. High juvenile mortality, low fecundity, and increased generation time should produce fossil populations of relatively few individuals. Inversely, low juvenile mortality, high fecundity, and shortened generation times should produce fossil populations of many individuals. Although one potential method would be to compare absolute abundances of individuals within a standard sample size (Cate and Evans, 1992), the vagaries of sedimentation and winnowing events makes these comparisons risky (Bailey, 1990).

An alternative would be to compare how prominent *D. subhemisphericus* was in each of the two crinoid paleocommunities, assuming that random processes of sampling and taphonomy maintain realistic species proportions between biofacies; these are the very abundance differences we sought to explain. Figure 3.7 and appendix 2 show that *D. subhemisphericus* is the most abundant crinoid in the Louisville sample, composing 26% of the crinoid fauna, while at Bolton it ranks fourth, comprising only 8% of the crinoid fauna. Although not conclusive, this dichotomy suggests fundamental differences in reproductive and survival rates between the two populations. These differences in fitness are consistent with filtration theory.

The stress experienced by *D. subhemisphericus* in the offshore environment was caused by morphological limitations in individual feeding efficiency and therefore was density independent. If resource limits are density independent, then individual resource use must be conserved regardless of population density; this is a departure from classic K-selected regimes in which resource limitations are competitive and density dependent (Boyce, 1984). Selection pressure in this limited - resource stress regime involves reducing growth rates, maintaining smaller body sizes, and reducing fecundity in an attempt to conserve individual resource use (Boyce, 1984). This selection regime would produce size paedomorphs (McKinney and McNamara, 1991), specifically neotenic ecophenotypes, in an attempt to maximize individual fitness by minimizing individual resource requirements. The documented responses clearly indicate that this crinoid underwent neotenic stress selection.

Environments with abundant resources harbor species which are more exploitive in some fashion. Classic r - selected species, because of unpredictable mortality schedules, mature precociously at a small size, produce abundant young, have high population densities, and have short life spans (McKinney and McNamara, 1991). However, individuals may also exploit abundant resources by rapid growth, attain large size, mature quickly, and maintain high lifetime fecundity (Boyce, 1984; McKinney, 1990; Stearns, 1992). This was the case for mussels and echinoids mentioned earlier. In these benign settings, accelerated development maximizes individual fitness and population growth, thus establishing a peramorphic selection regime. This clearly was the situation for *D. subhemisphericus* in the onshore environment.

One important point that was tacitly assumed throughout this analysis was that growth stages between environments were indeed equivalent. Any comparisons of growth rates are moot if the growth stages compared do not represent the same state of maturity. For instance, if the abundance of juveniles in the Bolton population represent precocious adults, a progenetic response could be inferred and growth rate comparisons invalid. However, the presence of small adults at Bolton is more indicative of neoteny.

An associated problem, which does not invalidate the results, is that if growth *and* maturation rates are reduced in the offshore environment, then the growth rate comparisons are actually between older forms at Bolton versus younger forms at Louisville. Thus, the net effect of direct comparisons used here is to introduce an error that *reduces* the actual differences between the populations, differences that are already quite significant.

Summary

Paleoautecology. Paleoecological analyses often use size-frequency data to infer specific life-history properties of populations, particularly patterns of mortality (Richards and Bambach, 1975; Walker and Parker, 1976; Miller and DuBar, 1988; Cate and Evans, 1992), although this approach has come under attack (Thayer, 1977; Cadee, 1988; Bailey, 1990). It is implicit in these size-frequency analyses that growth rate and size-at-maturity are highly constrained and that any deviations in the preserved sample represent early, even juvenile, mortality. Thus the implied response to stress is timing and rate of mortality, yielding specific age-based mortality profiles for populations in different environments. While this phenomenon certainly occurs, stress can alter individual growth rates producing mean phenotypic differences between populations, differences which can obscure size - derived, age - based mortality patterns. It is thus imperative to have some sense of how growth rates may differ between environments and to have size-independent indicators of maturity for a sound foundation on which to base inferences of life history variation.

Based on size - independent indicators of maturity, onshore and offshore populations of *Delocrinus subhemisphericus* differed significantly in growth rates, mean and maximum adult size, and juvenile mortality rates. The offshore reduction in growth rate, the resulting small size of adults, and high juvenile mortalities are all clear indications of stressful conditions. This pattern is consistent with decreased feeding efficiencies offshore and supports predictions of reduced fitness made for *D. subhemisphericus* based upon filtration feeding models. Additionally, stress response models of life history traits (Boyce, 1984; Stearns and Keolla, 1986) indicate that these conditions should increase generation times and reduce fecundity to ameliorate pressure brought on by decreased nutrient intake. The combination of high juvenile mortalities, reduced fecundity, and longer generation times should have resulted in lower population densities for stressed populations versus unstressed. This abundance pattern is confirmed for *D. subhemisphericus*; onshore populations are more abundant contributors to the crinoid paleocommunity than offshore, as extensively covered earlier in the chapter.

That some individuals were able to mature at fairly small sizes indicates some flexibility in development. This is not to imply that there was necessarily a correlated genetic - environmental response, but simply that there was some plasticity to the developmental program that allowed phenotypic modulation, resulting in small adult size, given certain environmental constraints. This flexibility could be viewed as adaptive for the species as a whole as a range of microevolutionary adaptations to local environmental conditions could greatly expand its potential habitat range. Based on theoretical and observed distribution patterns, *D. subhemisphericus* was best adapted and most characteristic of onshore environments. However, it is present in every crinoid - bearing facies of the Stanton Formation (Fig. 3.7, Appendix 2). While this widespread distribution may be related to other factors such as behavioral manipulation of the filtration fan (Lane and Burke, 1976), modest developmental flexibility should have been an important component of its generalized habitat distribution.

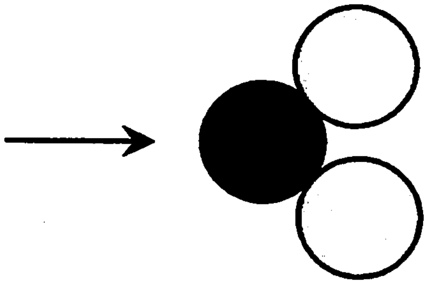
Evolutionary Prospectus. Environmentally - induced reduction in growth and delayed maturation produces size paedomorphs (McKinney and McNamara, 1991), or neotenic ecophenotypes, which are energy conservative strategies to survive resource - limited or stressful environments (Boyce, 1984; Parsons, 1991). Continued occupation of stressful habitats could select for specialized genotypes which maximize this strategy, thus abandoning the flexibility which enabled occupation of many environments by its generalist ancestors. In this way the stress response becomes fixed and genetic differentiation occurs (McKinney and McNamara, 1991). However, differentiation of *D. subhemisphericus* populations does not appear to have proceeded to this extreme.

Given the vast habitat differences and selection regimes affecting these two populations, it is paradoxical that divergence and speciation did not occur. The answer to this quandary may lie in the cyclicity of the Late Pennsylvanian. Rise and fall of sea - level during this interval forced the migration of depositional facies hundreds of miles across the North American continent (Heckel, 1980). This cyclicity has classically been invoked as a mechanism driving evolution (Moore, 1954, 1955). However, it is now suggested that cyclicity may actually inhibit speciation. In this view, species may have exhibited microevolutionary adaptations to prevailing local conditions during any particular cycle phase, but destruction and migration of habitats should have forced migrations of populations such that they were continually fragmented and recombined (Coope, 1979; Bartlein and Prentice, 1989; Bennett, 1990). Through continual recombination of populations, the likelihood for genetic fixation of specific phenotypes is reduced, resulting in stasis (Coope, 1979; Sheldon, 1990). In this way generalist species from cyclic sequences may display wide phenotypic variation among environments but may have a conservative evolutionary history (Sheldon, 1990).

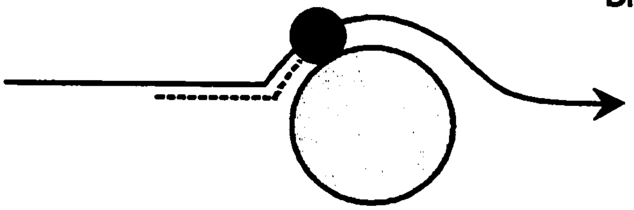
Vrba (1987) presents a somewhat similar model. Populations of resource generalists are able to adapt and migrate with climatically - induced environmental shifts, resulting in low speciation and extinction rates for these clades. In contrast, populations of resource specialists experience a mosaic of local extinction and range fragmentation during environmental shifts, resulting in high rates of speciation and extinction for these clades.

Preliminary analysis of *D. subhemisphericus* indicates that it ranges throughout all but the lowest Missourian and apparently well into the Virgilian Stage, an interval of approximately 10 Myr. It also appears that during the Missourian, only one other midcontinent *Delocrinus* species, *D. iolaensis*, can be considered originating from *D. subhemisphericus*. The evolutionary dynamics of *D. subhemisphericus* conforms well to the aforementioned evolutionary models in which ecological generalists in cyclic sequences have conservative phylogenetic histories.

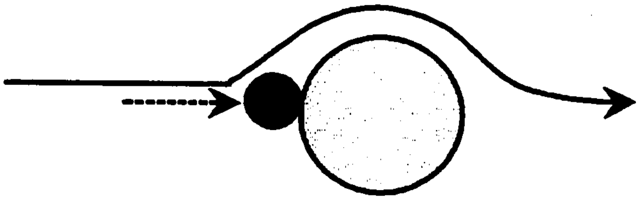
Figure 3.1) Schematic representation of filtration mechanisms. Light stippled circles are filter fibers, black circles are food particles, solid arrowed lines are flow lines, and dashed lines are particle paths. Sieving involves capturing particles larger than the filter pores and is not a mechanism of aerosol filtration. See text for explanation.



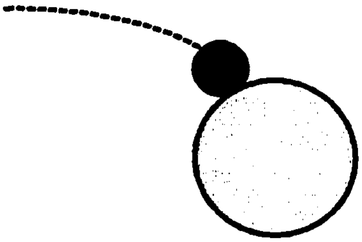
Sieving



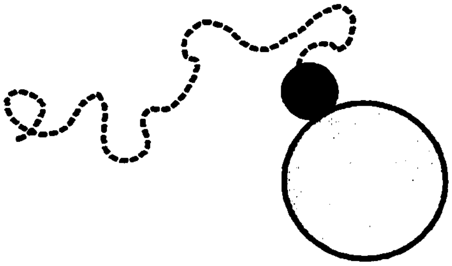
Direct Interception



Inertial Impaction

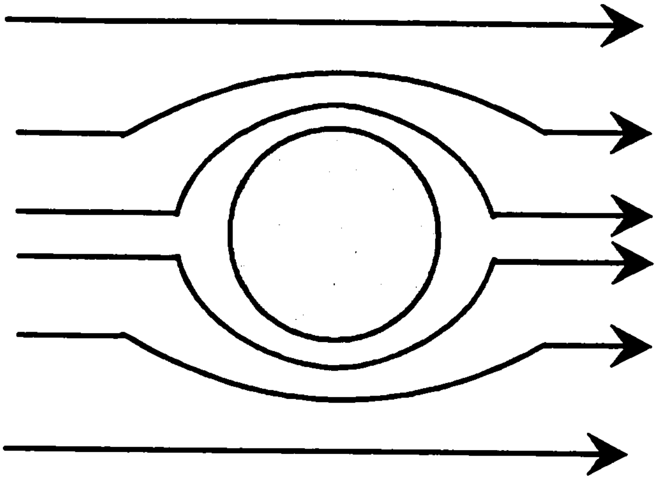


Gravitative Settling

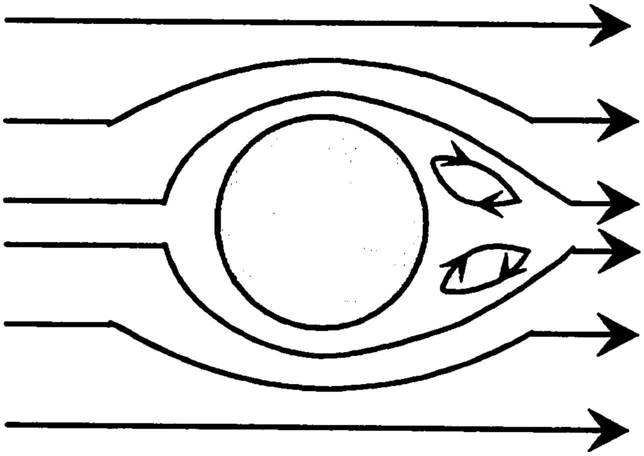


Motile Particle Capture

Figure 3.2) Behavior of fluid flow around crinoid tube feet (modified after Vogel, 1981). Reynolds numbers are generally low at this scale throughout the range of applicable flow rates. At typical flow rates, streamlines do not separate from around the tube foot and laminar flow is maintained (top). At higher flow velocities, streamlines separate on the leeward side of the tube foot and two counter current eddies develop, although flow is still uniform and non - turbulent (bottom).



Re < 10



10 < Re < 40

Figure 3.3) Influence of large versus small filter fibers on fluid streamlines. Large filter fibers (top) affect a greater thickness of fluid, compressing more severely a greater number of streamlines than small filter fibers (bottom). Particles entrained in more distant streamlines have a greater potential of touching a large filter fiber than small.

In dense mesh filtration fans, the regions of influence of neighboring filter fibers begin to touch, compounding the compression of streamlines and increasing the potential of particle capture. However, as filter density increases, filter gaps decrease and the volume of water sampled by the filter is reduced. This is a major point in the discussion on fluid flux.

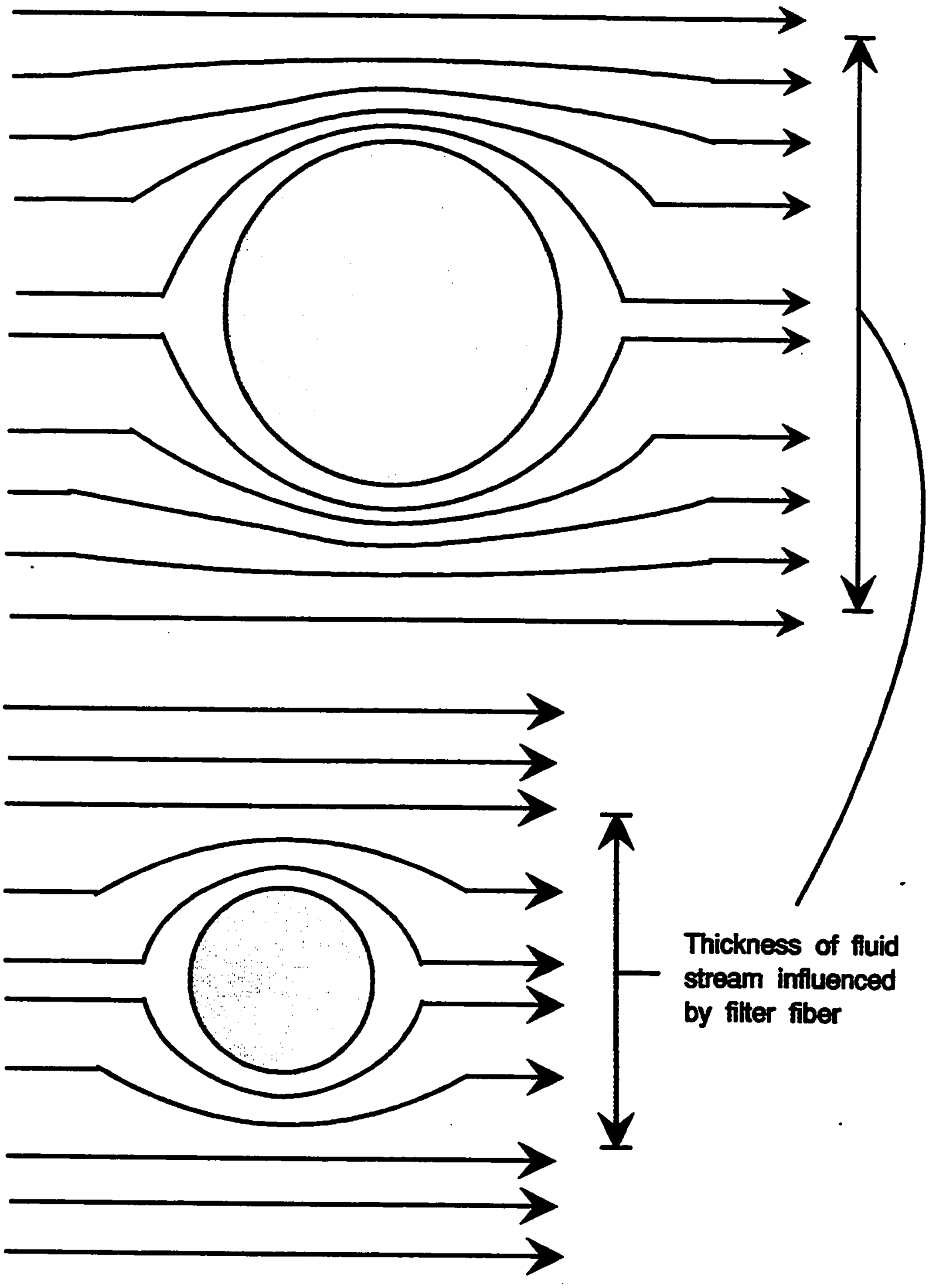
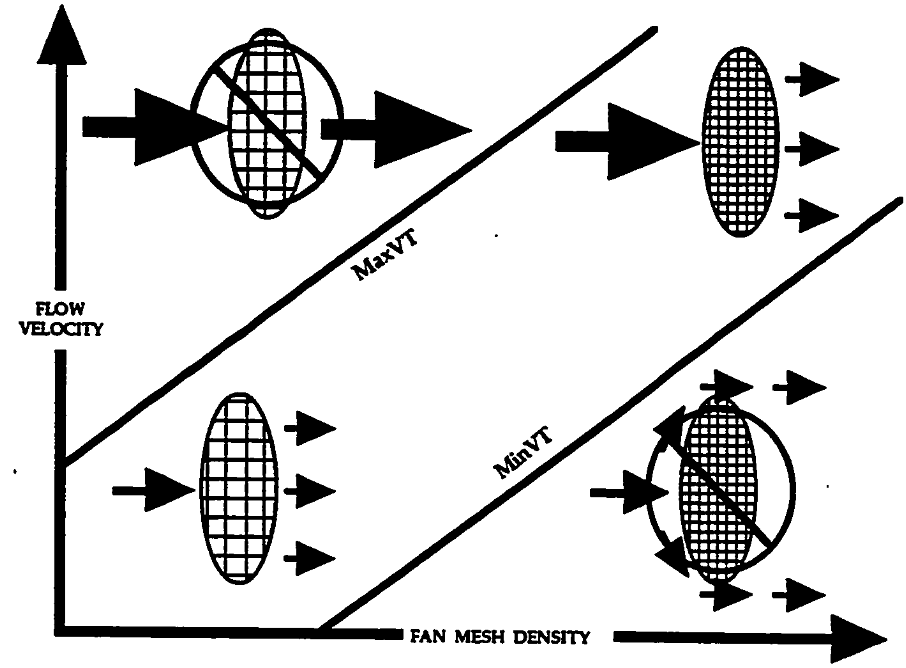
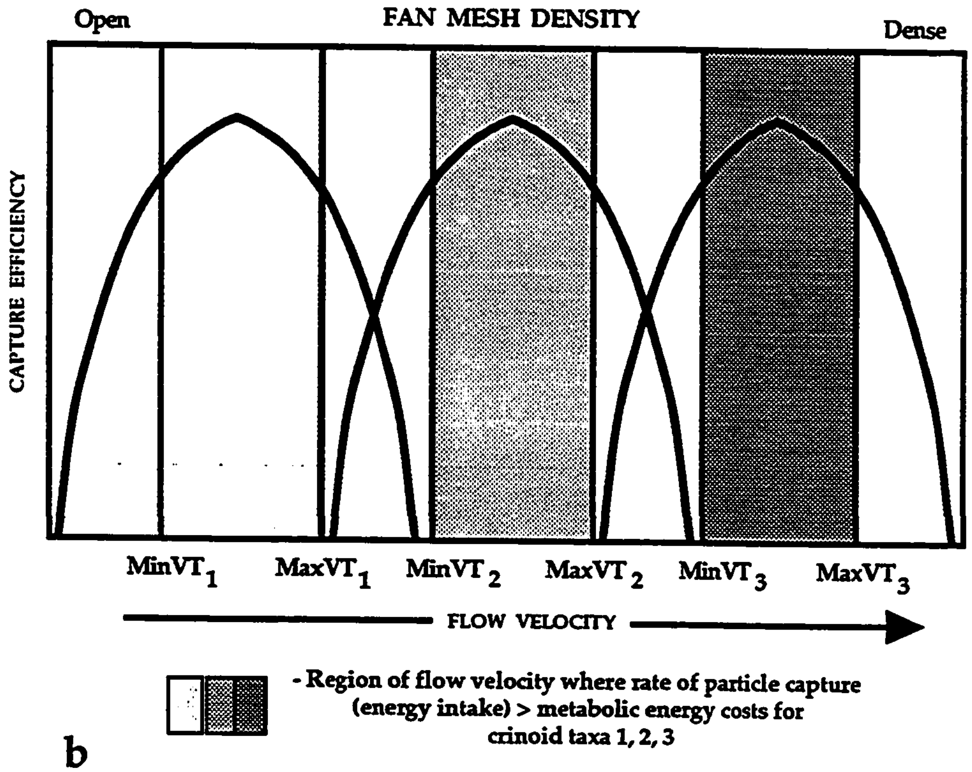

Thickness of fluid stream influenced by filter fiber

Figure 3.4) Relationships between filtration fan density and flow regime (adapted from Baumiller, 1990). a, Flow velocity versus fan mesh density. At low flow velocities, fluid flux is minimal for dense mesh crinoids, reducing their ability to effectively sample fresh fluid for food particles. Conversely, at high flow velocities open mesh crinoids cannot effectively retard flow, reducing the residence time of the fluid and inhibiting filtration. Thus, there is a positive correlation between flow velocities and fan types which defines a corridor of optimal filtration. The margins of this corridor correspond to MinVT and MaxVT.

b, Fan mesh density and flow velocity versus capture efficiencies. Different fan densities are optimal filters in different flow regimes. Thus, there should be a spectrum of fan types corresponding to differing flow regimes. Although this simple example displays clear separation and normal curves for resource utilization, in reality crinoids probably have peaks of differing heights and widths, defining specialist and generalist taxa.

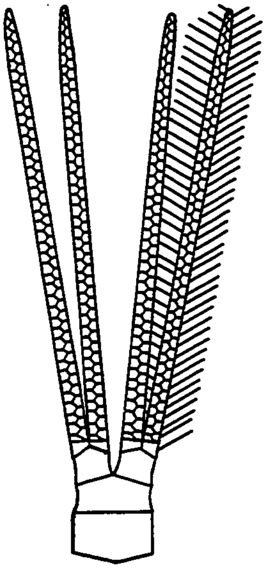

FLOW VELOCITY
MaxVT
MinVT
FAN MESH DENSITY

a

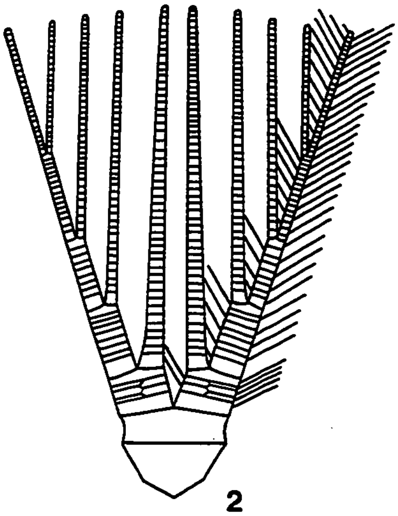

Open
FAN MESH DENSITY
Dense
CAPTURE EFFICIENCY
MinVT1
MaxVT1
MinVT2
MaxVT2
MinVT3
MaxVT3
FLOW VELOCITY
- Region of flow velocity where rate of particle capture (energy intake) > metabolic energy costs for crinoid taxa 1, 2, 3

b

Figure 3.5) Schematic of Late Paleozoic crinoid arm morphologies. View is of a typical single ray; pinnulate crinoids are shown with pinnules on right - most branch only. 1. Biserial, pinnulate, multiple branching arms producing very dense filtration fan, after *Ethelocrinus* sp. 2. Uniserial, pinnulate, multiple branching arms producing a fairly dense filtration fan, after *Eirmocrinus* sp. 3. Biserial, pinnulate arms with single bifurcation producing a fairly dense mesh filtration fan, after *Erisocrinus* sp. 4. Uniserial, pinnulate arms with multiple bifurcations producing an intermediate density filtration fan, after *Exoriocrinus* sp. 5. Uniserial, pinnulate arms with single bifurcation producing an open mesh filtration fan, after *Apographiocrinus* sp. 6. Ramulate, multiple bifurcating arms producing a very open mesh filtration fan, after *Euonychocrinus* sp. 7. Non - pinnulate arms with a single bifurcation producing a very open mesh filtration fan, after *Cibolocrinus* sp. 8. Non- pinnulate, non - branching arm producing a very open mesh filtration fan, after *Kallimorphocrinus* sp.



1



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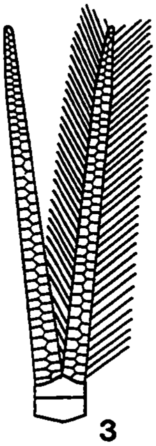

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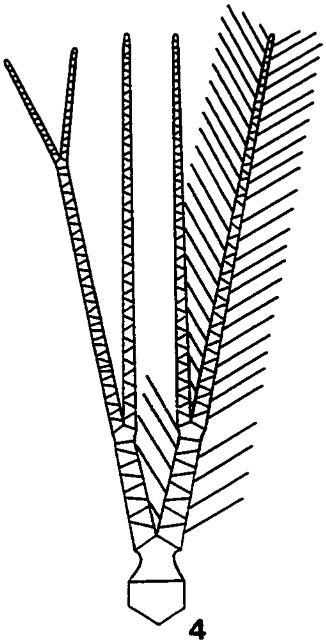

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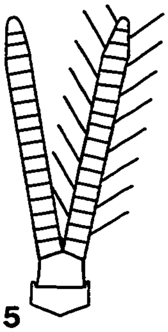

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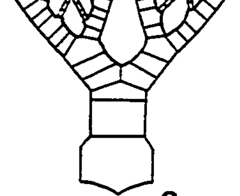

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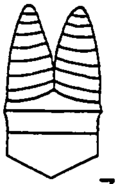

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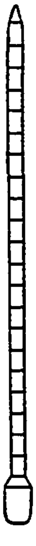


8

Figure 3.6) Photographs of selected fan - body types. *1. Exocrinus* sp. (UCGM 46494) small body type with large uniserial, pinnulate brachials and multiple bifurcations; crown height, 21.9 mm. *2. Polusocrinus* sp. (SUI 80144) large body type with uniserial, pinnulate brachials and a single bifurcation; crown height, 28.6 mm. *3. Allosocrinus* sp. (UNSM 13322) large body type with uniserial, pinnulate brachials and no bifurcations; crown height, 34.8 mm. *4. Paragazzisocrinus tarri* (UNSM) large body type with uniserial, pinnulate arms and single bifurcation; note fused, conical infrabasal circlet of this stemless crinoid; crown height, 24.8 mm.

1

3

2

4

Table 1) Criteria used for the assignment of Late Pennsylvanian crinoids into guilds.

	Pinnules	No. of Arms	Brachials	Body Size	Fan Type	Figure
Guild 1	yes	>10	biserial	large	very dense	5, *1*
Guild 2	yes	5 - 10	biserial	large	dense	5, *3*
Guild 3	yes	>10	uniserial	large	dense - intermediate	5, *2,4*
Guild 4	yes	5 - 10	uniserial	large	intermediate - open	6, *2 - 4*
Guild 5	yes	>10	uniserial	small	intermediate - open	6, *1*
Guild 6	yes	5 - 10	uniserial	small	open	5, *5*
Guild 7	no	variable	-	variable	very open	5, *6 - 8*

Table 2) Crinoid taxa identified from the Stanton Formation. These crinoids are assigned to a crinoid guild as defined in Table 1. Numbers on the right correspond to numbers on the R - mode dendrogram of the two - way cluster analysis of figure 3.7. Although camerates have been identified from the Stanton Formation, they are very rare and were not included further in the analysis.

				Guilds							
				1	2	3	4	5	6	7	
CAMERATES			Dichocrinus			●					-
			Dinacrocrinus		●						-
INADUNATES	CLADIDS	"ADVANCED CLADIDS" (POTERIOCRINES)	cromyocrinids	●							8
			Stellarocrinus	●							2
			Delocrinus		●						10
			Erisocrinus		●						20
			Graffhamicrinus		●						11
			Ulocrinus		●						14
			Exoriocrinus			●					5
			Glaukosocrinus			●					4
			laudonocrinids			●					18
			pirasocrinids			●					6
			Plummericrinus			●					3
			scytalocrinids			●					7
			"stenopecrinids"			●					16
			Terpnocrinus			●					13
			ampelocrinids				●				1
			cymbiocrinids				●				9
			Elibatocrinus				●				15
			Paragassizocrinus				●				27
		CYATHOCRINES	Exocrinus					●			26
			Galateacrinus					●			17
			Apographiocrinus						●		23
			graphiocrinids						●		12
			Lecythiocrinus							●	19
	DISPARIDS		Kallimorphocrinus							●	25
FLEXIBLES			Cibolocrinus							●	22
			Euonychocrinus							●	21
			Paramphicrinus							●	24

Designation in R-mode cluster analysis: ▲

Figure 3.7) Two - way cluster diagram of localities and crinoid taxa from the Stanton Formation. Dendrograms link individual objects and clusters at differing levels as indicated by the similarity scales adjacent to the dendrograms. The relative abundances of the different taxa within each sample are indicated; note shifting abundance peaks from upper left to lower right. This analysis identifies five taxonomic associations (R - mode clusters 1 - 5, left to right) and five sample associations, or biofacies (Q - mode clusters 1 - 5, top to bottom).

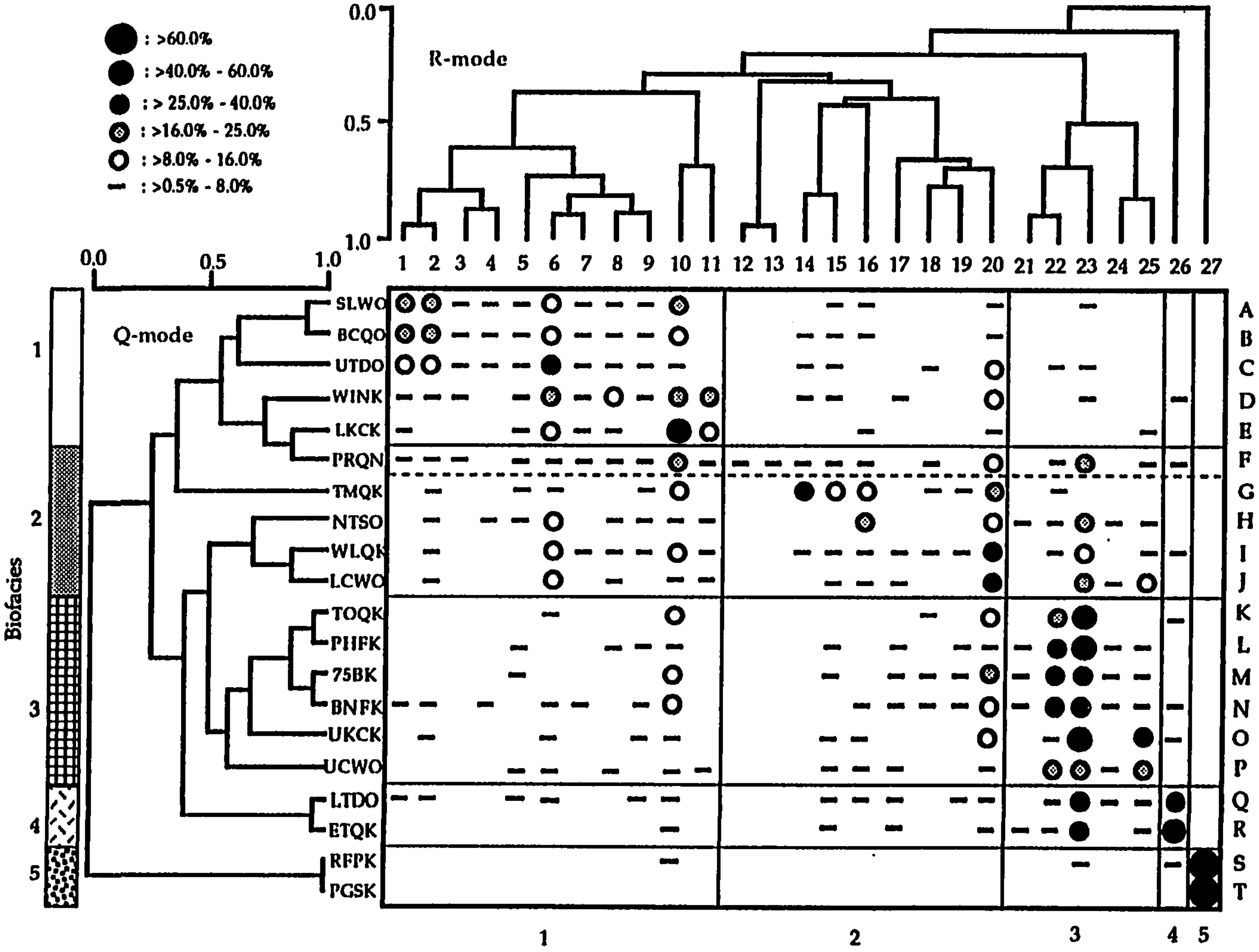

: >60.0%
: >40.0% - 60.0%
: > 25.0% - 40.0%
: >16.0% - 25.0%
: >8.0% - 16.0%
: >0.5% - 8.0%
R-mode
0.0
0.5
1.0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27
Q-mode
0.0
0.5
1.0
SLWO
BCQO
UTDO
WINK
LKCK
PRQN
TMQK
NTSO
WLQK
LCWO
TOQK
PHFK
75BK
BNFK
UKCK
UCWO
LTDO
ETQK
RFPK
PGSK
A B C D E F G H I J K L M N O P Q R S T
Biofacies
1
2
3
4
5

Figure 3.8) Q - mode Minimum Spanning Tree (MST) of the Stanton localities. MST orders localities in relative depth succession from nearshore biofacies 1 to offshore biofacies 5. See text for discussion.

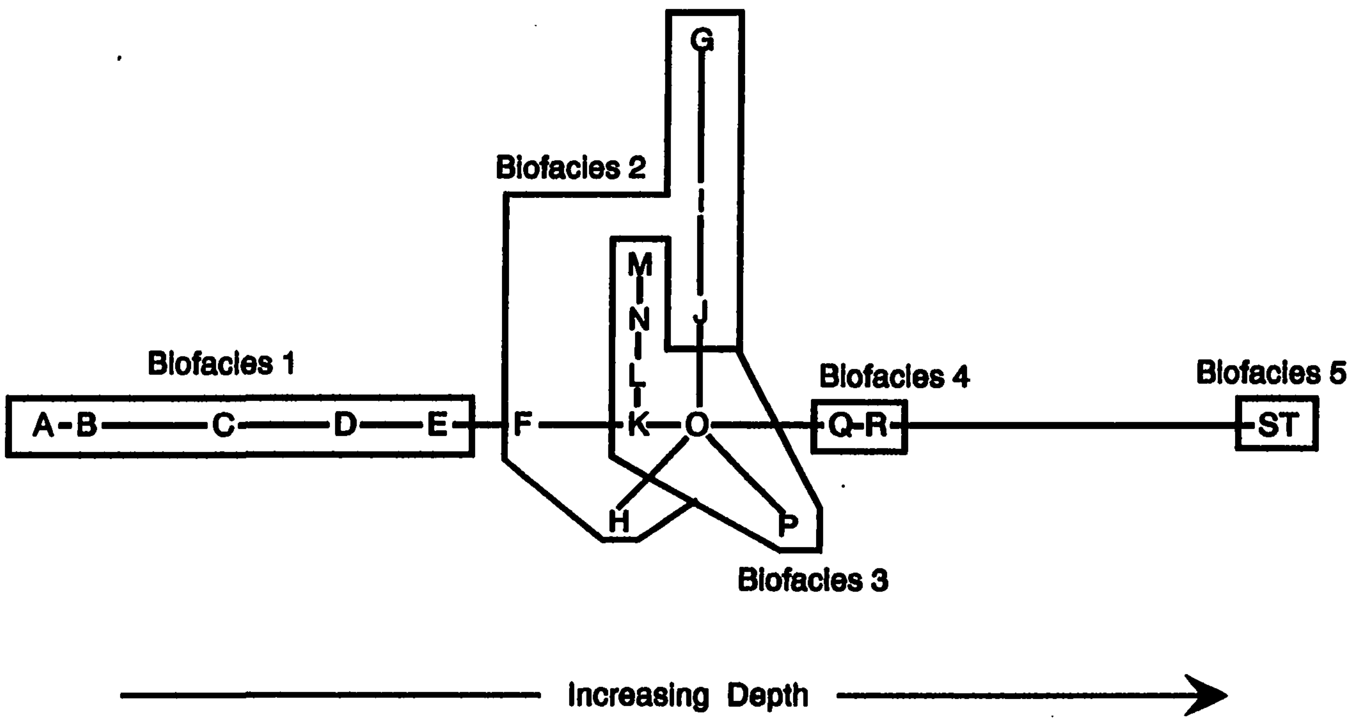
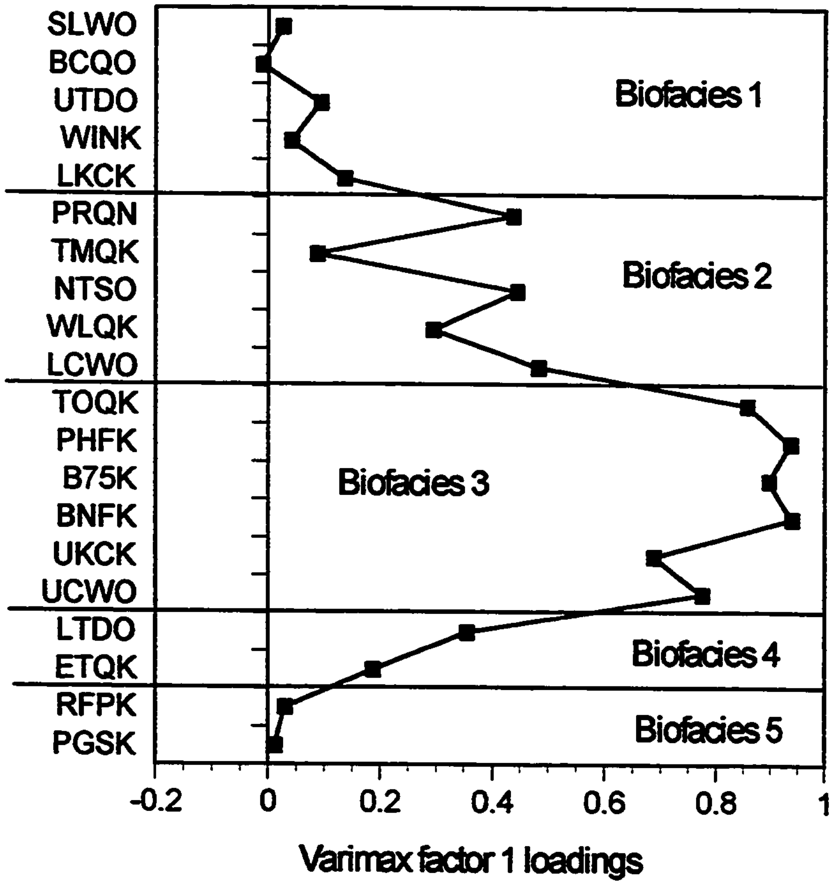

Biofacies 1
Biofacies 2
Biofacies 3
Biofacies 4
Biofacies 5
A-B
C
D
E
F
G
J
M
N
L
K
O
H
P
Q-R
ST
Increasing Depth

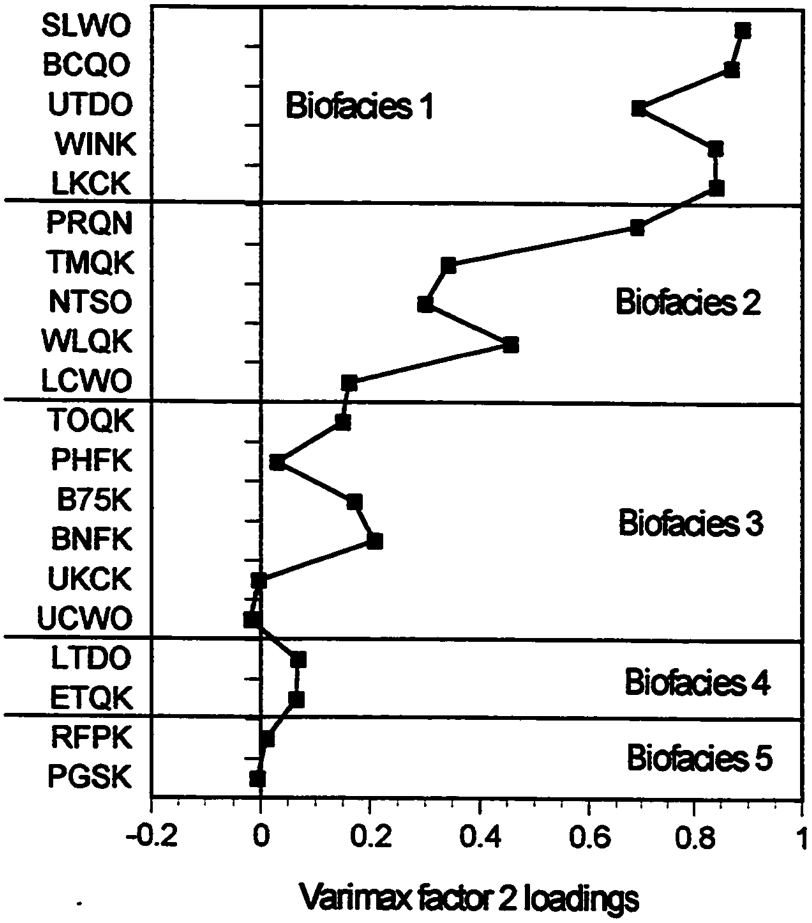
Figure 3.9) Factor one accounts for over 26% of the variance in the data set. Factor loadings are highest for samples of biofacies 3 and decline gradually toward zero for biofacies 1 and 5. This factor is dominantly controlled by the distribution of *Cibolocrinus* and *Apographiocrinus*, which have far and away the highest factor scores of all the variables.



Five highest varimax factor 1 variable scores:

1. Cibolocrinus - .676
2. Apographiocrinus - .653
3. Kallimorphocrinus - .198
4. Delocrinus - .154
5. Erisocrinus - .097

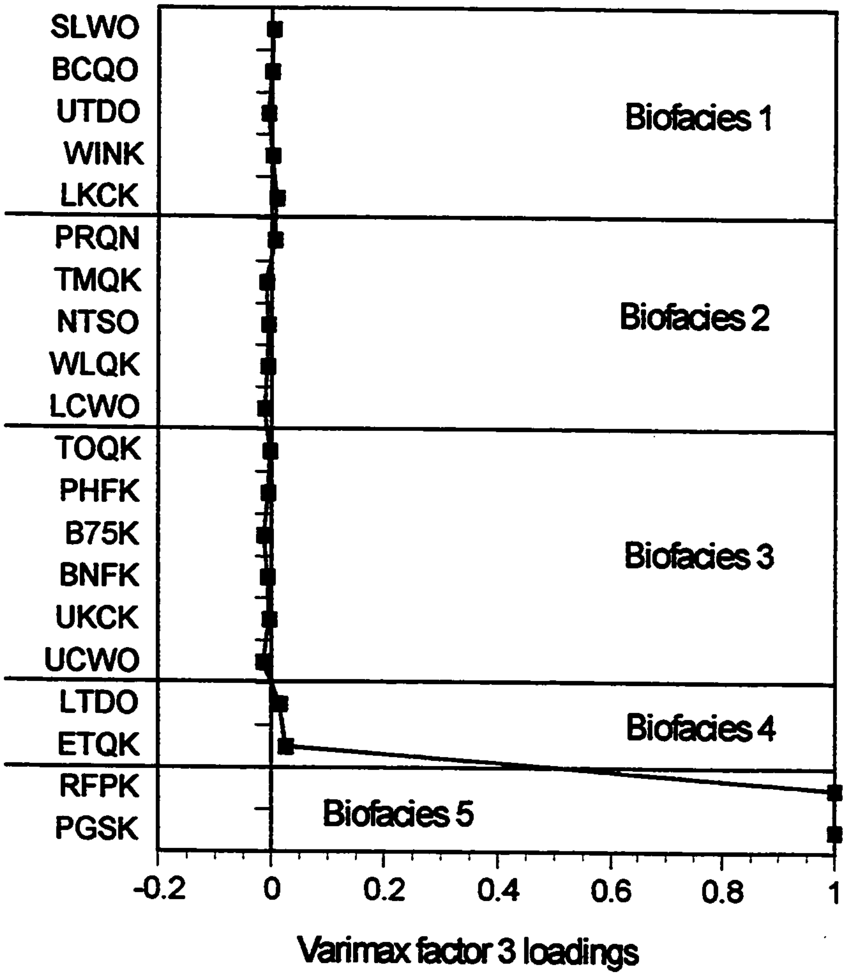
Figure 3.10) Factor two accounts for over 22% of the variance in the data set. Factor loadings are highest for samples of biofacies 1 and declines steadily to biofacies 5. This factor is dominated by large, pinnulate crinoids, most notably *Delocrinus* of guild 2 with significant contributions from members of guilds 1, 3, and 4.



Five highest varimax factor 2 variable scores:

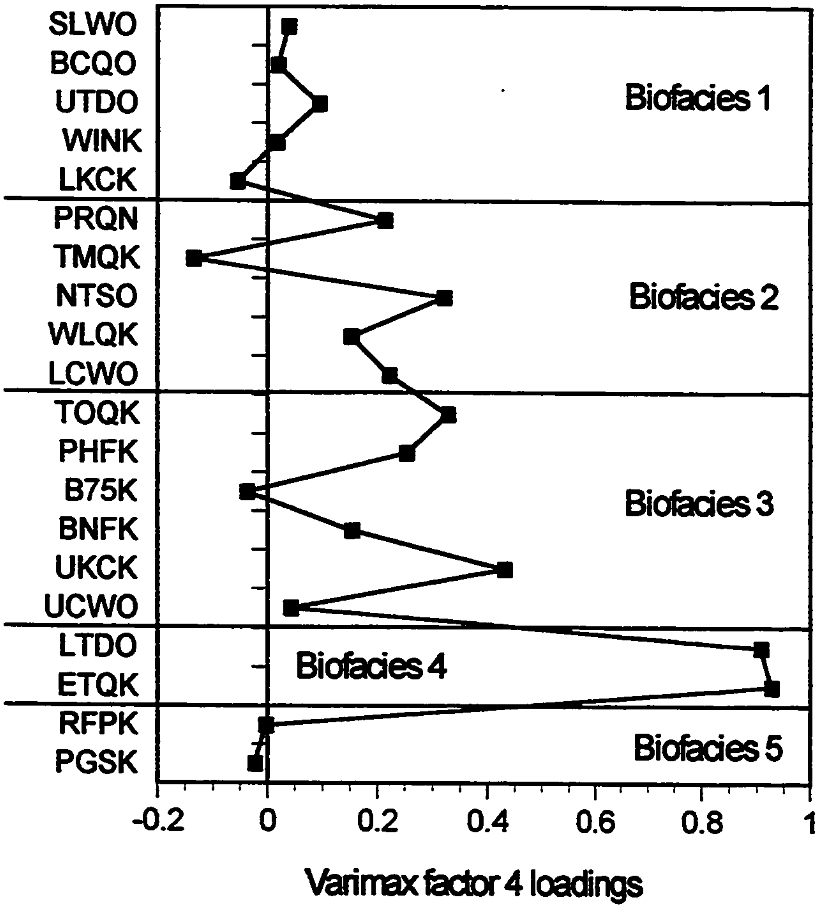
1. Delocrinus - .705
2. pirasocrinids - .449
3. ampelocrinids - .321
4. Stellarocrinus - .294
5. cromyocrinids - .171

Figure 3.11) Factor three accounts for almost 10% of the variance in the data set. This factor is identifying the monospecific biofacies 5, which is controlled entirely by *Paragazzisocrinus tarri*.



Highest varimax factor 3 variable scores:
1. Paragazzisocrinus - .999
* all others hover about .000

Figure 3.12) Factor four accounts for almost 12% of the variance in this data set. Factor loadings are highest for samples of biofacies 4 and are sporadic but generally low for the others. This factor is dominated by *Exocrinus* with a significant contribution from *Apographiocrinus*, members of guilds 5 and 6, respectively.



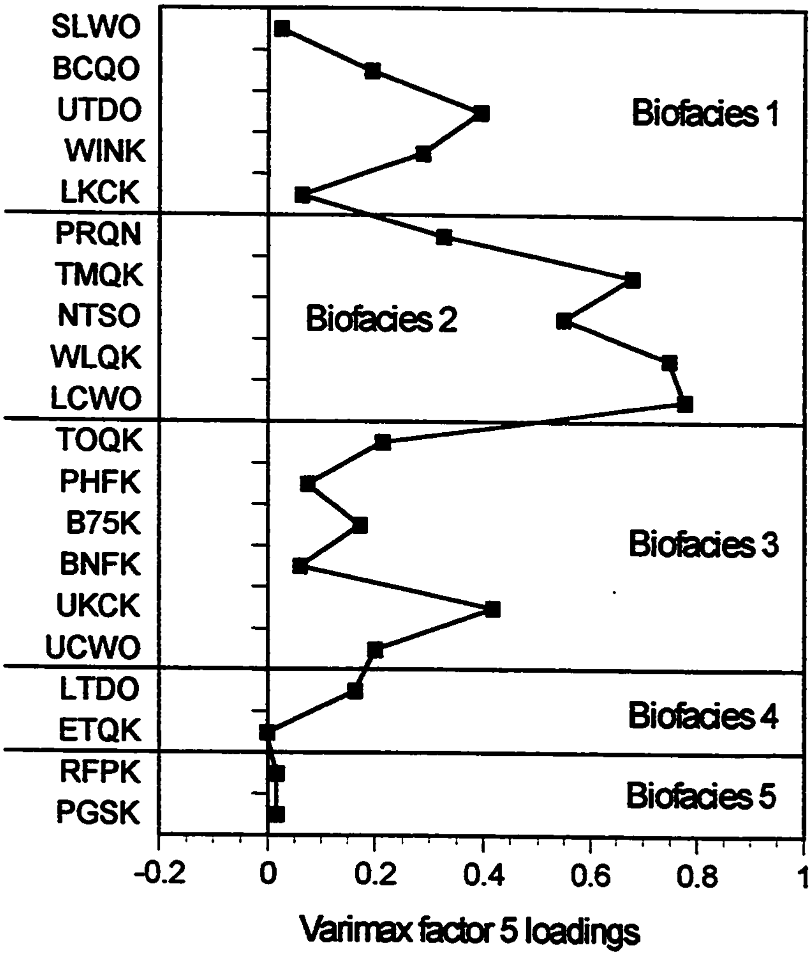
Extreme varimax factor 4 variable scores:

1. Exocrinus - .817
2. Apographiocrinus - .484

---

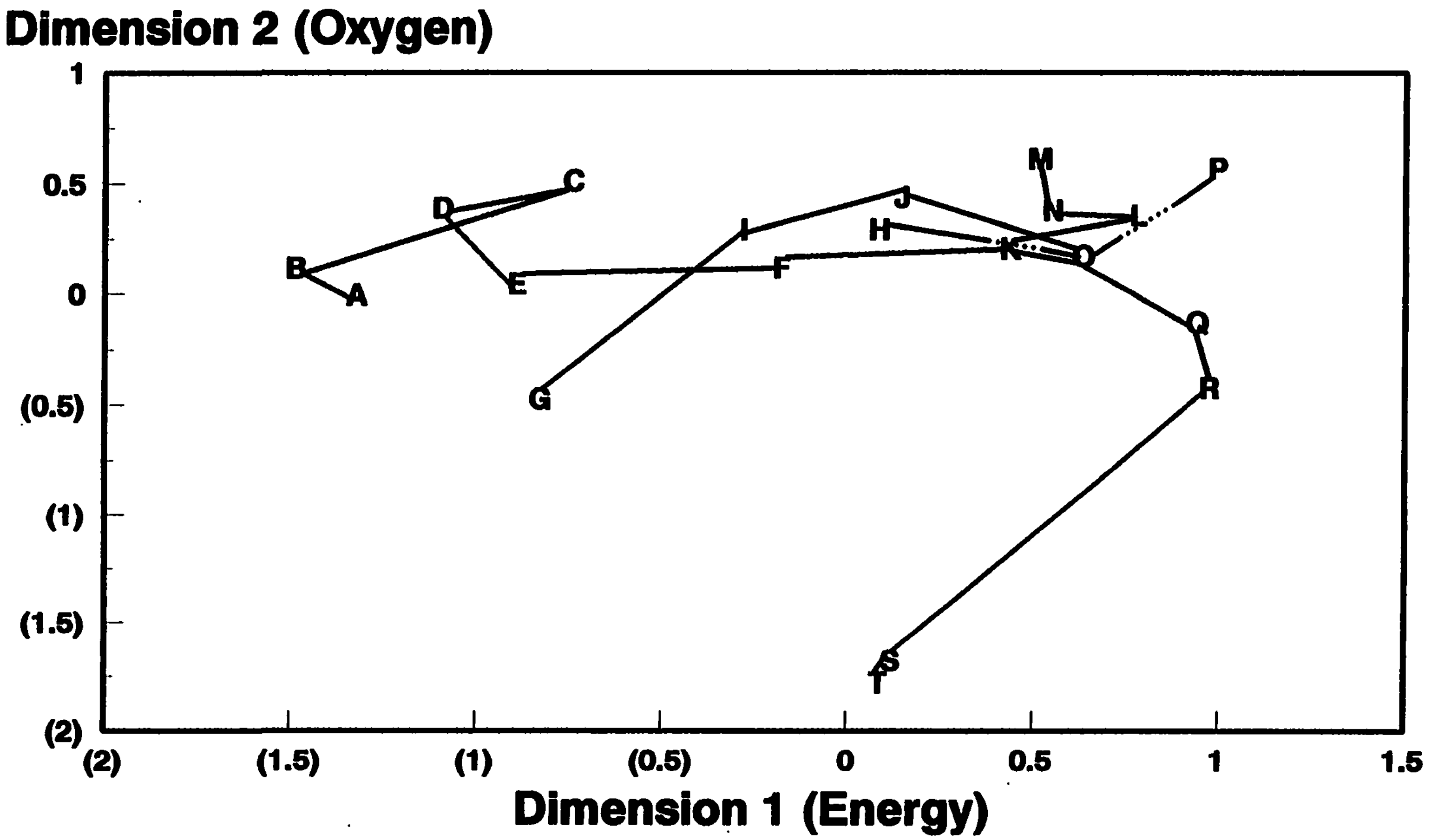
1. Cibolocrinus - (-.268)
2. Ulocrinus - (-.091)
3. Erisocrinus - (-.071)

Figure 3.13) Factor five accounts for over 13% of the variance in this data set. Factor loadings are highest for samples of biofacies 2 and are sporadic but lower for the others. This factor is strongly controlled by *Erisocrinus* of guild 2 with significant contributions by members of guild 3.



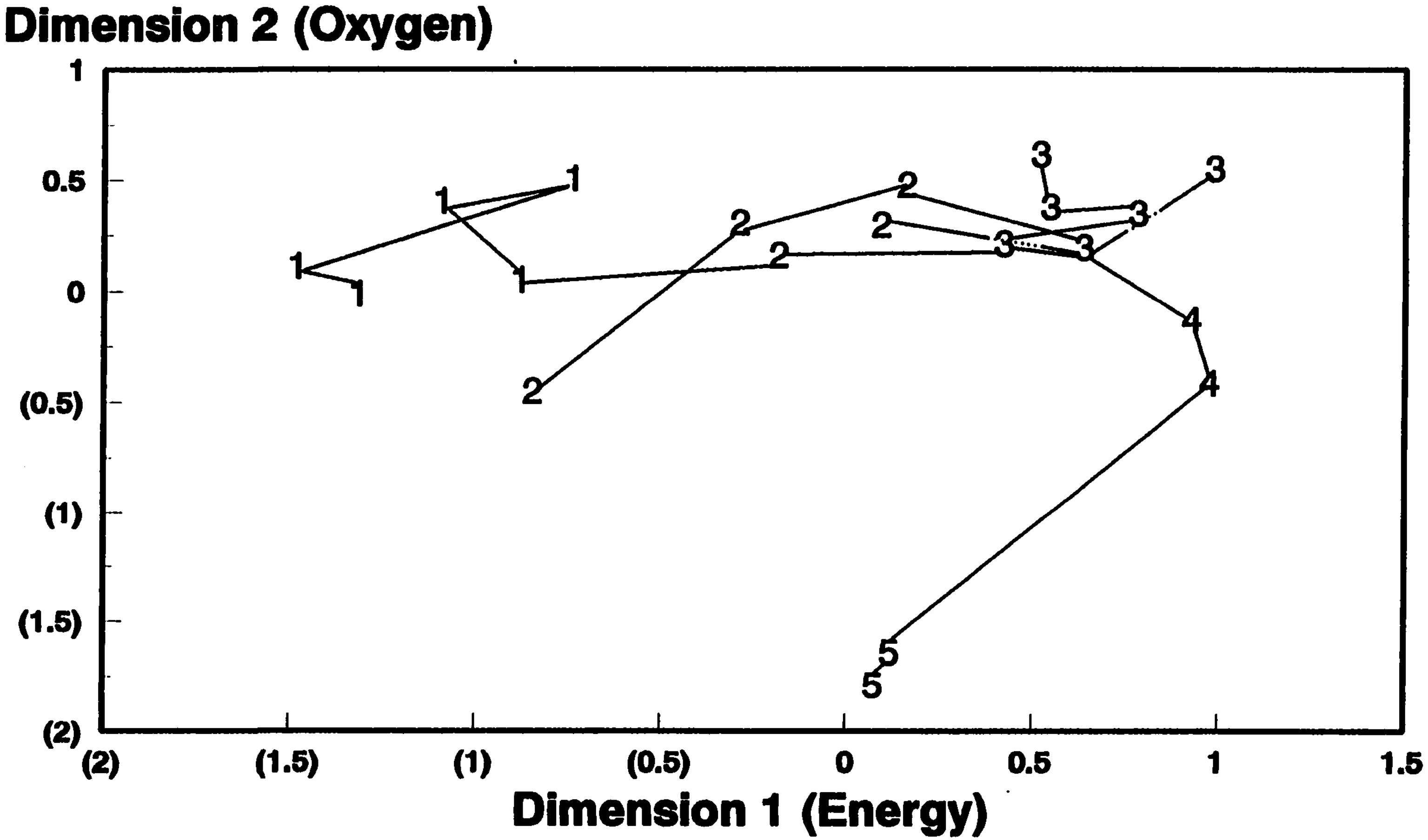
Five highest varimax factor 5 variable scores:
1. Erisocrinus - .764
2. Ulocrinus - .291
3. stenopecrinids - .271
4. pirasocrinids - .221
5. Kallimorphocrinus - .180

Figure 3.14) Q - mode Multidimensional Scaling (MDS) ordination of the Stanton localities. Samples are linked by the MST of figure 3.8. Letters correspond to the samples as labeled in the cluster analysis and MST. See text for discussion.



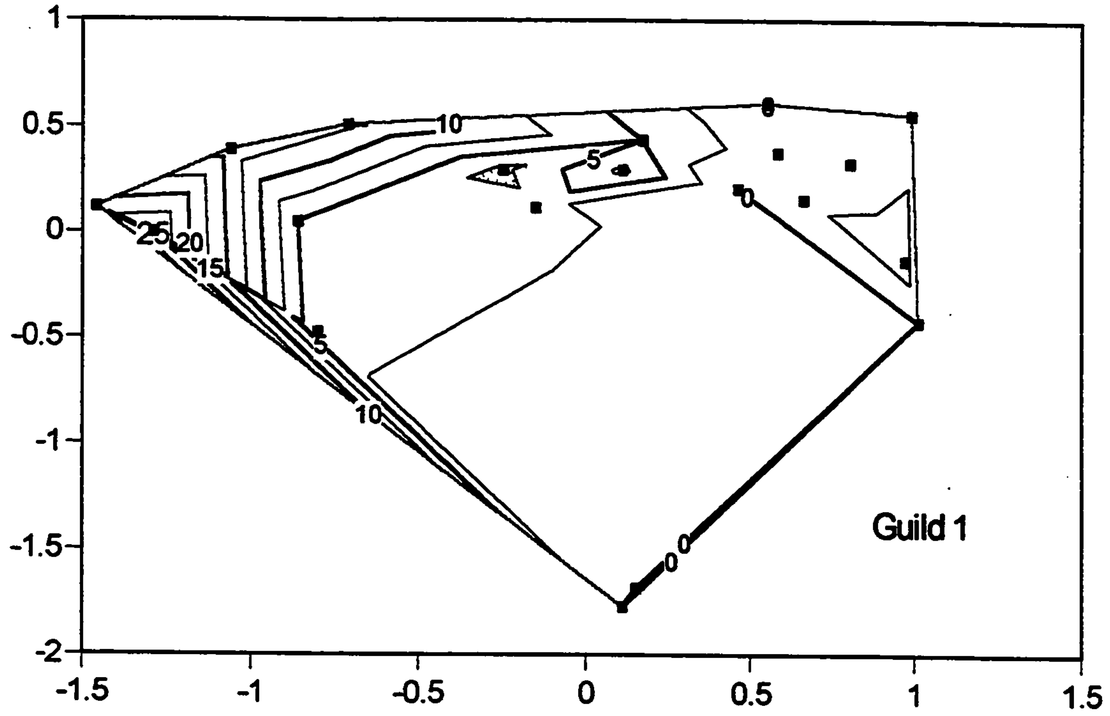
MDS stress=0.129

Figure 3.15) Q - mode MDS with MST linkage. Sample letters have been replaced by numbers corresponding to the cluster - defined biofacies. The spread of numbers clearly shows the gradational nature of the biofacies, yet each biofacies is generally confined to a "field" within the ordination. See text for discussion.



MDS stress=0.129

Figure 3.16) Abundance contours of guilds 1 and 2 on the Q - mode MDS ordination of the Stanton Formation. The large, dense fan crinoids of guild 1 are very restricted to the higher - energy field of the plot. The large, dense fan crinoids of guild 2 are much more dispersed and have non - trivial abundances into the low energy field. However, this guild is clearly most abundant in the higher energy field of the ordination.


Guild 1
10
5
25
20
15
5
10
0
0
0
0
1
0.5
0
-0.5
-1
-1.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5

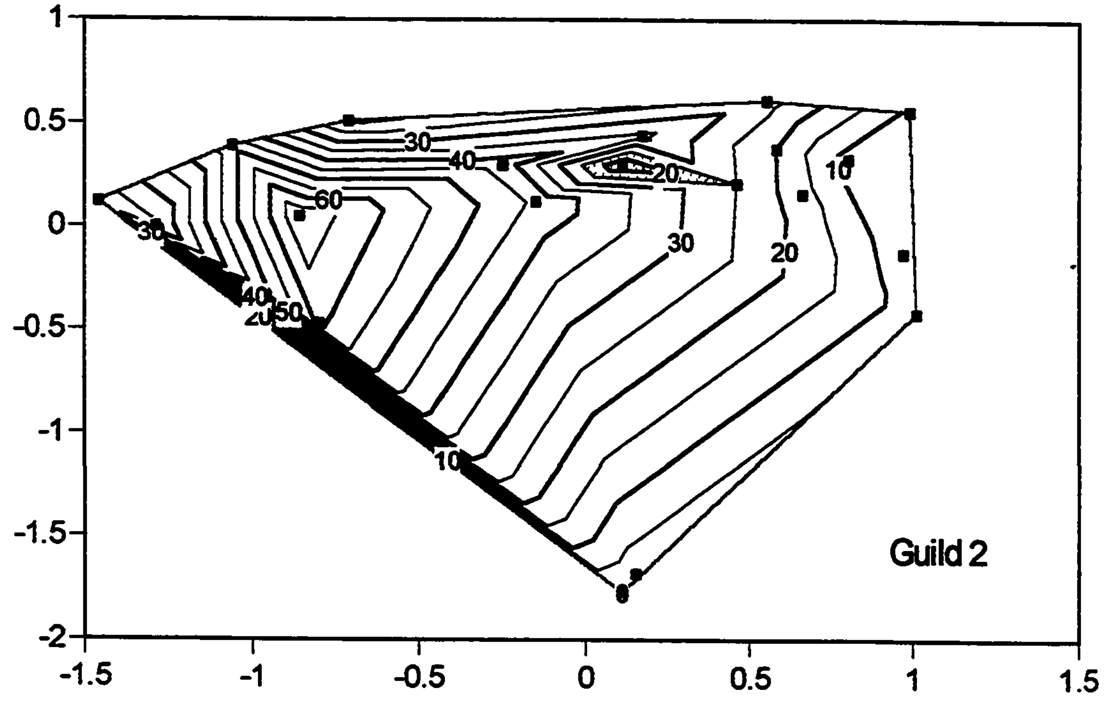
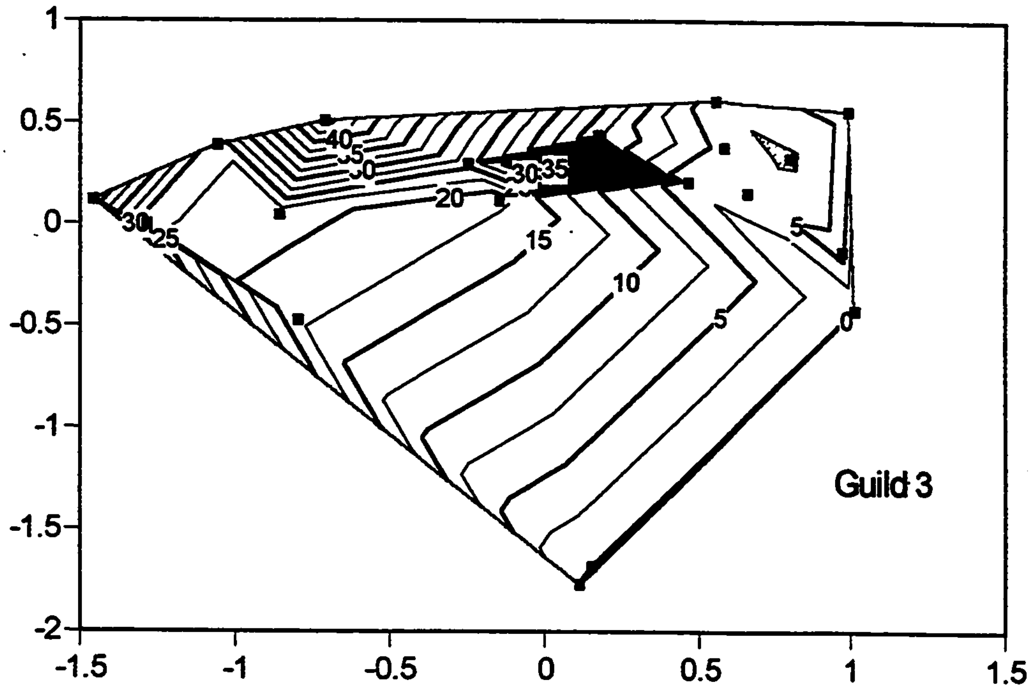

Guild 2
30
40
60
20
10
30
20
30
40
50
20
10
1
0.5
0
-0.5
-1
-1.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5

Figure 3.17) Abundance contours of guilds 3 and 4 (without *Paragazzisocrinus*) on the Q - mode MDS ordination of the Stanton Formation. The large, intermediate to dense fan crinoids of guild 3 are abundant in some of the samples in the high energy field, but the guild is more consistently abundant in the middle field of the ordination and are rather rare in the low energy field. Guild 4, composed of large but fairly open fan crinoids, is most abundant in the high energy field and rather unimportant in lower energy facies. This is an interesting phenomenon to be addressed in the Discussion.


Guild 3
40
35
30
20
30
35
30
25
15
10
5
5
0
1
0.5
0
-0.5
-1
-1.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5

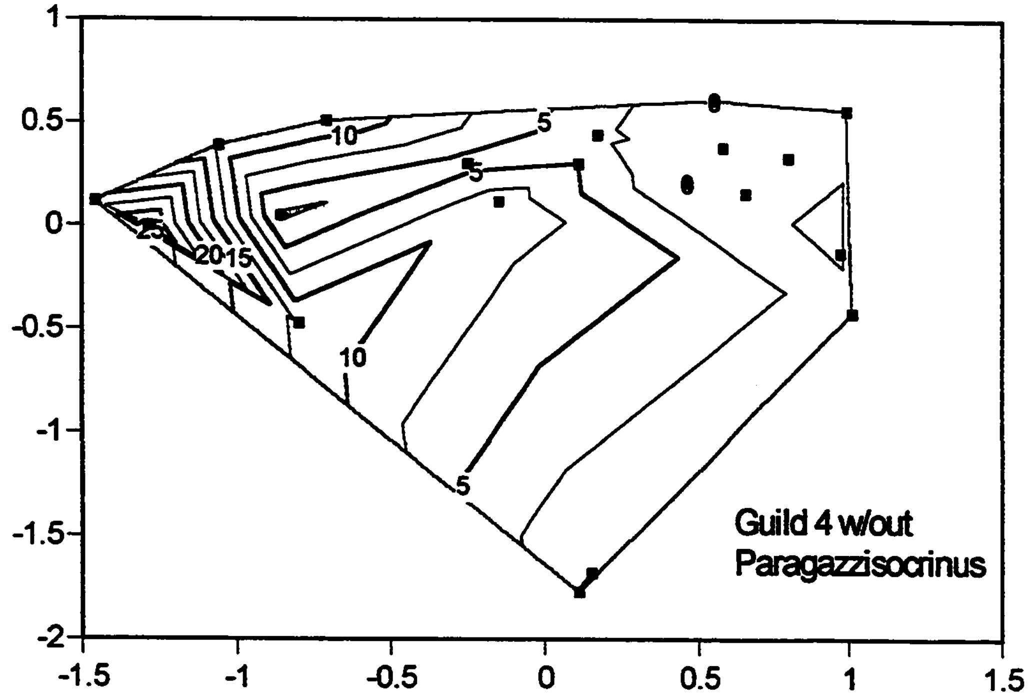
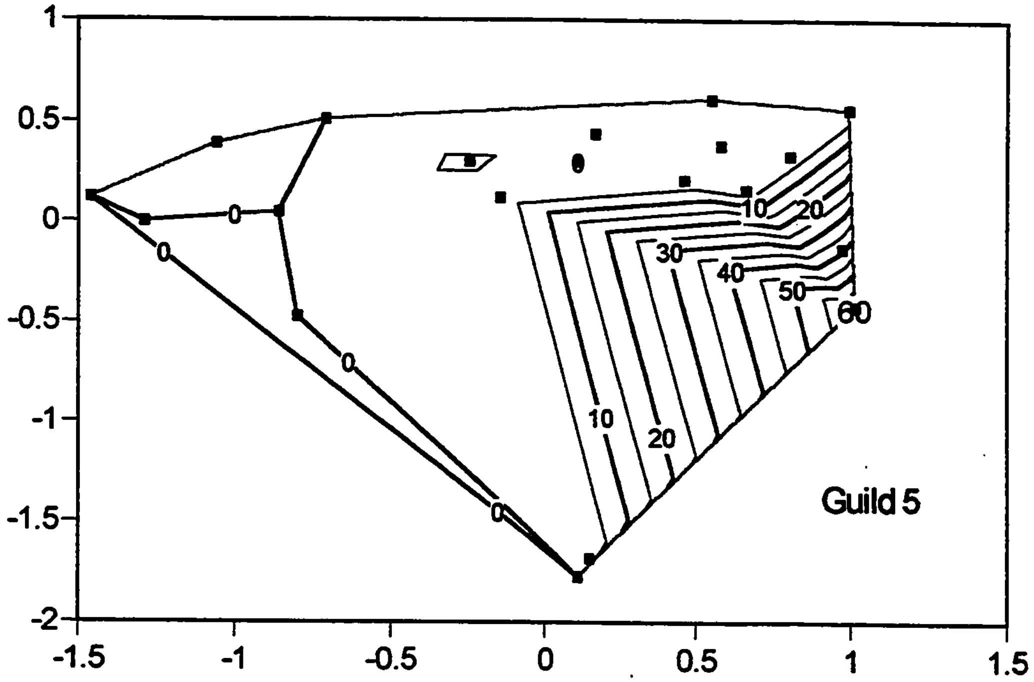

Guild 4 w/out
Paragazzisocrinus
10
5
5
25
20
15
10
5
1
0.5
0
-0.5
-1
-1.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5

Figure 3.18) Abundance contours of guilds 5 and 6 on the Q - mode MDS ordination of the Stanton Formation. Small, intermediate fan crinoids of guild 5 are very restricted to the low energy - dysaerobic field of the plot. The small, open fan crinoids of guild 6 are fairly wide spread over the moderate to low energy fields of the plot, but are clearly most abundant in the low energy field of the ordination.


Guild 5
1
0.5
0
-0.5
-1
-1.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
0
10
20
30
40
50
60

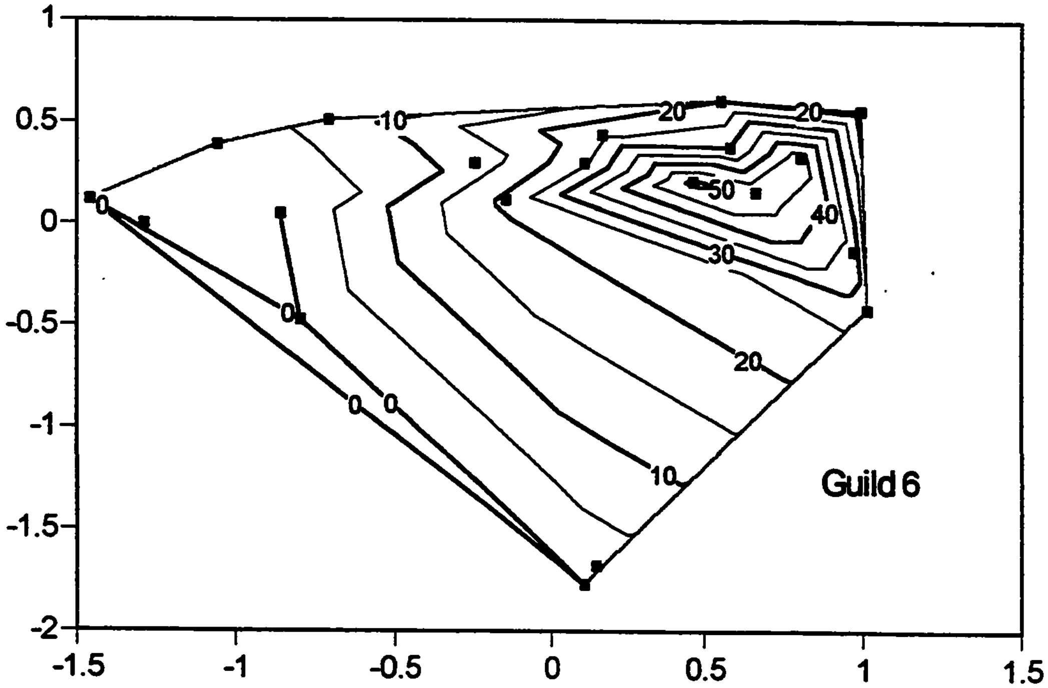
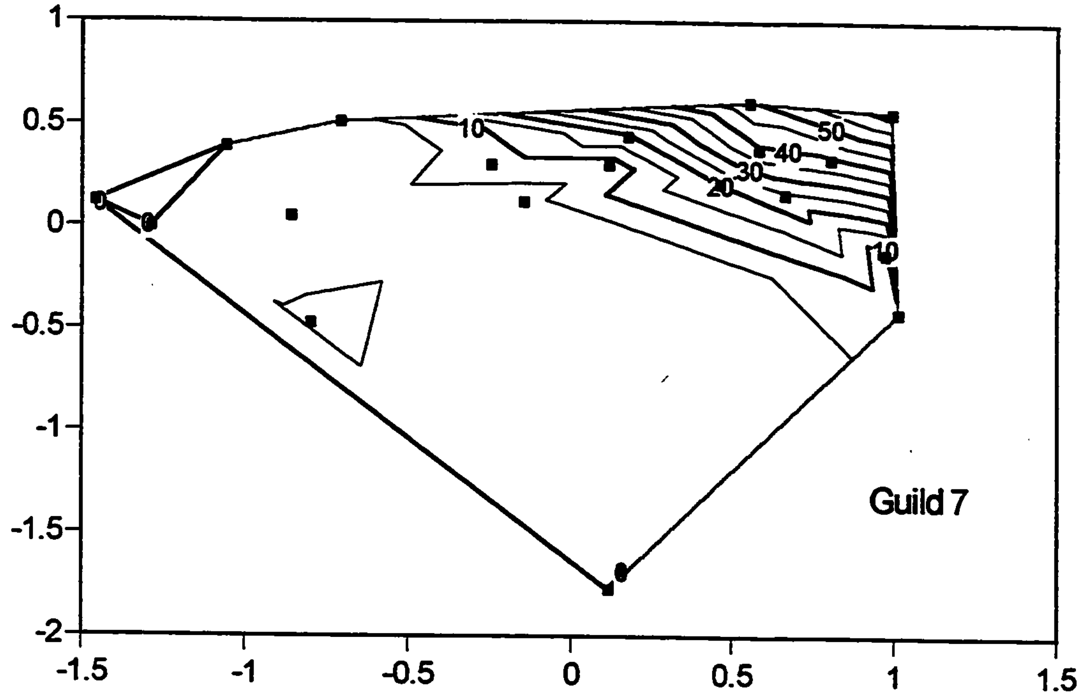
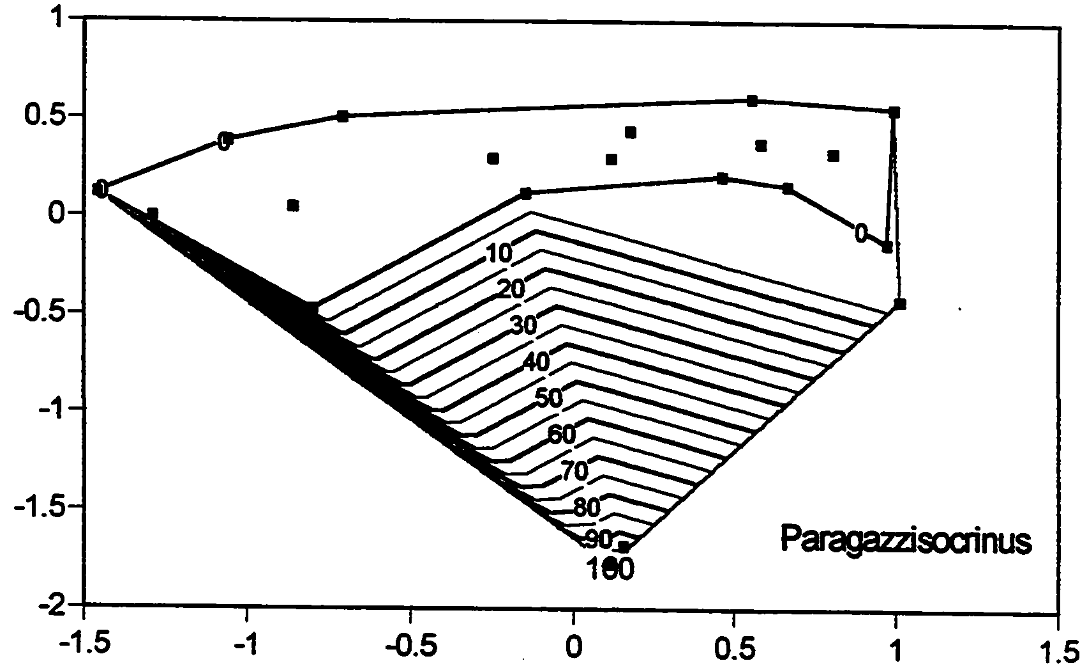

Guild 6
1
0.5
0
-0.5
-1
-1.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
0
10
20
30
40
50

Figure 3.19) Abundance contours of guild 7 and *Paragazzisocrinus* of guild 4 on the Q - mode MDS ordination of the Stanton Formation. Non - pinnulate crinoids of guild 7 are very restricted to the low energy field. *Paragazzisocrinus* is virtually the only taxa found in the extreme dysaerobic field of this ordination.



Guild 7
10
20
30
40
50
10
0
1
0.5
0
-0.5
-1
-1.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5



Paragazzisocrinus
0
10
20
30
40
50
60
70
80
90
100
1
0.5
0
-0.5
-1
-1.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5

Figure 3.20) Guild composition of biofacies from the Stanton Formation. Note the systematic reorganization of guilds between biofacies. See text for discussion.

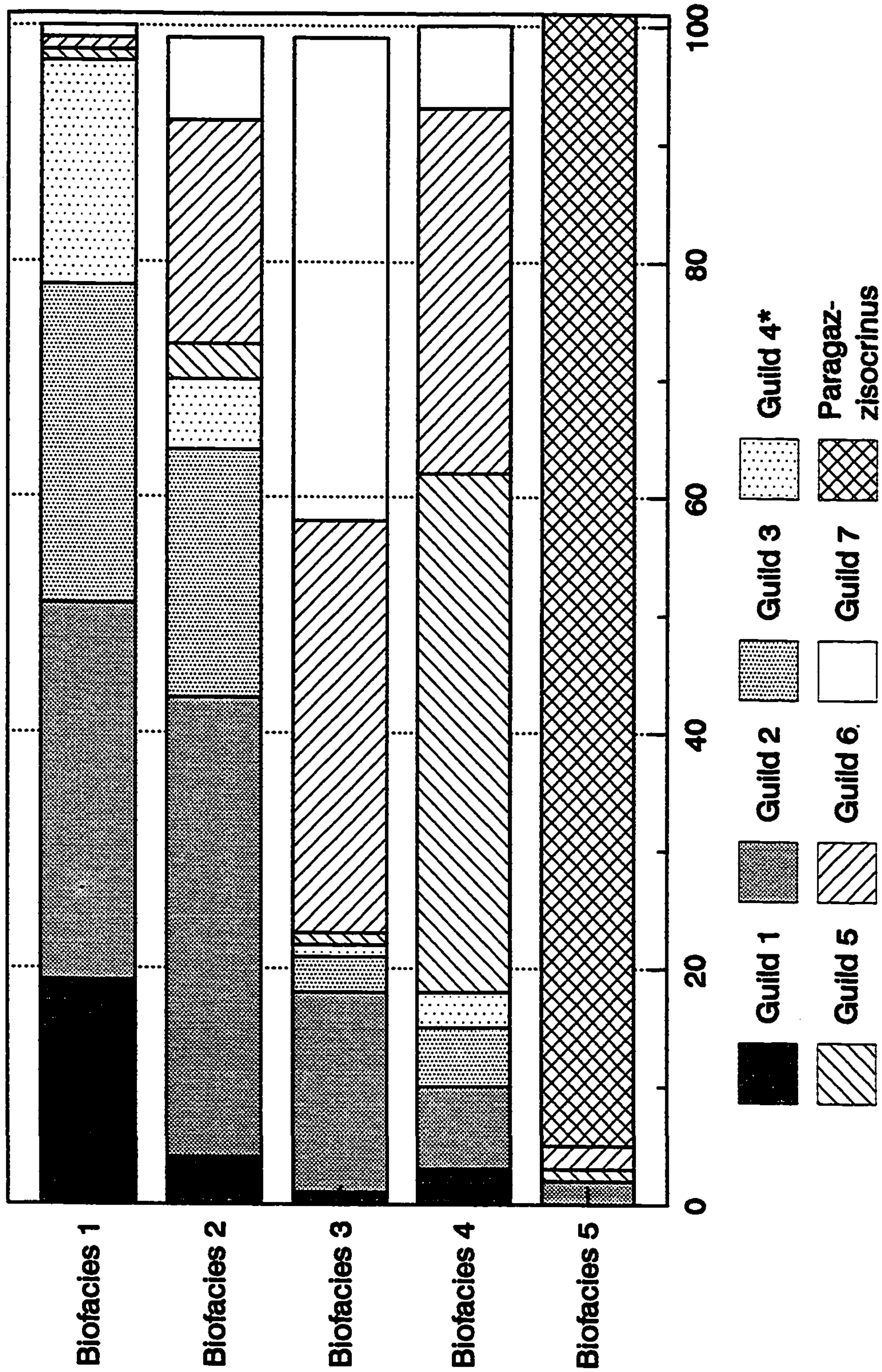

Biofacies 1
Biofacies 2
Biofacies 3
Biofacies 4
Biofacies 5
0
20
40
60
80
100
Guild 1
Guild 2
Guild 3
Guild 4*
Guild 5
Guild 6
Guild 7
Paragaz-
zisocrinus

Table 3) Diversity patterns between biofacies of the Stanton Formation. S = "species", or taxonomic richness; E = "equitability", measure of equality of species abundance; N = number of samples within biofacies; n = number of individuals within biofacies. Although taxonomic richness is rather high between biofacies 1 through 4, this diversity is more equitably structured for biofacies 1 and 2 and is increasingly more dominance structured for biofacies 3, 4, and 5.

Biofacies	1	2	3	4	5
S	21	26	22	23	4
E	0.80	0.81	0.63	0.53	0.12
N	5	5	6	2	2
n	539	2862	3739	1377	118

Table 4) Crinoid taxa identified from the Lansing Group. These crinoids are assigned to a crinoid guild as defined in Table 1. Numbers on the right correspond to numbers on the R - mode dendrogram of the two - way cluster analysis of figure 3.21. Although camerates have been identified from the Lansing Group, they are very rare and were not included further in the analysis.

Guilds

				1	2	3	4	5	6	7	
CAMERATES			Dichocrinus			●					-
			Dinacrocrinus		●						-
INADUNATES	CLADIDS	"ADVANCED CLADIDS" (POTERIOCRINES)	cromyocrinids	●							8
			Stellarocrinus	●							3
			Delocrinus		●						10
			Erisocrinus		●						15
			Graffhamicrinus		●						7
			Ulocrinus		●						14
			Exoriocrinus			●					5
			Glaukosocrinus			●					4
			laudonocrinids			●					17
			pirasocrinids			●					9
			Plummericrinus			●					6
			scytalocrinids			●					11
			"stenopecrinids"			●					16
			Terpnocrinus			●					12
			ampelocrinids				●				2
			cymbiocrinids				●				1
			Ellibatocrinus				●				13
			Paragassizocrinus				●				27
		CYATHOCRINES	Exocrinus					●			26
			Galateacrinus					●			18
			Apographiocrinus						●		20
			graphiocrinids						●		25
			Lecythiocrinus							●	19
	DISPARIDS		Kallimorphocrinus							●	24
FLEXIBLES			Cibolocrinus							●	22
			Euonychocrinus							●	21
			Paramphicrinus							●	23

Designation in R-mode cluster analysis and MDS: ▲

Figure 3.21) Two - way cluster diagram of localities and crinoid taxa from the Lansing Group. Samples of the Q - mode analysis are identified in table 5. Dendrograms link individual objects and clusters at differing levels as indicated by the similarity scales adjacent to the dendrograms. The relative abundances of the different taxa within each sample are indicated; note shifting abundance peaks from upper left to lower right. Like the cluster analysis of the Stanton Formation, this analysis identifies the five taxonomic associations (R - mode clusters 1 - 5, left to right) and five sample associations, or biofacies (Q - mode clusters 1 - 5, top to bottom). See text for discussion.

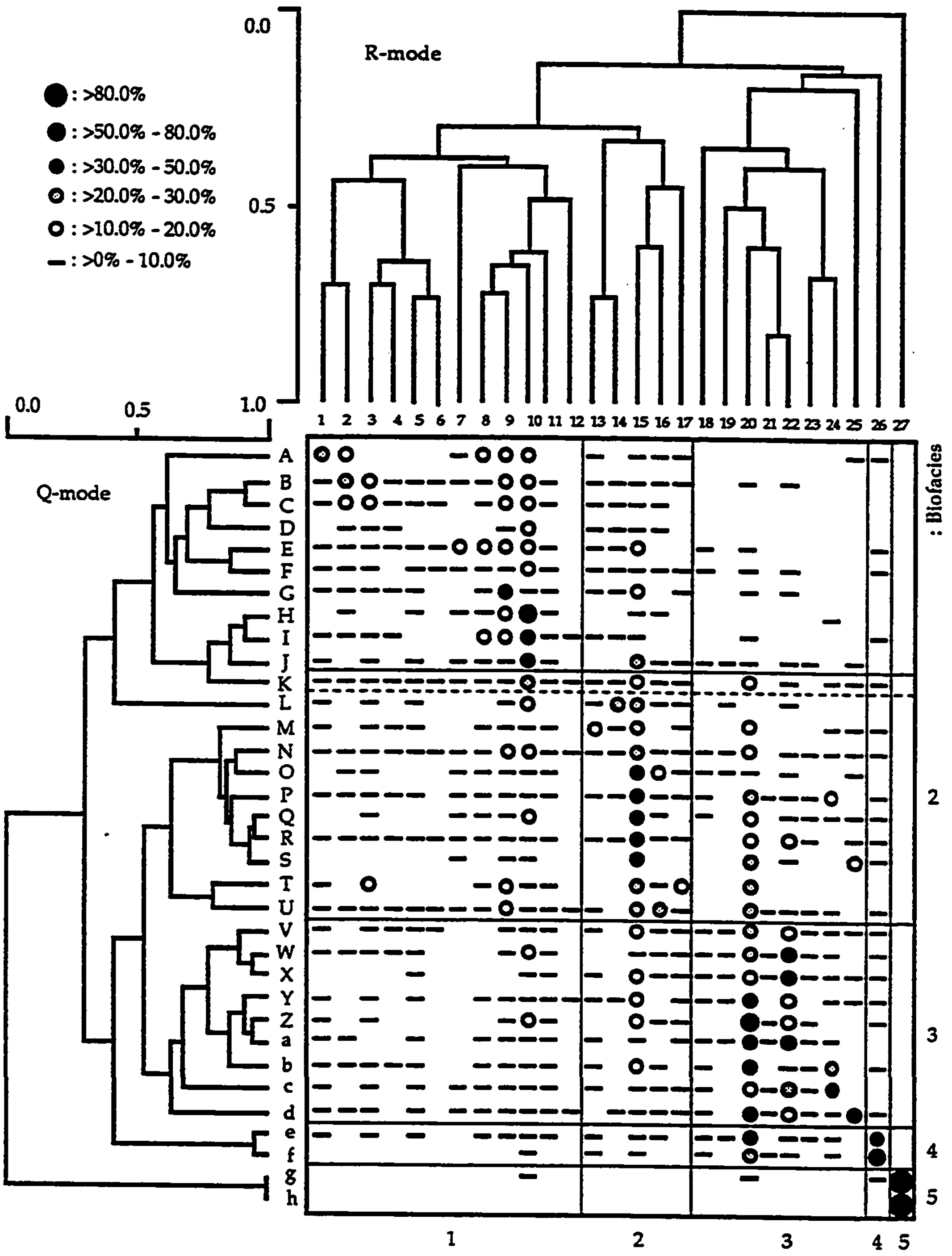

●: >80.0%
●: >50.0% - 80.0%
●: >30.0% - 50.0%
◎: >20.0% - 30.0%
○: >10.0% - 20.0%
—: >0% - 10.0%
R-mode
0.0
0.5
1.0
Q-mode
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27
A B C D E F G H I J K L M N O P Q R S T U V W X Y Z a b c d e f g h
: Biofacies
2
3
4
5
1 2 3 4 5

Table 5) Lansing Group localities and their Q - mode designations. Note that all formations have samples included in biofacies 1 through 3. See text for discussion.

Formation	Sample Locality Design.	Q - mode Designation	Biofacies
South Bend	LXQN	I	1
	ERQK	M	2
	ARCK	T	2
	RRWK	Y	3
Stanton	SLWO	B	1
	BCQO	C	1
	WINK	E	1
	UTDO	G	1
	LKCK	H	1
	PRQN	K	2
	TMQK	L	2
	WLQK	N	2
	LCWO	P	2
	NTSO	U	2
	BNFK	W	3
	75BK	X	3
	TOQK	Z	3
	PHFK	a	3
	UKCK	b	3
	UCWO	c	3
	LTDO	e	4
	ETQK	f	4
	RFPK	g	5
	PGSK	h	5
Plattsburg	CCQN	A	1
	CBMO	D	1
	TMBO	F	1
	O75K	J	1
	K96K	O	2
	K47K	Q	2
	N75K	R	2
	BRQK	S	2
	NFDK	V	3
	HPTO	d	3

Figure 3.22) R - mode MDS ordination of Lansing Group crinoids. Numbers correspond to taxonomic designations of table 4. Stress of .170 is considered a "good" fit to the original similarity matrix. R - mode clusters of the Lansing two - way cluster analysis are overlain on the ordination. See text for discussion.

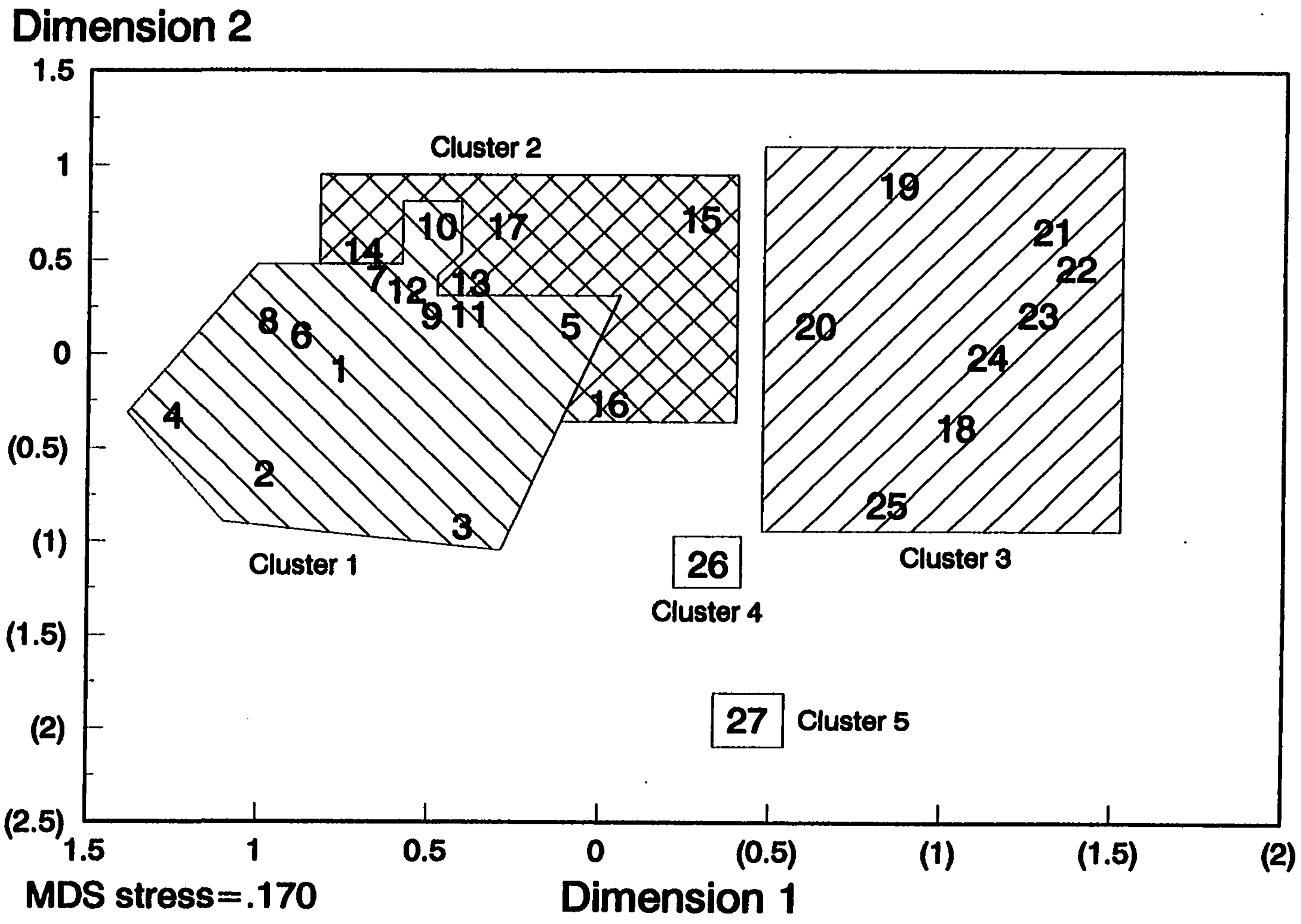

Dimension 2
1.5
1
0.5
0
(0.5)
(1)
(1.5)
(2)
(2.5)
Cluster 2
Cluster 1
Cluster 3
Cluster 4
Cluster 5
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
1.5
1
0.5
0
(0.5)
(1)
(1.5)
(2)
MDS stress=.170
Dimension 1

Figure 3.23) R - mode MDS ordination of Lansing Group crinoids. Taxonomic designations have been replaced by that individuals guild assignment. See text for discussion.

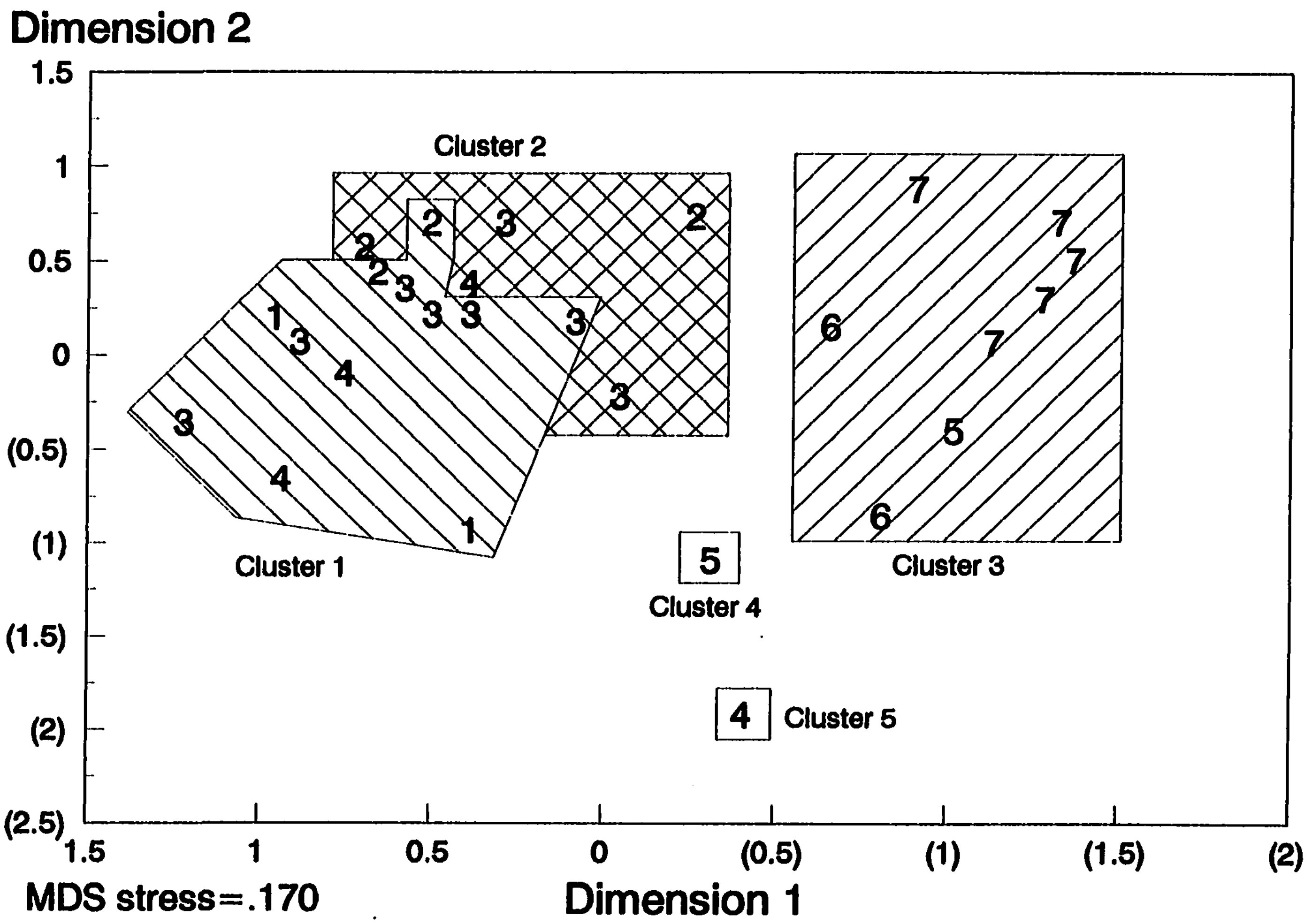

Dimension 2
1.5
1
0.5
0
(0.5)
(1)
(1.5)
(2)
(2.5)
Cluster 2
Cluster 1
Cluster 3
Cluster 4
Cluster 5
2
3
2
2
2
3
3
3
4
1
3
3
4
3
3
4
1
7
7
7
7
7
6
5
6
5
4
1.5
1
0.5
0
(0.5)
(1)
(1.5)
(2)
MDS stress=.170
Dimension 1

Figure 3.24) Q - mode MDS ordination of Lansing Group localities. Letters correspond to locality designations of table 5. Samples have been linked by a MST. Stress of .125 is considered a "good" fit to the original data matrix. See text for discussion.

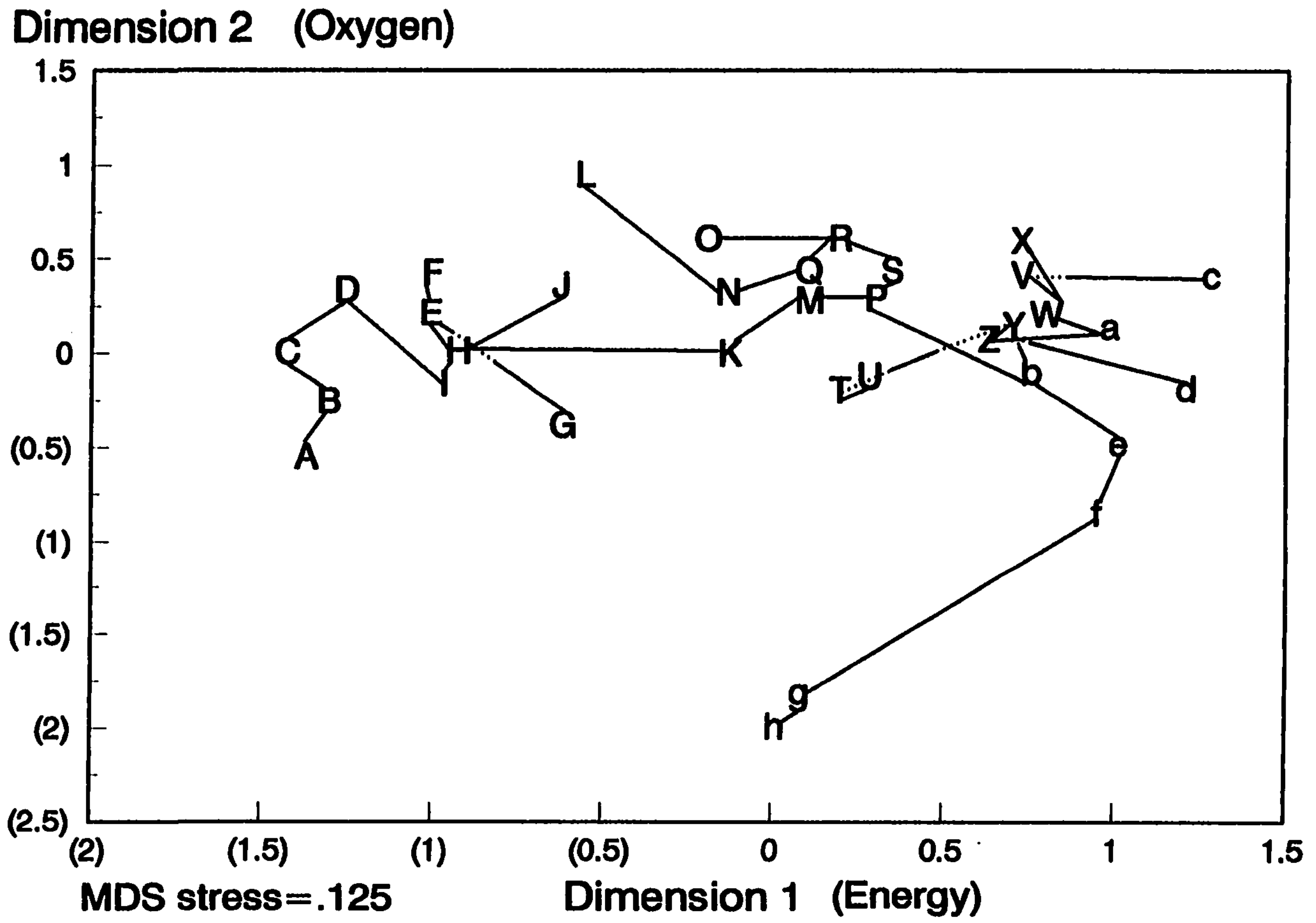

Dimension 2 (Oxygen)
1.5
1
0.5
0
(0.5)
(1)
(1.5)
(2)
(2.5)
(2)
(1.5)
(1)
(0.5)
0
0.5
1
1.5
MDS stress=.125
Dimension 1 (Energy)
A
B
C
D
E
F
H
I
J
G
L
K
N
O
Q
R
M
P
S
T
U
X
V
c
W
a
Z
Y
b
d
e
f
g
h

Figure 3.25) Q - mode MDS ordination of Lansing Group localities. Q - mode cluster defined biofacies are overlain on the ordination; note tight fit and separation of both ordination - and cluster - defined biofacies. See text for discussion.

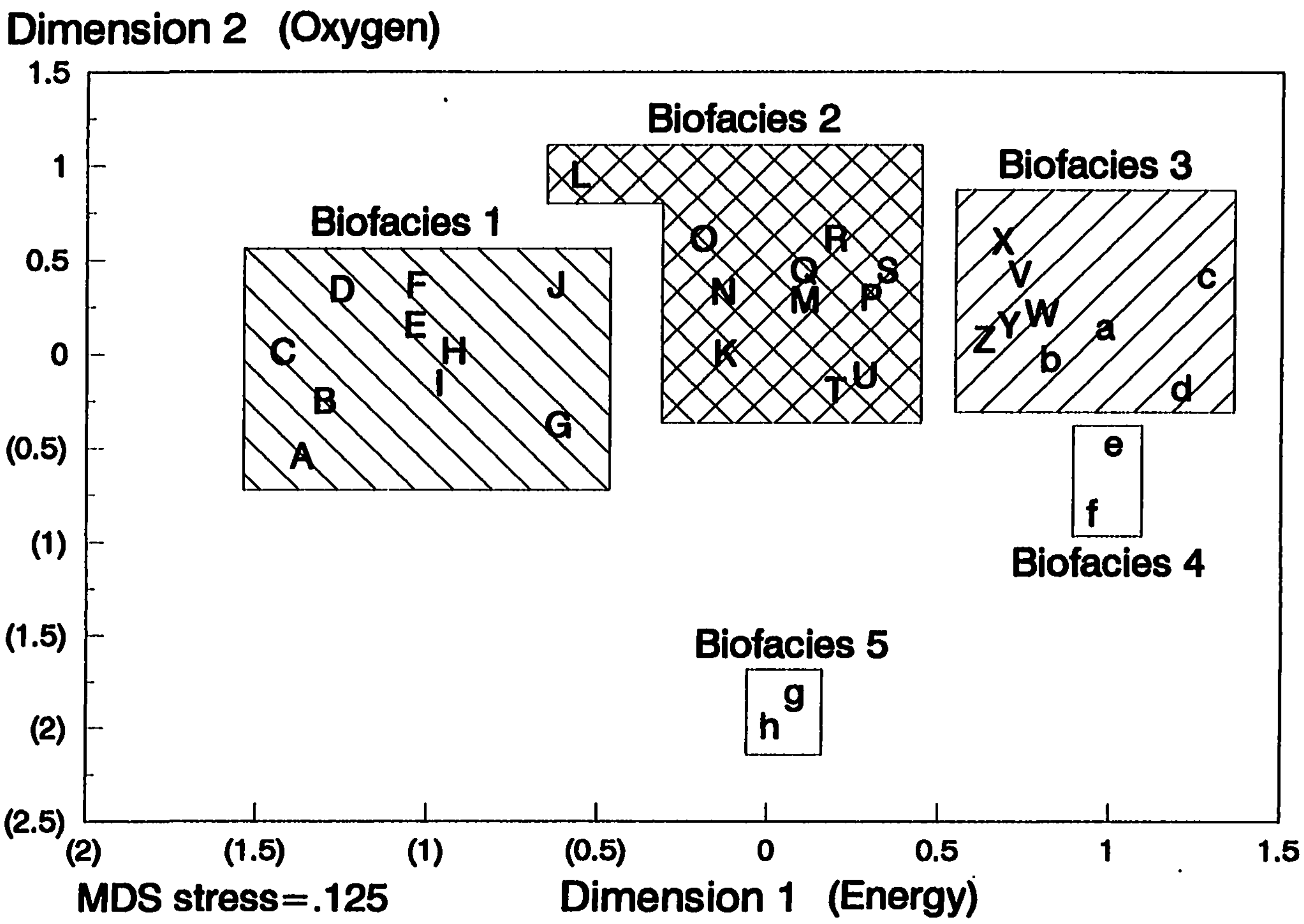

Dimension 2 (Oxygen)
1.5
1
0.5
0
(0.5)
(1)
(1.5)
(2)
(2.5)
(2)
(1.5)
(1)
(0.5)
0
0.5
1
1.5
MDS stress=.125
Dimension 1 (Energy)
Biofacies 1
A
B
C
D
E
F
H
I
J
G
Biofacies 2
L
O
N
K
R
Q
M
S
P
T
U
Biofacies 3
X
V
Z
Y
W
a
b
c
d
Biofacies 4
e
f
Biofacies 5
g
h

Table 6) Average factor loadings of biofacies 1 through 5 of the Lansing Group.

See text for discussion.

	Ave. Loadings of Samples				
	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Biofacies 1	0.0884	0.7992	-0.2103	0.0027	0.0251
Biofacies 2	0.3671	0.3098	-0.6777	0.0031	0.1884
Biofacies 3	0.8164	0.0633	-0.2566	-0.0021	0.1891
Biofacies 4	0.4323	0.0384	-0.0668	0.0174	0.6319
Biofacies 5	0.0102	0.0041	-0.0011	0.9994	0.0088

Extreme scores for each factor:

Factor 1	
Apographiocrinus -	0.709
Cibolocrinus -	0.584
Delocrinus -	0.255
Kallimorphocrinus -	0.192
graphiocrinids -	0.092

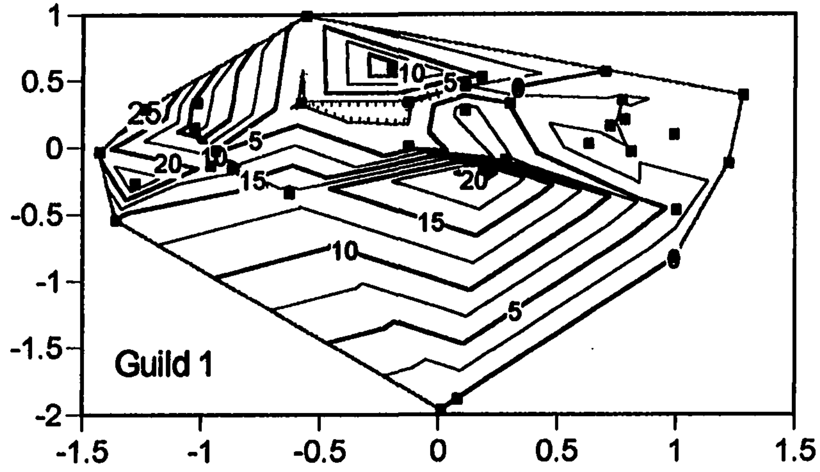
Factor 2	
Delocrinus -	0.717
pirasocrinids -	0.416
cromyocrinids -	0.296
ampelocrinids -	0.284
Stellarocrinus -	0.216

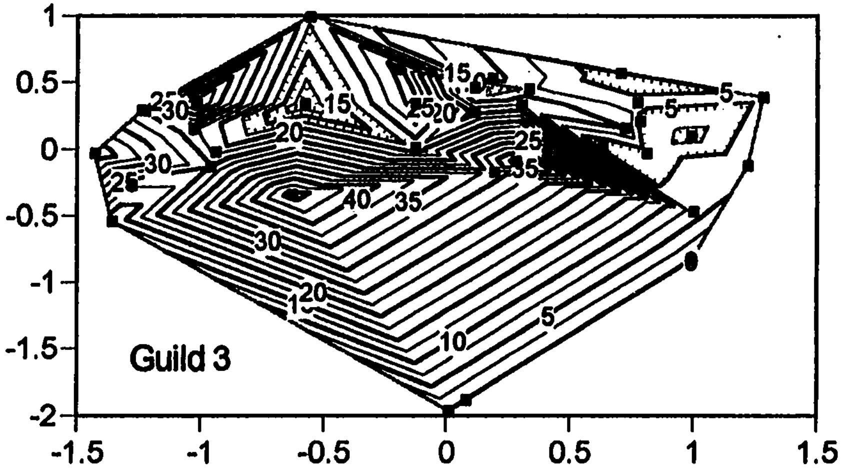
Factor 3	
Erisocrinus -	-0.952
stenopecrinids -	-0.174
Ulocrinus -	-0.120
Apographiocrinus -	-0.083
Elibatocrinus -	-0.067

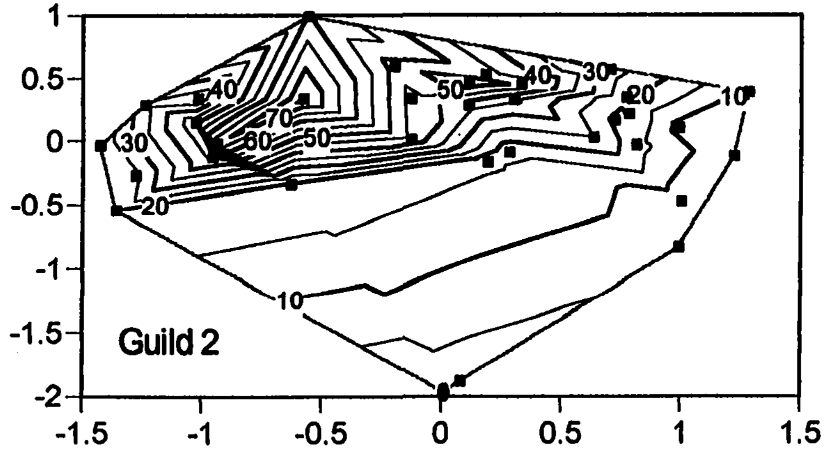
Factor 4	
Paragazzisocrinus -	0.999
all other scores hover about 0.000	

Factor 5	
Apographiocrinus -	0.539
Exocrinus -	0.426
-	-
Delocrinus -	-0.373
Cibolocrinus -	-0.365

Figure 3.26) Contour of guild abundances onto the Q - mode MDS ordination. Guild 1 is irregularly distributed between the high and moderate energy fields of the ordination. However, it is still rather rare in the low energy and dysaerobic fields of biofacies 3, 4, and 5. Guild 2 is more evenly abundant in the high - moderate energy fields but maintains an important contribution to biofacies 3 in the low energy field. Guild 3, like guild 1, is irregularly abundant in biofacies 1 and 2, but is rare in low and dysaerobic fields. Guild 4 is very important in the high energy field with low abundances in virtually all others fields of the ordination.


Guild 1
25
10
5
20
10
5
15
20
15
10
5
1
0.5
0
-0.5
-1
-1.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5


Guild 3
15
15
25
20
5
5
30
20
30
25
25
35
40
35
30
20
10
5
1
0.5
0
-0.5
-1
-1.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5


Guild 2
40
50
40
30
20
10
70
60
50
30
20
10
1
0.5
0
-0.5
-1
-1.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5

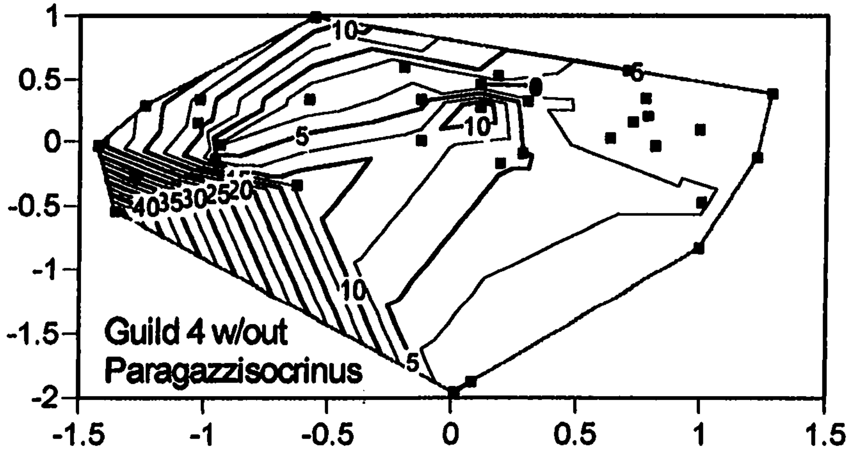
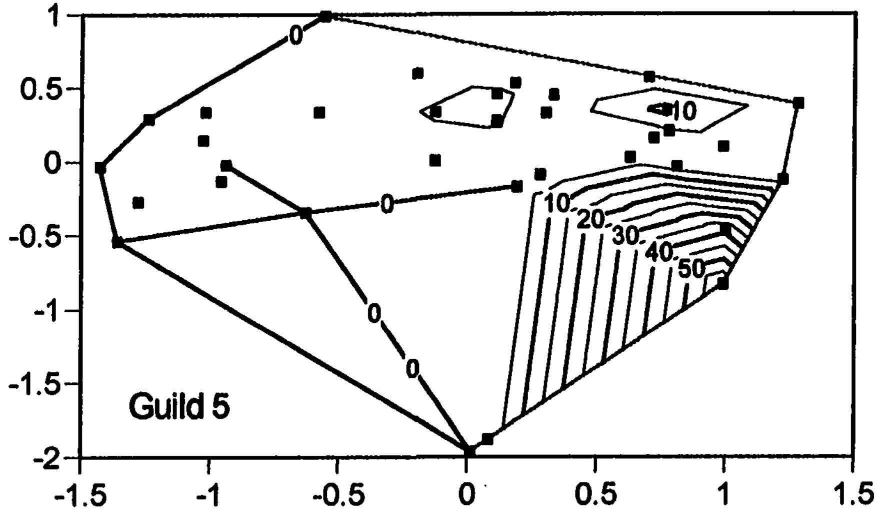
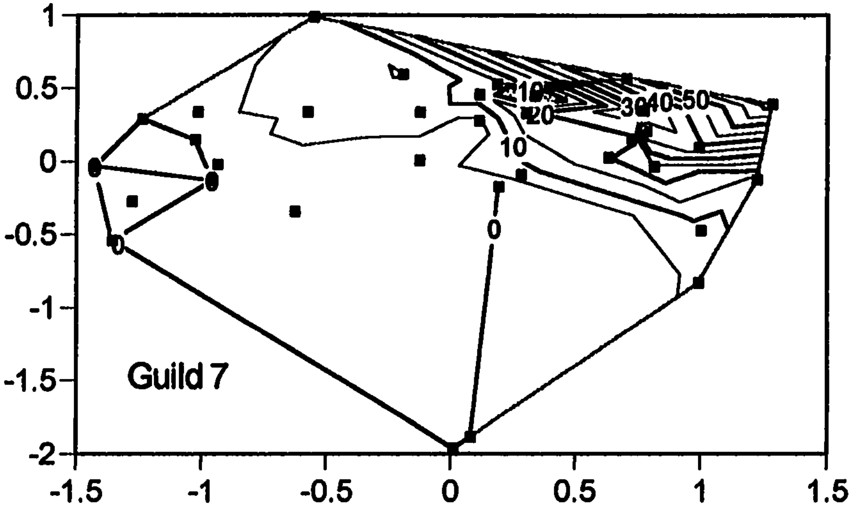
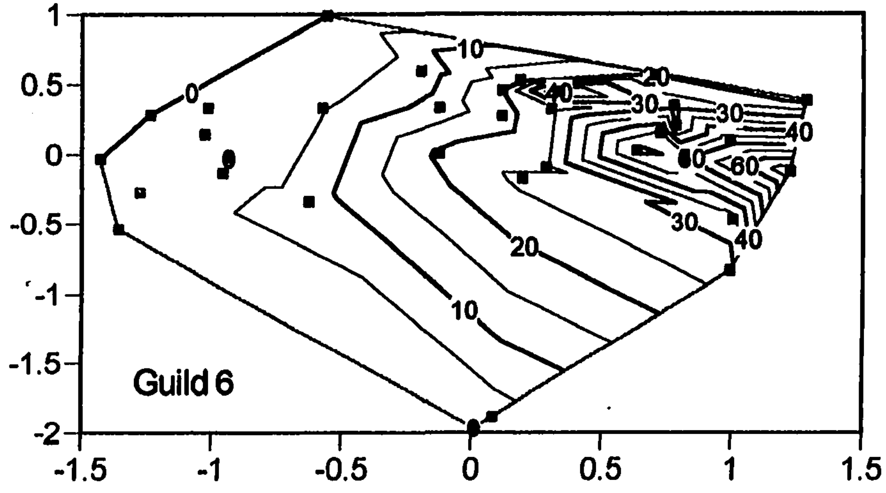

Guild 4 w/out Paragazzisocrinus
10
5
5
10
40
35
30
25
20
10
5
1
0.5
0
-0.5
-1
-1.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5

Figure 3.27) Contour of guild abundances onto the Q - mode MDS ordination. Guild 5 is virtually isolated in the transitional low energy - dysaerobic field of biofacies 4. Guild 6 is prominent in the low energy field of biofacies 3 with a diminishing contribution through the moderate energy field of biofacies 2. It is rare in the high energy field of biofacies 1. The non - pinnulate crinoids of guild 7 are quite confined to the low energy field of biofacies 3 and is virtually absent from all other biofacies. *Paragazzisocrinus* is restricted to the extreme dysaerobic field of biofacies 5.


Guild 5
1
0.5
0
-0.5
-1
-1.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
0
10
20
30
40
50


Guild 7
1
0.5
0
-0.5
-1
-1.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
0
10
20
30
40
50


Guild 6
1
0.5
0
-0.5
-1
-1.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
0
10
20
30
40
60

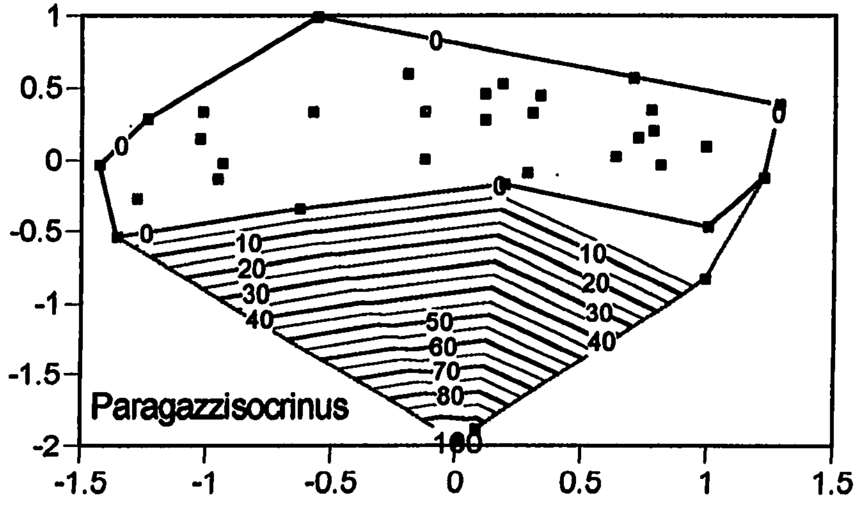

Paragazzisocrinus
1
0.5
0
-0.5
-1
-1.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
0
10
20
30
40
50
60
70
80
100

Figure 3.28) Distribution of guilds within biofacies of the Lansing Group. Note the systematic transition of large, pinnulate guilds for small, pinnulate and non - pinnulate guilds from biofacies 1 through 4.

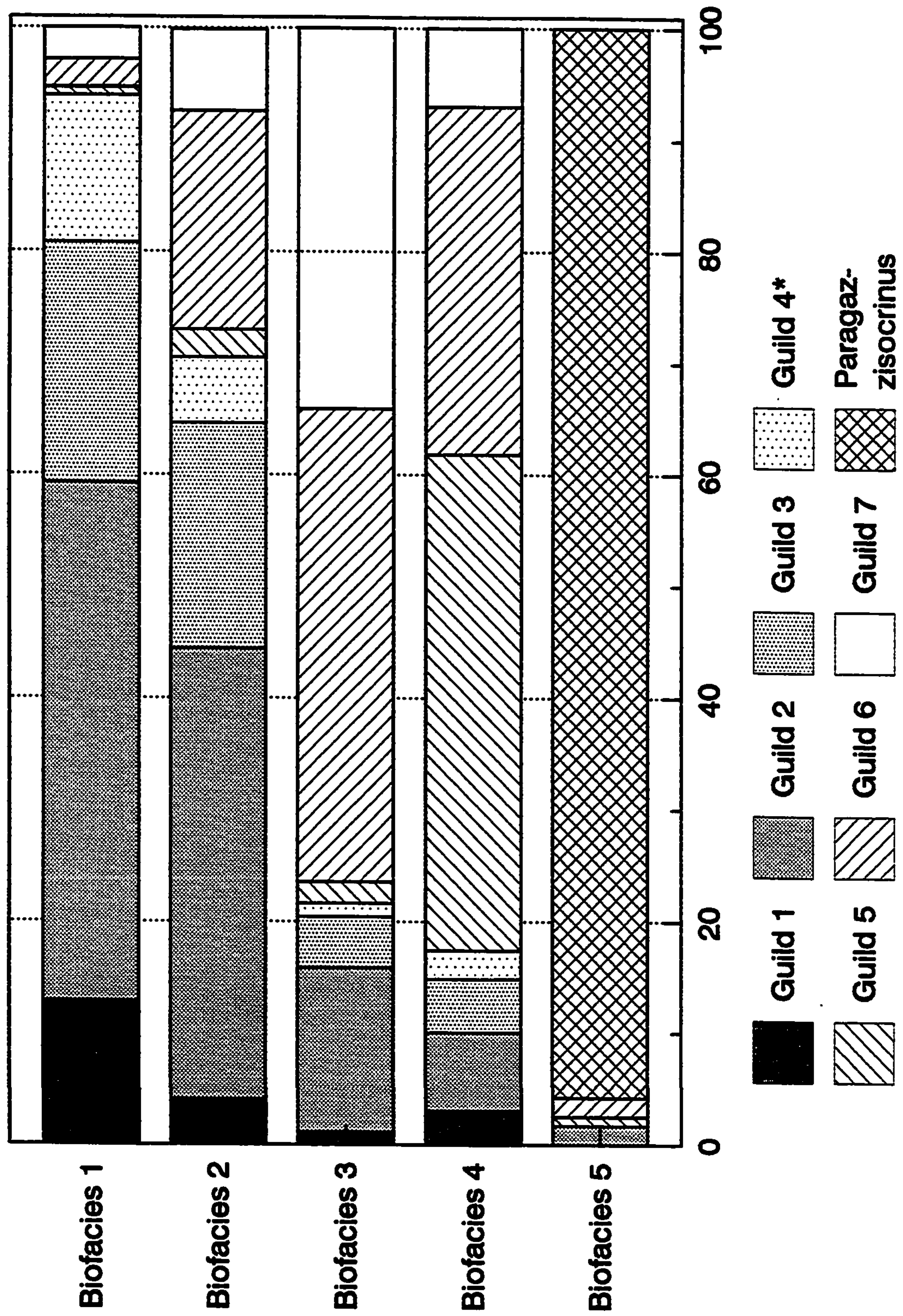

Biofacies 1
Biofacies 2
Biofacies 3
Biofacies 4
Biofacies 5
0
20
40
60
80
100
Guild 1
Guild 2
Guild 3
Guild 4*
Guild 5
Guild 6
Guild 7
Paragaz-
zisocrinus

Figure 3.29) Distribution of guilds within biofacies of the South Bend Formation. Note the systematic transition of large, pinnulate guilds for small, pinnulate and non - pinnulate guilds from biofacies 1 through 3, consistent with that observed for the Stanton and Lansing Group as a whole.

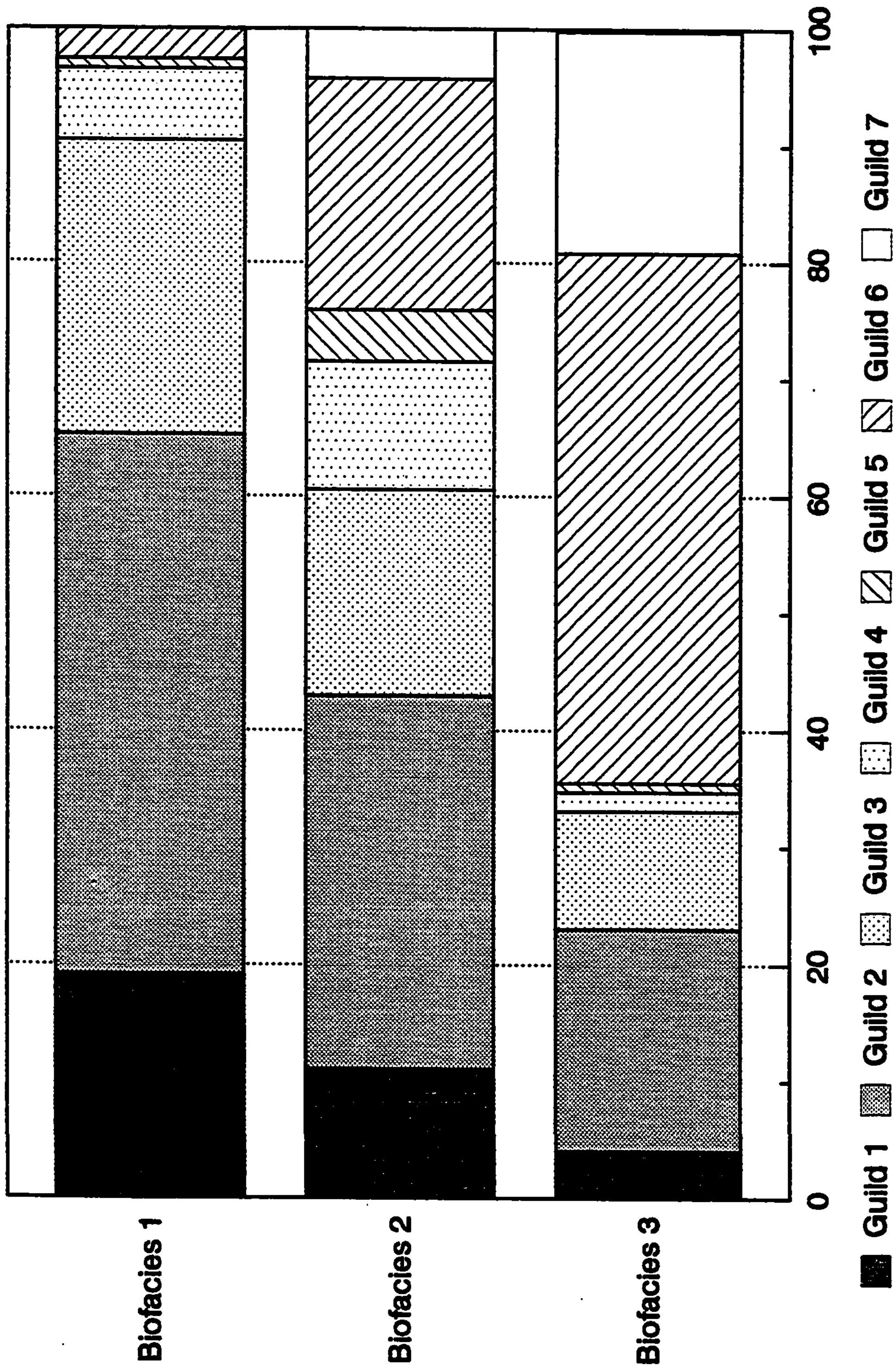

Biofacies 1
Biofacies 2
Biofacies 3
0
20
40
60
80
100
Guild 1
Guild 2
Guild 3
Guild 4
Guild 5
Guild 6
Guild 7

Figure 3.30) Distribution of guilds within biofacies of the Plattsburg Formation. Note the systematic transition of large, pinnulate guilds for small, pinnulate and non - pinnulate guilds from biofacies 1 through 3, consistent with biofacies patterns of all formations of the Lansing Group.

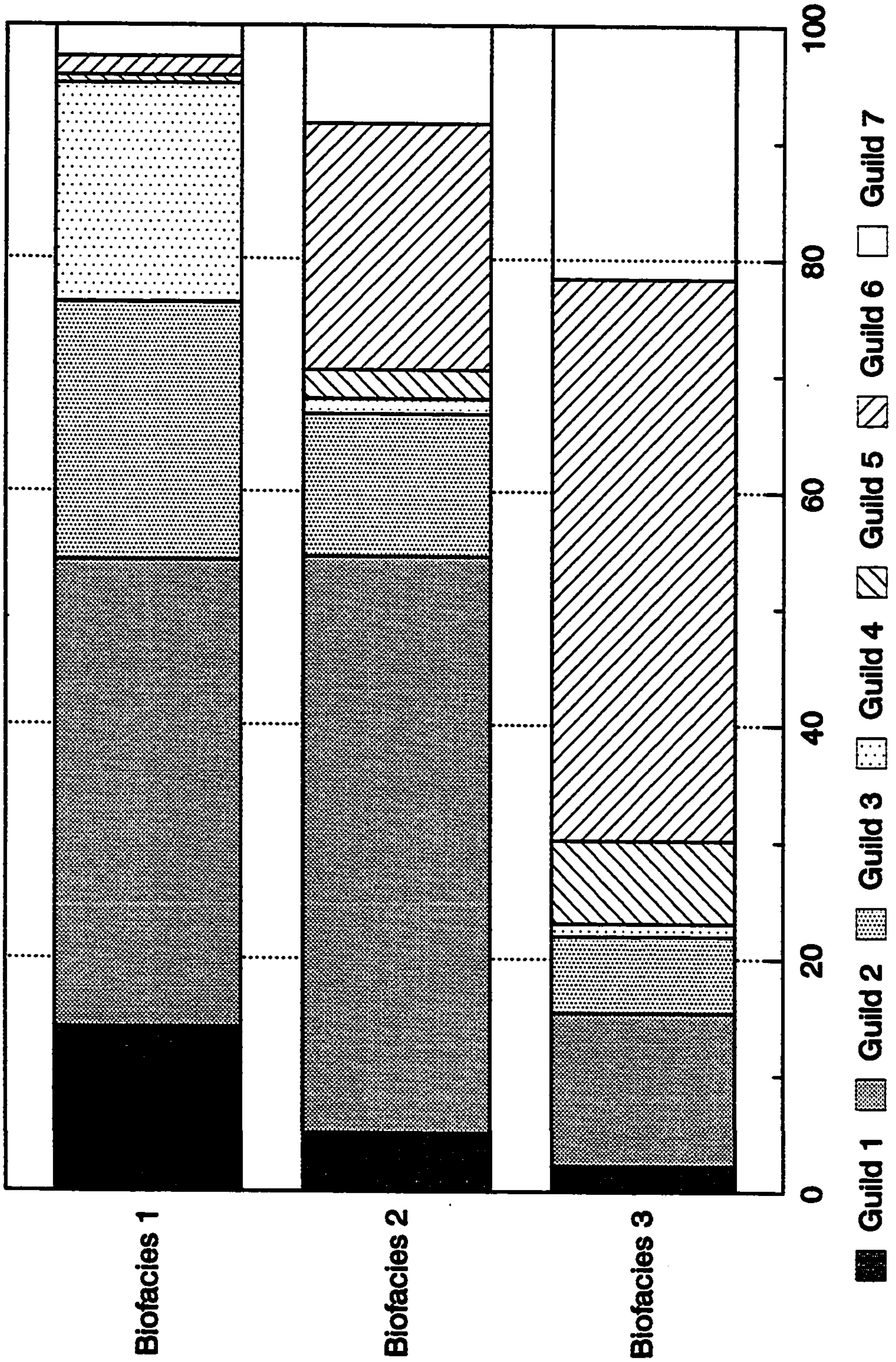

Biofacies 1
Biofacies 2
Biofacies 3
0
20
40
60
80
100
Guild 1
Guild 2
Guild 3
Guild 4
Guild 5
Guild 6
Guild 7

Table 7) Diversity patterns between biofacies of the Lansing Group. S = "species", or taxonomic richness; E = "equitability", measure of equality of species abundance; N = number of samples within biofacies; n = number of individuals within biofacies. Taxonomic richness has increased in biofacies 1 and 3 with the addition of samples from the Plattsburg and South Bend formations compared to the Stanton alone. However, even with *S* virtually equal between biofacies 1 through 4, diversity is still more equitably structured in biofacies 1 and 2 and is increasingly more dominance structured in biofacies 3, 4, and 5. A crinoid fauna from the Liberty Memorial Shale Formation in northeastern Kansas is included for comparison. This late regressive, prodeltaic fauna exhibits low taxonomic richness and uneven distribution of individuals contrasted with the nearshore fauna of biofacies 1. This simply points out the reduction in diversity experienced by crinoid paleocommunities at the nearshore terminus of the onshore - offshore environmental gradient.

Biofacies	1	2	3	4	5
S	25	26	25	23	4
E	0.76	0.79	0.66	0.53	0.12
N	10	11	9	2	2
n	1292	3396	5282	1377	118

Liberty Memorial Shale	% abund.	
Delocrinus	64.5	S = 8 E = 0.52 N = 5 n = 287
cromyocrinids	16.7	
ampelocrinids	13.2	
pirasocrinids	2.1	
Elibatocrinus	1.7	
Kallimorphocrinus	0.7	
Erisocrinus	0.7	
cymbiocrinids	0.3	

Table 8) Summary of analytical results of Stearns and Koella (1986).

	Size at Maturity	Lifetime Fecundity	Age at Maturation
Slow, Stressed Growth	Small, due to reduced rate of growth	Low, proportional to size reduction from normal	Increases to maximize slow growth to reduce spontaneous juvenile mortality, maintaining r
Rapid, Optimal Growth	Large, due to rapid growth	High, related to increased size at maturity	Decreases to reduce generation time, maximizing r

Figure 3.31) Lithologic section at Bolton, Kansas. Silty clastics of the Vilas Formation are overlain by a thin horizon of foram- and cyanobacteria - encrusted shell material ("Ottonosia" facies) of the lower Captain Creek. The distinctive sponge-rich wackestone composes the upper Captain Creek. This unit is overlain by the black, phosphatic facies of the Eudora Shale. Arrow marks crinoidal horizon.

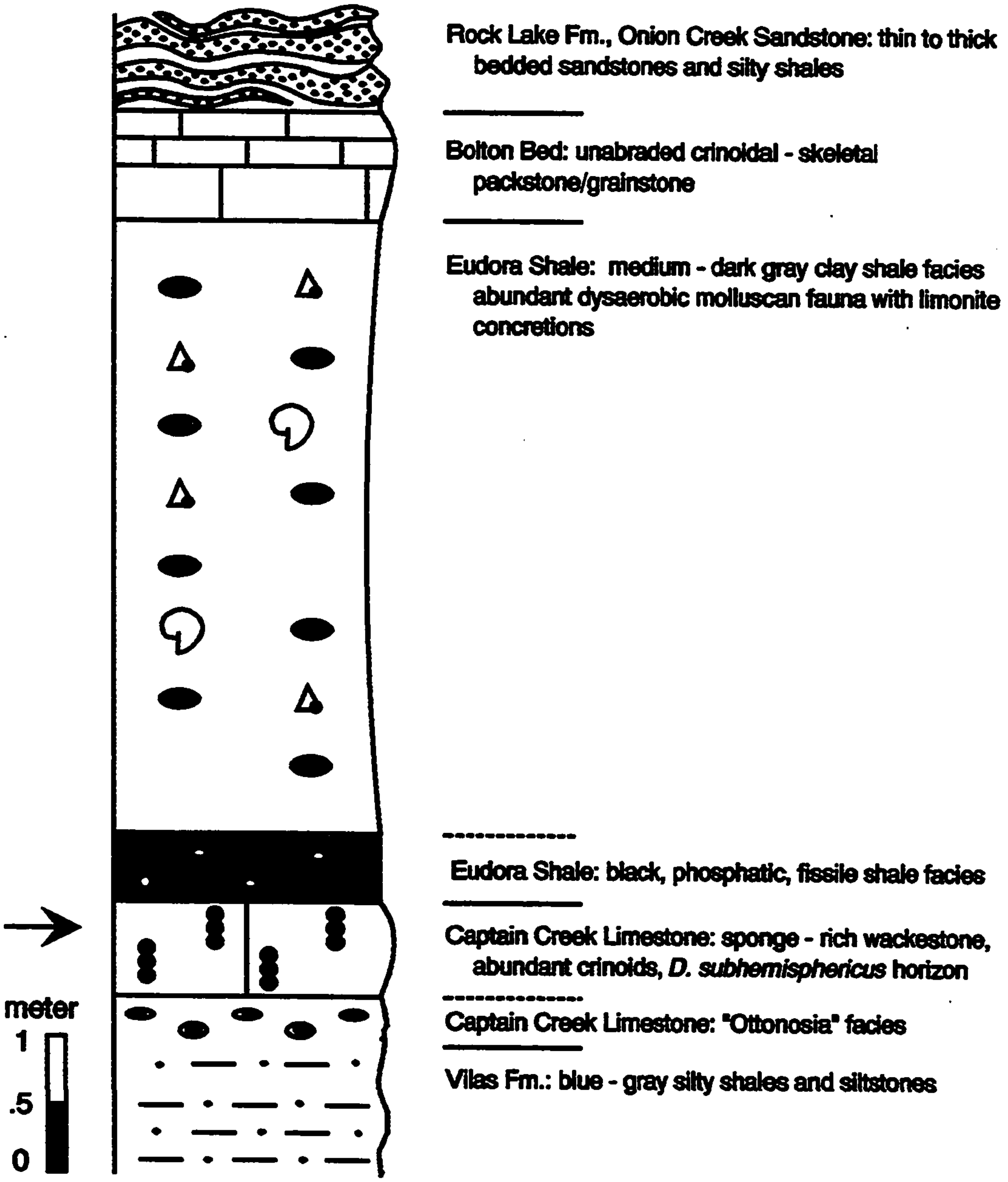

Rock Lake Fm., Onion Creek Sandstone: thin to thick bedded sandstones and silty shales
Bolton Bed: unabraded crinoidal - skeletal packstone/grainstone
Eudora Shale: medium - dark gray clay shale facies abundant dysaerobic molluscan fauna with limonite concretions
Eudora Shale: black, phosphatic, fissile shale facies
Captain Creek Limestone: sponge - rich wackestone, abundant crinoids, *D. subhemisphericus* horizon
Captain Creek Limestone: "Ottonosia" facies
Vilas Fm.: blue - gray silty shales and siltstones
meter
1
.5
0

Figure 3.32) Lithologic section at Louisville, Nebraska. The Kiewitz Bed and upper Stoner represent a shoaling carbonate ramp capped by a well - developed paleosol. Arrow marks crinoidal horizon.

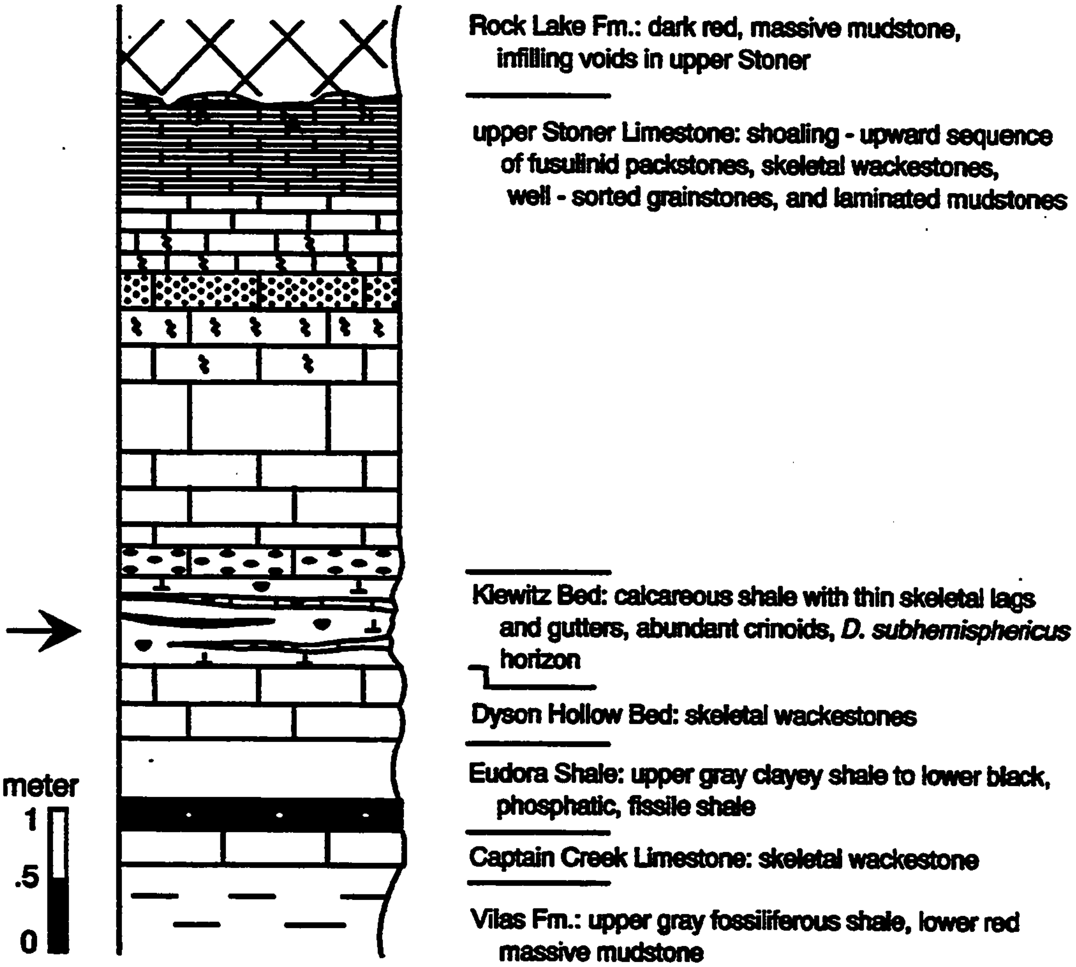

Rock Lake Fm.: dark red, massive mudstone, infilling voids in upper Stoner
upper Stoner Limestone: shoaling - upward sequence of fusulinid packstones, skeletal wackestones, well - sorted grainstones, and laminated mudstones
Klewitz Bed: calcareous shale with thin skeletal lags and gutters, abundant crinoids, *D. subhemisphericus* horizon
Dyson Hollow Bed: skeletal wackestones
Eudora Shale: upper gray clayey shale to lower black, phosphatic, fissile shale
Captain Creek Limestone: skeletal wackestone
Vilas Fm.: upper gray fossiliferous shale, lower red massive mudstone
meter
1
.5
0

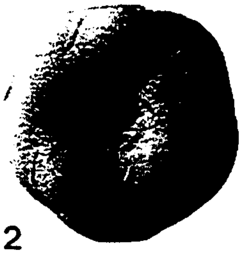
Figure 3.33) *Delocrinus subhemisphericus* growth stages. J1 and J2 specimens from Bolton, A specimen from Louisville.

1 - *3*) Oral (*1*), posterior (*2*), and aboral (*3*) views of early juvenile (J1) growth stage; cup width, 11.1 mm. Note tumid plates and pronounced dimples (UCGM 46495).

4 - *6*) Oral (*4*), posterior (*5*), and aboral (*6*) views of late juvenile (J2) growth stage; cup width, 12.0 mm. Note suppression of plate tumidity, but retention of dimples (UCGM 46496).

7 - *8*) Oral (*7*) and aboral (*8*) views of mature (A) growth stage; cup width, 16.3 mm. Note smooth suturing of entire cup (UCGM 46497).

1



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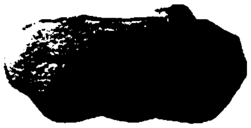

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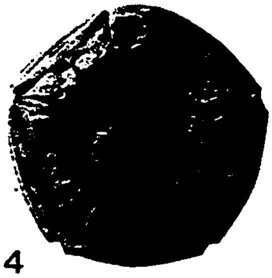
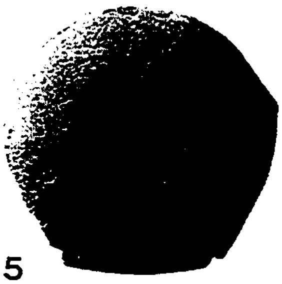
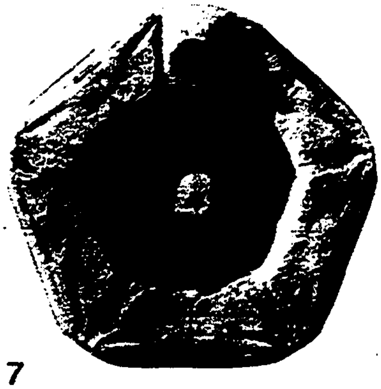


4

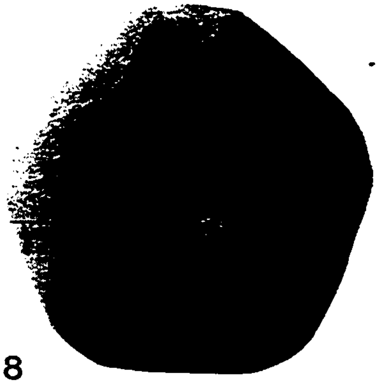


5

6

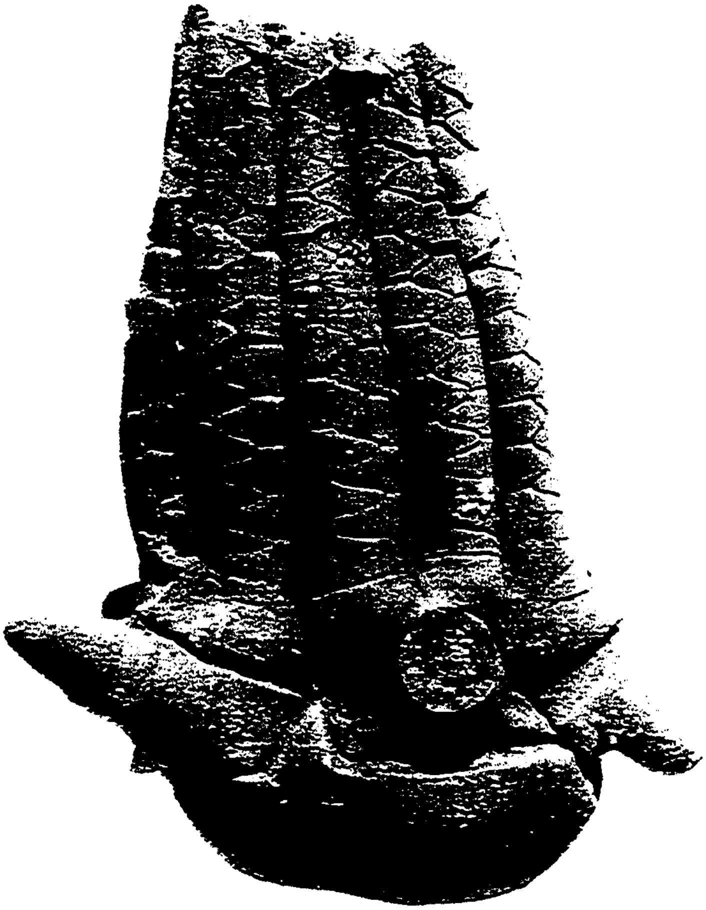


7



8

Figure 3.34) Crown and camera lucida of cup of *Delocrinus subhemisphericus*. Crown showing dense filtration fan of ten, biserial, pinnulate arms; crown height, 34.5 mm (UCGM 46498). Dorsal cup (UCGM 46497) width (Wc) was measured from anterior (A ray) to posterior (anal X). Widths of isolated radial plates (Wr) were measured lateral margin to lateral margin along the upper articulating surface.



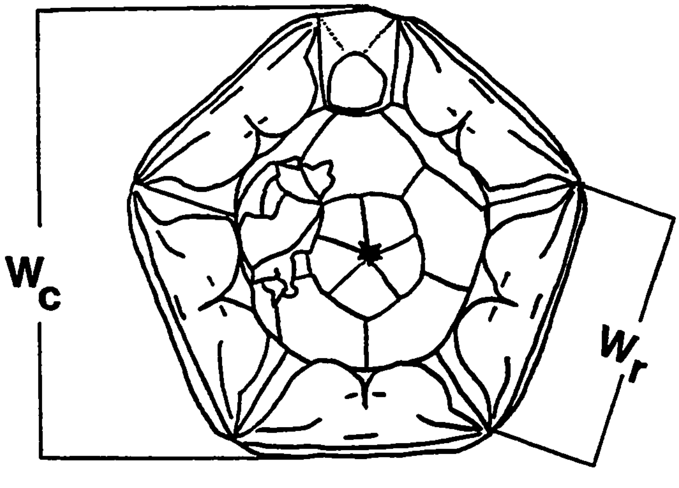
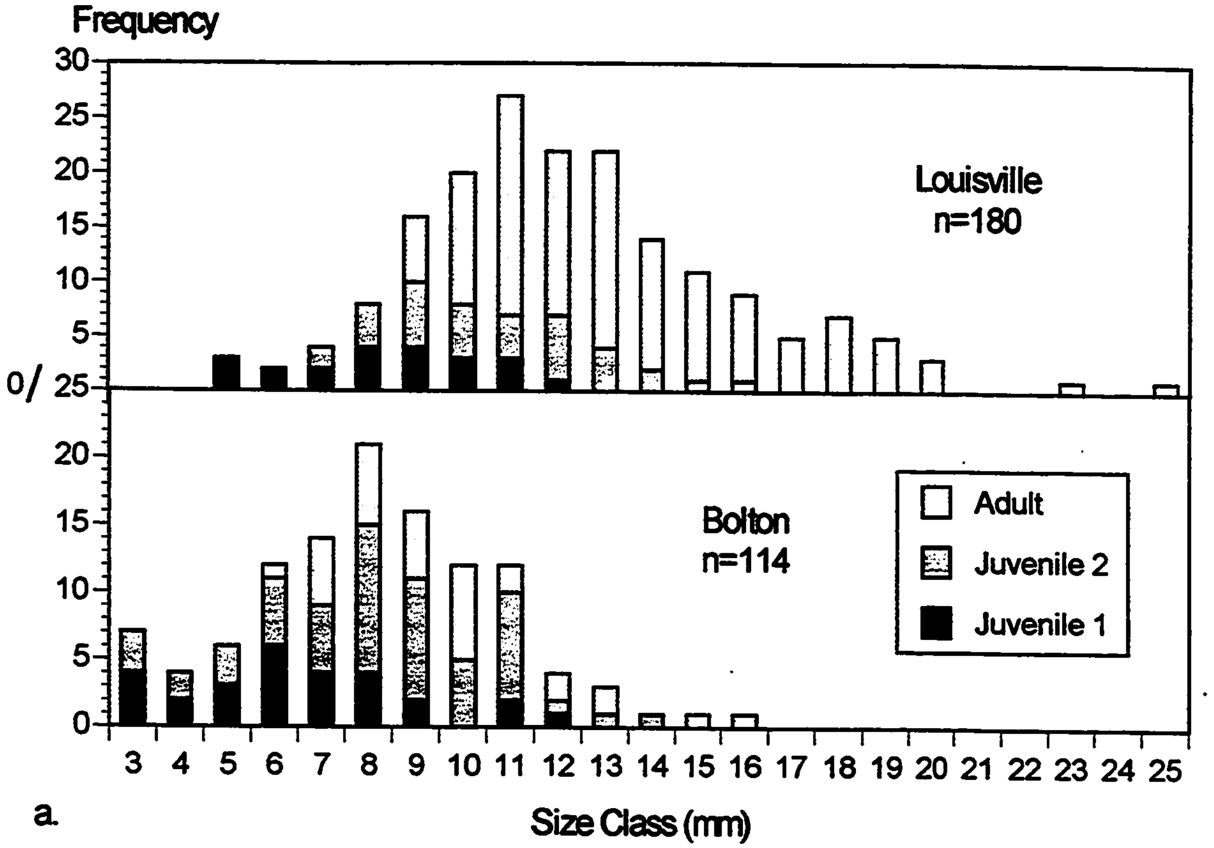

W_c
W_r

Figure 3.35) Size frequency data of *D. subhemisphericus*. a. Size frequency histograms of *D. subhemisphericus*. Maturity classes defined in figure 3.38. b. Cumulative log percent of size classes.


Frequency
30
25
20
15
10
5
0/ 25
20
15
10
5
0
Louisville
n=180
Bolton
n=114
Adult
Juvenile 2
Juvenile 1
3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
a.
Size Class (mm)

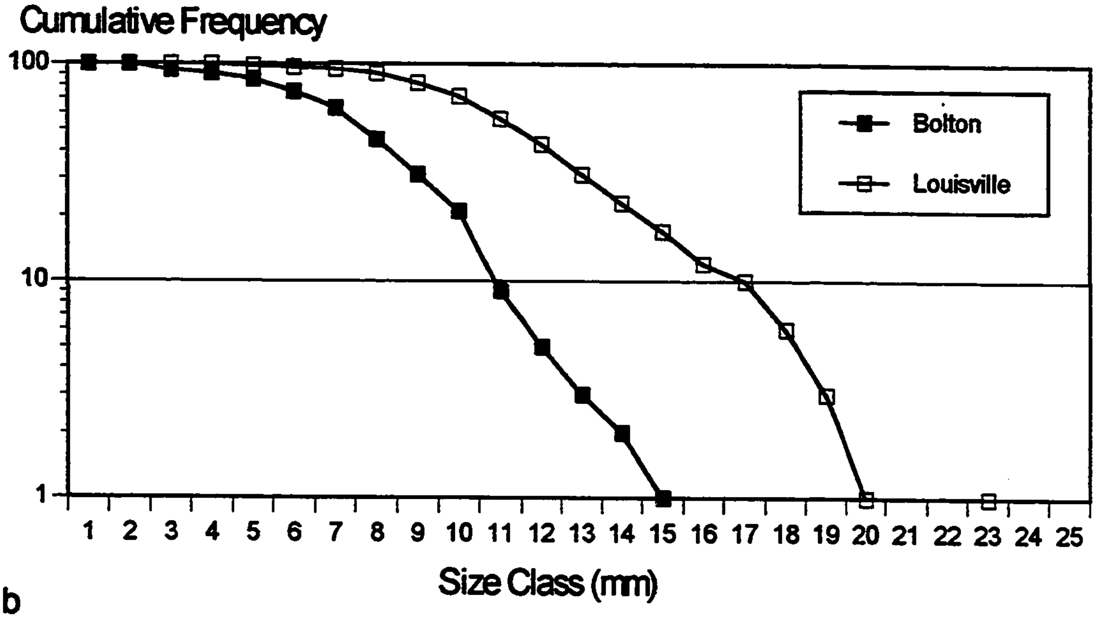
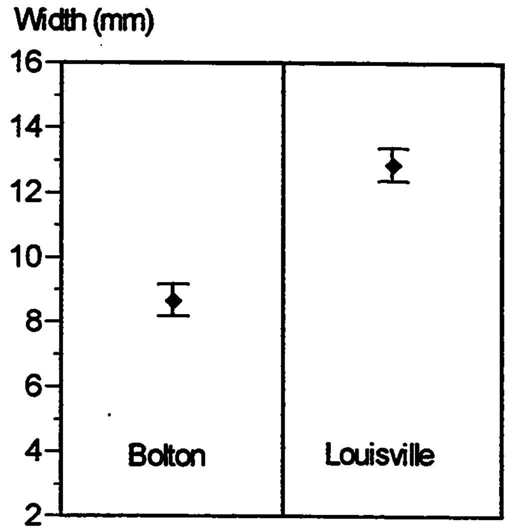
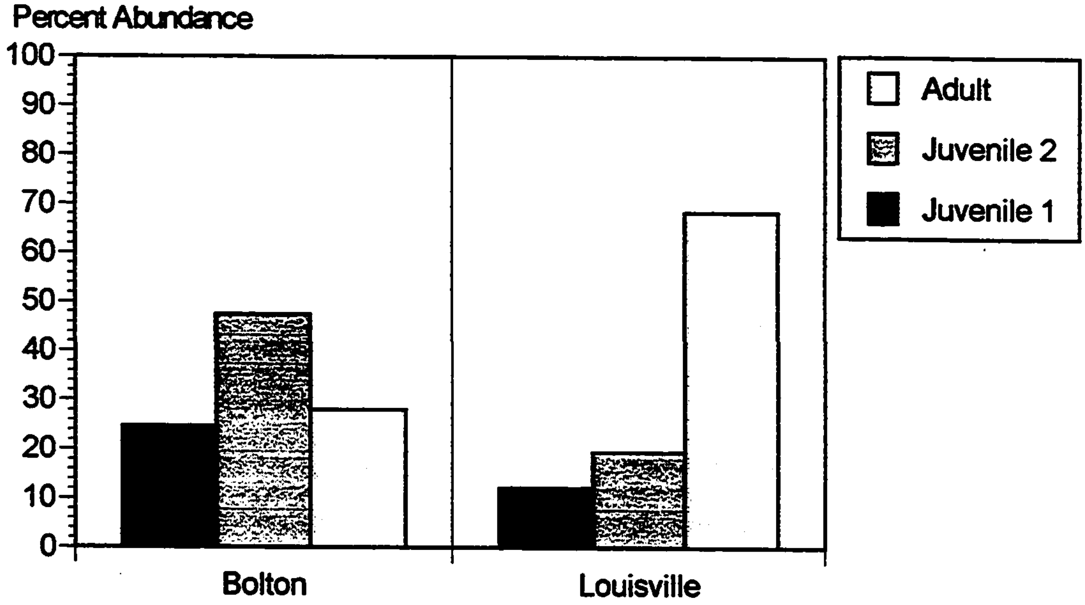

Cumulative Frequency
100
10
1
Bolton
Louisville
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
Size Class (mm)
b

Figure 3.36) Mean cup size and maturity histograms. a. Ninety - five percent confidence interval for total cup size. The two populations are significantly different in their overall mean size. b. Percent frequency histogram of maturity classes between the two populations. The Bolton population is dominated by juveniles while Louisville is dominated by adults.

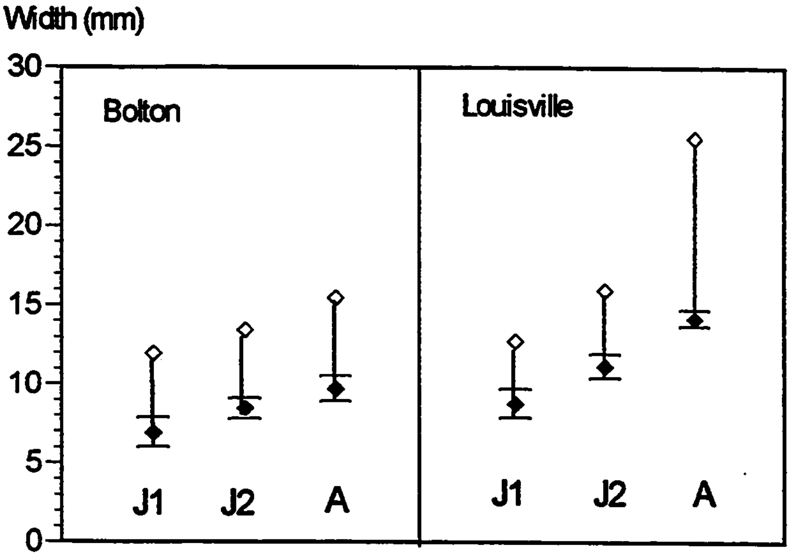

Width (mm)
16
14
12
10
8
6
4
2
Bolton
Louisville

a

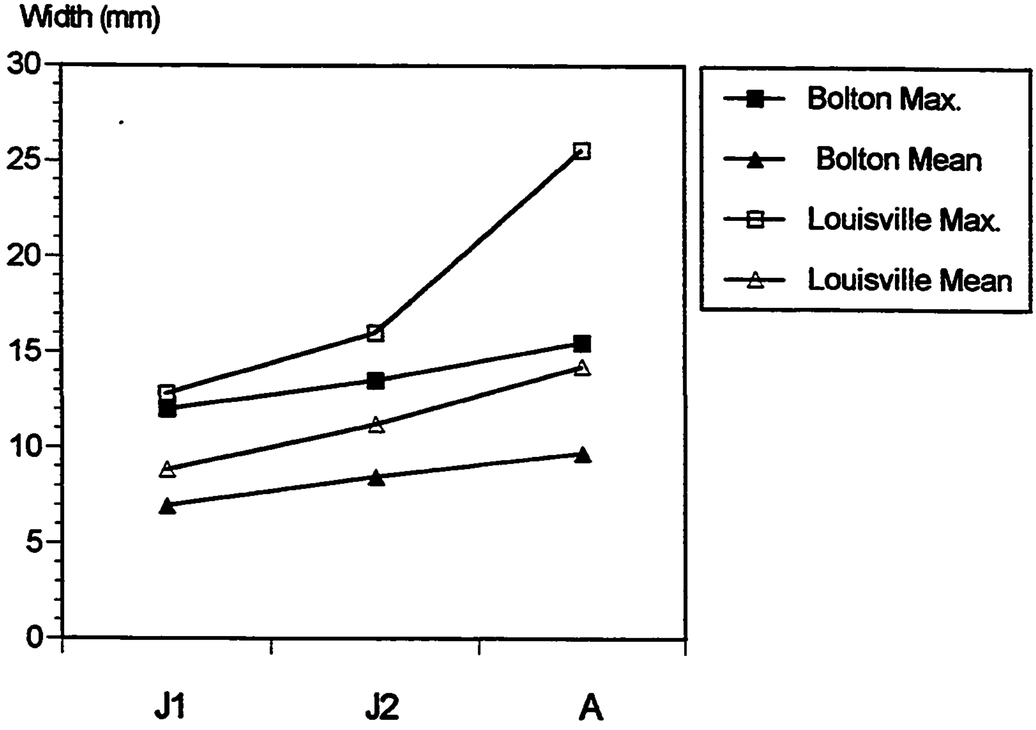

Percent Abundance
100
90
80
70
60
50
40
30
20
10
0
Bolton
Louisville
Adult
Juvenile 2
Juvenile 1

b

Figure 3.37) Body size of maturity classes. a. Mean (solid diamond), 95% confidence interval (bars), and maximum body size (open diamond) for the three maturity classes between the two populations. Note that successive growth stages are significantly different in size at Louisville while they overlap at Bolton. b. Growth plot of mean and maximum sizes for the two populations. Note the divergence of the curves at older growth stages, particularly the divergence between the maximum size attained by adults between the two localities.

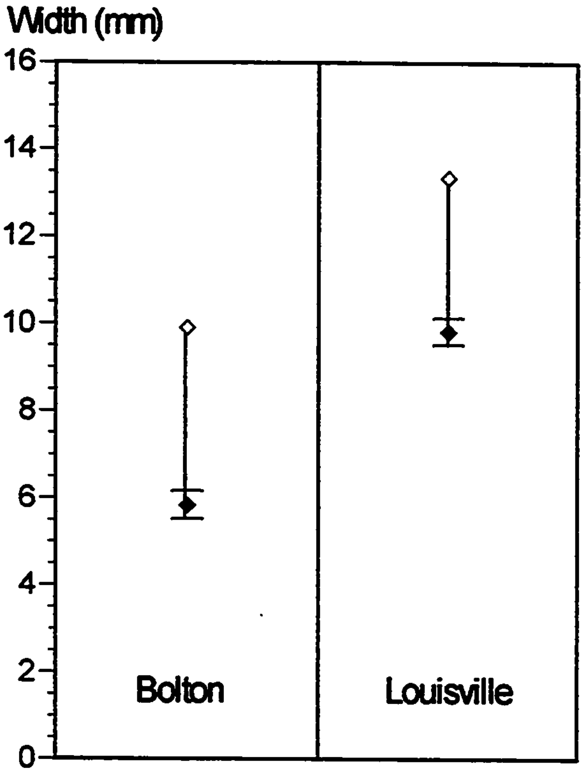

Width (mm)
30
25
20
15
10
5
0
Bolton
Louisville
J1
J2
A
J1
J2
A

a


Width (mm)
30
25
20
15
10
5
0
Bolton Max.
Bolton Mean
Louisville Max.
Louisville Mean
J1
J2
A

b

Figure 3.38) Isolated radial size. Mean (solid diamond), 95% confidence interval (bars), and maximum (open diamond) sizes of isolated radial plates of *D. subhemisphericus* from the two localities. The size differences of the disarticulated radials parallel the size differences of the dorsal cups (Fig. 3.41), indicating that differential disarticulation of various size classes did not occur.


Width (mm)
16
14
12
10
8
6
4
2
0
Bolton
Louisville

CHAPTER 4

SUMMARY

Crinoids of the Upper Pennsylvanian Lansing Group are not randomly distributed among environments, but rather are tied to specific hydrographic energy regimes based upon the density of their filtration fan and body size: large and/or dense fan crinoids are most abundant in high energy, nearshore facies while small and/or open fan crinoids are most abundant in low energy, offshore facies. This general pattern of crinoid distribution is consistent with predictions made by filtration theory.

Diversity patterns along the onshore - offshore gradient are also consistent with filtration theory: highest diversity/evenness in fully marine nearshore and mid - depth settings, lowest diversity/evenness in extreme nearshore and offshore settings. However, this is not a product of simple winnowing of stenotopic nearshore taxa progressively offshore, as is predicted by filtration theory. There is an actual replacement of numerous characteristically nearshore taxa for fewer characteristically offshore taxa from onshore to offshore with overlap in mid - depth settings. This contradiction to filtration theory is even more profound when the widespread distribution of the dense fan crinoids *Delocrinus subhemisphericus* and *Erisocrinus typus* is noted. It is here proposed that these crinoids manipulated their filtration fans in response to prevailing flow conditions which allowed them to exploit a wide range of habitats.

The association of taxonomic and morphologic groups of crinoids with particular depositional environments consistently recurs throughout the cycles of the Lansing Group. These recurring taxonomic and morphologic associations define crinoid biofacies which are named for the crinoid guild which dominates it:

The Dense Fan Biofacies is found in early transgressive, late regressive, and/or elevated shelf and basinal settings disposed to shallow, higher energy conditions.

The High Guild Diversity Biofacies encompasses a variety of "mid - depth" settings ranging from early regressive shelf, mid/late transgressive shelf, and early transgressive basinal settings.

The Open Fan Biofacies is diagnostic of mid/late transgressive basinal or transitional late transgressive - highstand shelf settings indicative of offshore, low energy conditions.

The Small Calyx, Pinnulate Biofacies is found in mildly dysaerobic basinal deposits associated with the transition from dysaerobic to aerobic highstand facies.

The Mature Molluscan - *Paragazzisocrinus* Biofacies is intimately associated with basinal, highstand dysaerobic molluscan faunas as previously identified by Boardman et al. (1984).

Available evidence does not support the model that these biofacies were highly integrated units which tracked paleobathymetric zones with changing sea level. Instead, taxa appear to have responded independently to changing environmental conditions, with particular environments being consistently staffed by taxa best adapted to the prevailing conditions.

The asymmetric deployment of biofacies within cyclic sequences is the strongest evidence that taxa are responding independently to consistently recurring conditions. The Open Fan Biofacies is only found in the transgressive systems tracts of cyclothems; it has yet to be identified from any regressive systems tract. This indicates that the characteristic association of taxa which defines this biofacies only occurs with rising sea level and does not recur, or track back out, with falling sea level. This pattern also provides some insight into the dynamics of transgression and regression. The restriction of a biofacies to one hemicycle suggests a more complex sequence of environmental and climatic events than simple rise and fall of sea level.

Coordinated shifts in abundance patterns of taxa among depositional environments is what structures biofacies. The change in abundance of individual taxa is inferred to be a response to reduced fitness as more stressful environments are encountered. However, decreases in abundance between environments is only one response to stress. A marginal, offshore population of *Delocrinus subhemisphericus* experienced high juvenile mortality, reduced growth rates, stunted adults, and apparently reduced fecundity, compared to a population from more optimal nearshore conditions. This response pattern can serve as a model for assessing the response of other crinoid species to stressful conditions.

These biofacies and phenotypic response patterns provide a template for the analysis of Late Paleozoic crinoid evolutionary ecology. Some potential questions include: Can these same morphology - based biofacies be identified in other basins and paleobiogeographic provinces? How temporally recognizable are these morphology - based biofacies? Which biofacies experience the most taxonomic volatility? Are new taxonomic associations within biofacies assembled from existing species or are new or immigrant species involved? How ecologically variable are various taxa through time? Are there contrasting evolutionary dynamics between generalist and specialist taxa? Is there any relationship between intraspecific stress response patterns and modes of speciation?

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Appendix 1) South Bend Formation raw data and biofacies - guild tables.

	LXQN	ERQK	CARK	RRWK	Total
cromyo.	21	1	1	3	26
Stellaro.	1	5	3	7	16
Delo.	44	7	1	3	55
Eriso.	6	16	2	43	67
Ulo.	3	3	0	1	7
Terpno.	3	0	0	1	4
Glaukoso.	3	1	0	0	4
laudono.	0	1	2	4	7
Exorio.	0	1	0	2	3
piraso.	15	3	2	15	35
scytalo.	8	4	1	3	16
stenope.	0	0	1	0	1
ampelo.	1	0	0	0	1
Elibato.	3	8	0	3	14
cymbio.	3	1	1	1	6
Exo.	1	4	0	1	6
Galatea.	0	0	0	1	1
Apographio.	3	12	5	102	122
graphio.	0	1	0	10	11
Kallimorpho.	0	3	1	10	13
Lecythio.	0	0	0	7	7
Cibolo.	0	0	0	30	30
Total	115	71	20	247	452

Biofacies	Guild	Taxa	Rank w/in Guild	Rank w/in Biofacies	% Abundance w/in Biofacies
Biofacies 1 Shoreward facies of early transgression and late regression	Guild 2 - 46.1% of Biofacies 1	Delocrinus	1	1	38.3
		Erisocrinus	2	5	5.2
		Ulocrinus	3	7	2.6
		Graffhamicrinus	-	-	0.0
	Guild 3 - 25.2% of Biofacies 1	pirasocrinids	1	3	13.0
		scytalocrinids	2	4	7.0
		Terpnocrinus	3	9	2.6
		Glaukosocrinus	4	10	2.6
		laudonocrinids	-	-	0.0
		Plummericrinus	-	-	0.0
		Exoriocrinus	-	-	0.0
		stenopecrinids	-	-	0.0
	Guild 1 - 19.1% of Biofacies 1	cromyocrinids	1	2	18.3
		Stellarocrinus	2	14	0.9
	Guild 4 - 6.1% of Biofacies 1	Elibatocrinus	1	6	2.6
		cymbiocrinids	2	8	2.6
		ampelocrinids	3	12	0.9
		Paragazzisocrinus	-	-	0.0
	Guild 6 - 2.6% of Biofacies 1	Apographiocrinus	1	11	2.6
		graphiocrinids	-	-	0.0
	Guild 5 - .9% of Biofacies 1	Exocrinus	1	13	0.9
		Galateacrinus	-	-	0.0
	Guild 7 - 0.0% of Biofacies 1	Kallimorphocrinus	-	-	0.0
		Lecythiocrinus	-	-	0.0
		Paramphicrinus	-	-	0.0
		Cibolocrinus	-	-	0.0
		Euonychocrinus	-	-	0.0

Biofacies	Guild	Taxa	Rank w/in Guild	Rank w/in Biofacies	% Abundance w/in Biofacies
Biofacies 2 Mid-shelf facies of early to mid transgression and early to mid regression	Guild 2 - 31.9% of Biofacies 2	Erisocrinus	1	1	19.8
		Delocrinus	2	4	8.8
		Ulocrinus	3	11	3.3
		Graffhamicrinus	-	-	0.0
	Guild 6 - 19.8% of Biofacies 2	Apographiocrinus	1	2	18.7
		graphiocrinids	2	15	1.1
	Guild 3 - 17.6% of Biofacies 2	pirasocrinids	1	6	5.5
		scytalocrinids	2	7	5.5
		laudonocrinids	3	10	3.3
		Glaukosocrinus	4	14	1.1
		Exoriocrinus	5	16	1.1
		stenopecrinids	6	17	1.1
		Terpnocrinids	-	-	0.0
		Plummericrinus	-	-	0.0
	Guild 4 - 11.0% of Biofacies 2	Elibatocrinus	1	3	8.8
		cymbiocrinids	2	13	2.2
		Paragazzisocrinus	-	-	0.0
		ampelocrinus	-	-	0.0
	Guild 1 - 11.0% of Biofacies 2	Stellarocrinus	1	5	8.8
		cromyocrinids	2	12	2.2
	Guild 7 - 4.4% of Biofacies 2	Kallimorphocrinus	1	8	4.4
		Lecythiocrinus	-	-	0.0
		Paramphicrinus	-	-	0.0
		Cibolocrinus	-	-	0.0
		Euonychocrinus	-	-	0.0
	Guild 5 - 4.4% of Biofacies 2	Exocrinus	1	9	4.4
		Galateacrinus	-	-	0.0

Biofacies	Guild	Taxa	Rank w/in Guild	Rank w/in Biofacies	% Abundance w/in Biofacies
Biofacies 3 Offshore - oxic facies of mid to late transgression and highstand	Guild 6 - 45.3% of Biofacies 3	Apographiocrinus	1	1	41.3
		graphiocrinids	2	6	4.0
	Guild 2 - 19.0% of Biofacies 3	Erisocrinus	1	2	17.4
		Delocrinus	2	11	1.2
		Ulocrinus	3	19	0.4
		Graffhamicrinus	-	-	0.0
	Guild 7 - 19.0% of Biofacies 3	Cibolocrinus	1	3	12.1
		Kallimorphocrinus	2	5	4.0
		Lecythiocrinus	3	7	2.8
		Paramphicrinus	-	-	0.0
		Euonychocrinus	-	-	0.0
	Guild 3 - 10.1% of Biofacies 3	pirasocrinids	1	4	6.1
		laudonocrinids	2	9	1.6
		scytalocrinids	3	13	1.2
		Exoriocrinus	4	14	0.8
		Terpnocrinus	5	15	0.4
		Glaukosocrinus	-	-	0.0
		Plummericrinus	-	-	0.0
		stenopecrinus	-	-	0.0
	Guild 1 - 4.0% of Biofacies 3	Stellarocrinus	1	8	2.8
		cromyocrinids	2	12	1.2
	Guild 4 - 1.6% of Biofacies 3	Elibatocrinus	1	10	1.2
		cymbiocrinids	2	16	0.4
		Paragazzisocrinus	-	-	0.0
		ampelocrinus	-	-	0.0
	Guild 5 - .8% of Biofacies 3	Exocrinus	1	17	0.4
		Galateacrinus	2	18	0.4

Appendix 2) Stanton Formation raw data and biofacies - guild tables.

	PRQN	LKCK	UKCK	WLQK	TMQK	WINK	PHFK	PGSK	RFPK	BNFK	75BK	TOQK	ETQK	LCWO	UCWO	LTDO	UTDO	NTSO	BCQO	SLWO	Total
cromyo.	32	2	1	4	0	12	5	0	0	0	0	0	0	12	5	2	3	11	2	17	108
Stellaro.	8	0	10	9	1	6	0	0	0	2	0	1	0	11	4	40	6	16	7	46	167
Delo.	361	22	15	77	4	24	32	0	2	29	79	69	17	15	10	11	5	14	6	49	841
Graffhami.	82	4	0	8	0	23	0	0	0	0	0	0	0	5	13	0	0	4	0	1	140
Eriso.	141	3	74	180	7	14	35	0	0	21	143	65	7	149	52	60	7	36	2	10	1006
Ulo.	25	0	0	8	9	2	0	0	0	0	0	0	0	1	0	1	1	0	1	1	49
Terpno.	15	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	18
Glaukoso.	5	0	2	1	0	0	0	0	0	1	0	0	0	1	0	0	2	2	3	8	25
laudono.	40	0	0	45	1	0	1	0	0	1	5	6	0	2	3	0	1	1	0	1	107
Plummeri.	11	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	4	2	4	24
Exorio.	19	1	2	2	1	1	7	0	0	1	14	0	0	1	6	3	3	12	2	7	82
piraso.	93	6	7	79	1	25	1	0	0	3	0	5	0	38	12	20	23	34	5	33	385
scytalo.	38	1	1	8	0	3	3	0	0	3	2	1	0	1	3	13	2	1	1	2	83
stenope.	32	1	8	29	3	0	0	0	0	2	2	2	0	16	22	29	0	75	3	3	227
Paragazziso.	0	0	0	0	0	0	0	33	80	0	0	0	1	0	0	0	0	0	0	0	114
ampelo	21	1	1	3	0	5	0	0	0	2	0	1	0	2	0	11	4	10	5	62	128
Elibato.	74	0	3	15	3	1	10	0	0	0	4	0	2	12	19	12	1	1	2	2	161
cymbio.	26	0	4	7	1	9	4	0	0	1	0	1	0	1	1	10	3	6	2	7	83
Exo.	32	0	11	21	0	2	0	0	1	7	2	5	213	2	0	375	0	1	0	1	673
Galatea.	0	0	1	15	0	1	6	0	0	5	7	0	2	3	8	21	0	0	0	0	69
Apographio.	277	0	261	73	0	1	382	0	2	73	159	272	99	111	150	331	5	80	0	2	2278
graphio.	12	0	0	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	16
Kallimorpho.	39	1	122	5	0	0	25	0	0	3	30	0	12	66	273	45	0	11	0	0	632
Lecythio.	0	0	0	31	1	0	14	0	0	7	25	0	0	0	0	6	0	0	0	0	84
Paramphi.	0	0	2	1	0	0	7	0	0	4	32	2	0	21	41	16	0	8	0	0	134
Cibolo.	8	0	6	5	1	0	241	0	0	77	283	101	5	1	196	8	1	3	0	1	937
Euonycho.	0	0	0	0	0	0	21	0	0	5	25	2	3	1	3	1	0	3	0	0	64
Total	1391	42	531	632	33	130	794	33	85	247	813	533	361	472	821	1016	67	334	43	257	8635

Biofacies	Guild	Taxa	Rank w/in Guild	Rank w/in Biofacies	% Abundance w/in Biofacies
Biofacies 1 Shoreward facies of early transgression and late regression	Guild 2 - 32.5% of Biofacies 1	Delocrinus	1	1	19.7
		Erisocrinus	2	6	6.7
		Graffhamicrinus	3	7	5.2
		Ulocrinus	4	16	0.9
	Guild 3 - 26.7% of Biofacies 1	pirasocrinids	1	2	17.1
		Exoriocrinus	2	9	2.6
		Glaukosocrinus	3	10	2.4
		scytalocrinids	4	11	1.7
		Plummericrinus	5	13	1.3
		stenopecrinids	6	14	1.3
		laudonocrinids	7	18	0.4
		Terpnocrinus	-	-	0
	Guild 4 - 19.3% of Biofacies 1	ampelocrinids	1	3	14.3
		cymbiocrinids	2	8	3.9
		Elibatocrinus	3	15	1.1
		Paragassizocrinus	-	-	0
	Guild 1 - 18.7% of Biofacies 1	Stellarocrinus	1	4	12.1
		cromyocrinids	2	5	6.7
	Guild 6 - 1.5% of Biofacies 1	Apographiocrinus	1	12	1.5
		Contocrinus	-	-	0
	Guild 5 - .8% of Biofacies 1	Exocrinus	1	17	0.6
		Galateacrinus	2	21	0.2
	Guild 7 - .6% of Biofacies 1	Cibolocrinus	1	19	0.4
		Kallimorphocrinus	2	20	0.2
		Lecythiocrinus	-	-	0
		Euonychocrinus	-	-	0
		Paramphicrinus	-	-	0

Biofacies	Guild	Taxa	Rank w/in Guild	Rank w/in Biofacies	% Abundance w/in Biofacies
Biofacies 2 Mid-shelf facies of early to mid transgression and early to mid regression	Guild 2 - 39.3% of Biofacies 2	Erisocrinus	1	2	17.9
		Delocrinus	2	3	16.5
		Graffhamicrinus	3	8	3.5
		Ulocrinus	4	14	1.5
	Guild 3 - 21.5% of Biofacies 2	pirasocrinids	1	4	8.6
		stenopecrinids	2	5	5.4
		laudonocrinids	3	9	3.1
		scytalocrinids	4	12	1.7
		Exoriocrinus	5	17	1.2
		Terpnocrinus	6	20	0.6
		Plummericrinus	7	23	0.6
		Glaukosocrinus	8	25	0.3
	Guild 6 - 19.4% of Biofacies 2	Apographiocrinus	1	1	18.9
		Contocrinus	2	24	0.5
	Guild 7 - 7.2% of Biofacies 2	Kallimorphocrinus	1	6	4.2
		Lecythiocrinus	2	18	1.1
		Paramphicrinus	3	19	1
		Cibolocrinus	4	22	0.6
		Euonychocrinus	5	26	0.1
	Guild 4 - 6.4% of Biofacies 2	Elibatocrinus	1	7	3.7
		cymbiocrinids	2	15	1.4
		ampelocrinids	3	16	1.3
		Paragassizocrinus	-	-	0
	Guild 1 - 3.6% of Biofacies 2	cromyocrinids	1	10	2.1
		Stellarocrinus	2	13	1.6
	Guild 5 - 2.6% of Biofacies 2	Exocrinus	1	11	2
		Galateacrinus	2	21	0.6

Biofacies	Guild	Taxa	Rank w/in Guild	Rank w/in Biofacies	% Abundance w/in Biofacies
Biofacies 3 Offshore - oxic facies of mid- to late - transgression	Guild 7 - 41.4% of Biofacies 3	Cibolocrinus	1	2	24.2
		Kallimorphocrinus	2	3	12.1
		Paramphicrinus	3	6	2.4
		Euonychocrinus	4	7	1.5
		Lecythiocrinus	5	8	1.2
	Guild 6 - 34.7% of Biofacies 3	Apographiocrinus	1	1	34.7
		Contocrinus	-	-	0
	Guild 2 - 17.0% of Biofacies 3	Erisocrinus	1	4	10.4
		Delocrinus	2	5	6.3
		Graffhamicrinus	3	17	0.3
		Ulocrinus	-	-	0
	Guild 3 - 3.4% of Biofacies 3	stenopecrinids	1	10	1
		Exoriocrinus	2	11	0.8
		pirasocrinids	3	12	0.7
		laudonocrinids	4	16	0.4
		scytalocrinids	5	18	0.3
		Glaukosocrinus	6	22	0.1
		Plummericrinus	-	-	0
		Terpnocrinus	-	-	0
	Guild 5 - 1.4% of Biofacies 3	Galateacrinus	1	13	0.7
		Exocrinus	2	14	0.7
	Guild 4 - 1.4% of Biofacies 3	Elibatocrinus	1	9	1
		cymbiocrinids	2	20	0.3
		ampelocrinids	3	21	0.1
		Paragassizocrinus	-	-	0
	Guild 1 - .75% of Biofacies 3	Stellarocrinus	1	15	0.5
		cromyocrinids	2	19	0.3

Biofacies	Guild	Taxa	Rank w/in Guild	Rank w/in Biofacies	% Abundance w/in Biofacies
Biofacies 4 Offshore - dysoxic facies of late transgression and early regression; associated with epifaunal suspension feeders	Guild 5 - 44.4% of Biofacies 4	Exocrinus	1	1	42.7
		Galateacrinus	2	13	1.7
	Guild 6 - 31.2% of Biofacies 4	Apographiocrinus	1	2	31.2
		Contocrinus	-	-	0
	Guild 2 - 7% of Biofacies 4	Erisocrinus	1	3	4.9
		Delocrinus	2	7	2
		Ulocrinus	3	22	0.1
		Graffhamicrinus	-	-	0
	Guild 7 - 6.9% of Biofacies 4	Kallimorphocrinus	1	4	4.1
		Paramphicrinus	2	10	1.2
		Cibolocrinus	3	12	0.9
		Lecythiocrinus	4	16	0.4
		Euonychocrinus	5	17	0.3
	Guild 3 - 4.8% of Biofacies 4	stenopecrinids	1	6	2.1
		pirasocrinids	2	9	1.5
		scytalocrinids	3	13	0.9
		Exoriocrinus	4	18	0.2
		Plummericrinus	5	20	0.1
		Terpnocrinus	-	-	0
		Glaukosocrinus	-	-	0
		laudonocrinids	-	-	0
	Guild 1 - 3.1% of Biofacies 4	Stellarocrinus	1	5	2.9
		cromyocrinids	2	19	0.1
	Guild 4 - 2.6% of Biofacies 4	Elibatocrinus	1	11	1
		ampelocrinids	2	14	0.8
		cymbiocrinids	3	15	0.7
		Paragassizocrinus	4	20	0.1

Biofacies	Guild	Taxa	Rank w/in Guild	Rank w/in Biofacies	% Abundance w/in Biofacies
Biofacies 5 Offshore - dysoxic facies of highstand and early regression; associated with nekto - benthic & deposit - feeding mollusks	Guild 4 - 95.8% of Biofacies 5	Paragassizocrinus	1	1	95.8
		ampelocrinids	-	-	0
		cymbiocrinids	-	-	0
		Elibatocrinus	-	-	0
	Guild 6 - 1.7% of Biofacies 5	Apographiocrinus	1	2	1.7
		Contocrinus	-	-	0
	Guild 2 - 1.7% of Biofacies 5	Delocrinus	1	3	1.7
		Erisocrinus	-	-	0
		Ulocrinus	-	-	0
		Graffhamicrinus	-	-	0
	Guild 5 - .8% of Biofacies 5	Exocrinus	1	4	0.8
		Galateacrinus	-	-	0
	Guild 7 - 0% of Biofacies 5	Kallimorphocrinus	-	-	0
		Paramphicrinus	-	-	0
		Cibolocrinus	-	-	0
		Lecythiocrinus	-	-	0
		Euonychocrinus	-	-	0
	Guild 3 - 0% of Biofacies 5	stenopecrinids	-	-	0
		pirasocrinids	-	-	0
		scytalocrinids	-	-	0
		Exoriocrinus	-	-	0
		Plummericrinus	-	-	0
		Terpnocrinus	-	-	0
		Glaukosocrinus	-	-	0
		laudonocrinids	-	-	0
	Guild 1 - 0% of Biofacies 5	Stellarocrinus	-	-	0
		cromyocrinids	-	-	0

Appendix 3) Plattsburg Formation raw data and biofacies - guild tables.

	CCQN	O75K	N75K	K47K	K96K	NFDK	BRQK	TMBO	HPTO	CBMO	Total
cromyo.	13	8	2	1	5	0	0	11	4	2	46
Stellaro.	0	1	6	1	8	4	0	7	13	1	41
Delo.	14	190	9	10	5	9	4	16	33	2	292
Graffhami.	1	14	6	2	5	0	1	11	3	0	43
Eriso.	3	105	61	28	40	20	44	12	22	1	336
Ulo.	0	0	2	0	0	0	0	1	3	1	7
Terpno.	0	0	0	0	0	0	0	0	3	0	3
Glaukoso.	0	0	1	0	0	1	0	5	0	1	8
laudono.	3	11	1	0	2	1	0	3	5	0	26
Plummeri.	0	0	1	0	0	1	0	6	0	0	8
Exorio.	0	1	4	0	0	1	0	5	10	0	21
piraso.	12	13	5	2	10	2	1	12	27	1	85
scytalo.	0	1	1	0	1	1	0	2	10	0	16
stenope.	1	16	5	1	14	1	7	12	30	1	88
ampelo.	17	0	2	0	1	0	0	6	3	1	30
Elibato.	1	0	2	0	0	1	0	1	1	1	7
cymbio.	24	1	3	0	0	1	0	8	4	0	41
Exo.	0	0	2	2	0	4	1	1	19	0	29
Galatea.	0	1	0	3	1	12	0	2	12	0	31
Apographio.	0	6	26	12	6	30	27	1	398	0	506
graphio.	1	13	4	3	1	9	13	0	393	0	437
Kallimorpho.	0	0	0	1	0	12	0	0	13	0	26
Lecythio.	0	3	0	0	1	1	0	0	0	0	5
Paramphi.	0	2	2	2	0	1	0	0	22	0	29
Cibolo.	0	23	20	7	4	27	2	5	127	0	215
Euonycho.	0	0	0	0	0	0	0	0	2	0	2
Total	90	409	165	75	104	139	100	127	1157	12	2378

Biofacies	Guild	Taxa	Rank w/in Guild	Rank w/in Biofacies	% Abundance w/in Biofacies
Biofacies 1 Shoreward facies of early transgression and late regression	Guild 2 - 40.1% of Biofacies 1	Delocrinus	1	1	22.8
		Erisocrinus	2	2	11.7
		Graffhamicrinus	3	9	3.3
		Ulocrinus	4	13	2.3
	Guild 3 - 22.1% of Biofacies 3	pirasocrinids	1	4	8.6
		stenopecrinids	2	7	5.7
		Glaukosocrinus	3	10	3.1
		laudonocrinids	4	14	2.1
		Plummericrinus	5	15	1.2
		Exoriocrinus	6	17	1.0
		scytalocrinids	7	20	0.5
		Terpnocrinus	-	-	0.0
	Guild 4 - 18.8% of Biofacies 1	cymbiocrinids	1	5	8.3
		ampelocrinids	2	6	8.0
		Elibatocrinus	3	11	2.6
		Paragassizocrinus	-	-	0.0
	Guild 1 - 14.0% of Biofacies 1	cromyocrinids	1	3	10.4
		Stellarocrinus	2	8	3.5
	Guild 7 - 2.7% of Biofacies 1	Cibolocrinus	1	12	2.4
		Lecythiocrinus	2	22	0.2
		Paramphicrinus	3	23	0.1
		Kallimorphocrinus	-	-	0.0
		Euonychocrinus	-	-	0.0
	Guild 6 - 1.6% of Biofacies 1	graphiocrinids	1	16	1.1
		Apographiocrinus	2	18	0.6
	Guild 5 - .7% of Biofacies 1	Galateacrinus	1	19	0.5
		Exocrinus	2	21	0.2

Biofacies	Guild	Taxa	Rank w/in Guild	Rank w/in Biofacies	% Abundance w/in Biofacies
Biofacies 2 Mid-shelf facies of early to mid transgression and early to mid regression	Guild 2 - 49.4% of Biofacies 2	Erisocrinus	1	1	39.2
		Delocrinus	2	3	6.9
		Graffhamicrinus	3	9	3.0
		Ulocrinus	4	21	0.3
	Guild 6 - 21.2% of Biofacies 2	Apographiocrinus	1	2	16.1
		graphiocrinids	2	6	5.1
	Guild 3 - 12.2% of Biofacies 2	stenopecrinids	1	5	6.2
		pirasocrinids	2	7	4.1
		laudonocrinids	3	14	0.6
		Exoriocrinus	4	15	0.6
		scytalocrinids	5	18	0.4
		Plummericrinus	6	23	0.2
		Glaukosocrinus	7	24	0.2
		Terpnocrinus	-	-	0.0
	Guild 7 - 8.4% of Biofacies 2	Cibolocrinus	1	4	6.8
		Paramphicrinus	2	13	1.0
		Kallimorphocrinus	3	19	0.3
		Lecythiocrinus	4	22	0.2
		Euonychocrinus	-	-	0.0
	Guild 1 - 5.0% of Biofacies 2	Stellarocrinus	1	8	3.2
		cromyocrinids	2	10	1.8
	Guild 5 - 2.5% of Biofacies 2	Galateacrinus	1	11	1.2
		Exocrinus	2	12	1.2
	Guild 4 - 1.3% of Biofacies 2	ampelocrinids	1	16	0.5
		cymbiocrinids	2	17	0.5
		Elibatocrinus	3	20	0.3
		Paragassizocrinus	-	-	0.0

Biofacies	Guild	Taxa	Rank w/in Guild	Rank w/in Biofacies	% Abundance w/in Biofacies
Biofacies 3 Offshore - oxic facies of mid to late transgression and highstand	Guild 6 - 48.2% of Biofacies 3	Apographiocrinus	1	1	28.0
		graphiocrinids	2	2	20.2
	Guild 7 - 21.8% of Biofacies 3	Cibolocrinus	1	3	15.2
		Kallimorphocrinus	2	5	4.9
		Paramphicrinus	3	12	1.3
		Lecythiocrinus	4	18	0.4
		Euonychocrinus	5	26	0.1
	Guild 2 - 13.1% of Biofacies 3	Erisocrinus	1	4	8.1
		Delocrinus	2	7	4.7
		Graffhamicrinus	3	24	0.1
		Ulocrinus	4	25	0.1
	Guild 5 - 7.1% of Biofacies 3	Galateacrinus	1	6	4.8
		Exocrinus	2	8	2.3
	Guild 3 - 6.6% of Biofacies 3	pirasocrinids	1	10	1.9
		stenopecrinids	2	11	1.7
		Exoriocrinus	3	13	0.8
		scytalocrinids	4	14	0.8
		laudonocrinids	5	15	0.6
		Glaukosocrinus	6	19	0.4
		Plummericrinus	7	20	0.4
		Terpnocrinus	8	23	0.1
	Guild 1 - 2.2% of Biofacies 3	Stellarocrinus	1	9	2.0
		cromyocrinids	2	21	0.2
	Guild 4 - 1.1% of Biofacies 3	cymbiocrinids	1	16	0.5
		Elibatocrinus	2	17	0.4
		ampelocrinids	3	22	0.1
		Paragassizocrinus	-	-	0.0