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Community Paleoecology of the Pennsylvanian Winchell Formation, North-Central Texas

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Community Paleoecology of the Pennsylvanian Winchell Formation, North-Central Texas

by

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O Lord, what a variety of things you have made!

In wisdom you have made them all.

The earth is full of your creatures.

Here is the ocean, vast and wide,

teeming with life of every kind,

both great and small.

Psalms 104: 24-25

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Community Paleoecology of the Pennsylvanian Winchell Formation, North-Central Texas

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Abstract

Many previous fossil community studies have focussed on biodiversity issues without examining community structure and dynamics. The research herein investigates how much community information beyond biodiversity can be recovered.

An echinoid Lagerstätten in the Lake Brownwood Spillway locality of the Pennsylvanian (Missourian) Winchell Formation contains four new species of echinoids. Archaeocidarids also host *Crurithyris* and bryozoan epibionts on their spines. The relationship between the echinoids and epibionts was commensal, benefitting the epibionts. Epibionts received associational defense, transport, water currents, settlement sites, and decreased competition.

Four recurring community types occurred in Winchell outcrops from the Lake Brownwood Spillway, Perrin, and RP1, and in Kansas outcrops from the Kansas City, Lansing, and Shawnee Groups. Large productids, *Neospirifer*, echinoids, and *Aviculopinna* are characteristic fauna of communities in argillaceous

limestones. In shales, highly abundant bryozoans, small attaching brachiopods, and crinoids characterize one community type, whereas small attaching brachiopods and tubuliporate bryozoans plus *Neospirifer,* productids, and *Myalina* typify a different community type. In fine grain limestones, abundant *Composita* and echinoids, along with *Antiquatonia* and bryozoans characterize another community type. Other distinct, non-recurring communities included those containing abundant echinoids in the Brownwood black shale Lagerstätte; *Composita* and *Acanthopecten* in packstone layers in the Brownwood black shale, and diverse bivalves plus *Parajuresania* and *Minilya* in concretions at Brownwood.

Insights into community structure, not just changes in community diversity through time, are possible with detailed sampling and analysis. Ordination analyses revealed limestone/shale patterns in scatterplots and a ternary gradient arrangement of unbaffled, fenestellid-baffled, and phylloid algae-baffled communities. Competition is inferred to occur between large productid brachiopods. Spatial competition is directly seen in fenestellid-baffled shale communities as interspecific overgrowths and non-interference by conspecifics. Epibiosis is very common in all shale communities and provides evidence for unpreserved substrates, but the biotic or abiotic nature of these host surfaces is unknown.

Cluster analyses were performed on Brownwood samples using Bambach's (1983) guild classification, guilds based on the potential for strong competitive interactions, and individual taxa. Guild and taxon analyses agree on large-scale community types, but differ in sample arrangement within units and lithologies. Researcher bias in sampling appears to be minimal.

Table of Contents

List of Tables xii

List of Figures xiii

Chapter 1: Community 1

Influences on Community 2

Paleoecology and the Community 3

Chapter 2: Echinoid Lagerstätten from the Pennsylvanian Winchell Formation, Lake Brownwood Spillway, Brownwood, Texas 8

Echinoid Taxonomy 8

Introduction 8

Geology and Depositional Environments 10

Discovery, Collection, and Preparation 12

Paleoecology 20

Systematic Description 22

Epibionts on *Archaeocidaris*: Paleoecological Interactions 51

Introduction 51

Materials and Methods 53

Results 57

Discussion 65

Epibiont Assemblage 65

Interactions between Epibionts and Archaeocidarids 68

Conclusions, Chapter 2 75

Chapter 3: Community Paleoecology of the Winchell Formation near Brownwood, Texas and Other Contemporaneous Localities 77

Introduction 77

Definition of Community 79

Geology and Background 83

This Study 87
Taphonomy 97
Methods 100
Results 106
Cluster and Ordination Analysis 106
Relative Abundance and Presence-Absence Data 106
Partial (Culled) Data 118
Brachiopod or Bryozoan Data Only 132
Brownwood Samples 143
Units and Localities 147
Ecological Patterns 151
Discussion 161
Patterns in the Data 161
Use of Whole Community Data 175
Conclusions, Chapter 3 177
Implications for Paleoecology 177
Results of this Study 179
Chapter 4: Human Artifacts in Paleocommunity Analysis 183
Bambach Guilds, Competitors, or Taxa? Community Analysis Using Different Classifications 183
Introduction 183
Geology and Methods 185
Results 188
Discussion 192
Researcher Specialty Bias on Data Collection 194
Introduction 194
Geology and Methods 195
Results 196
Discussion 199
Conclusions, Chapter 4 200

Chapter 5: The Echinoid Ball 202

Appendix 1: Community Definitions and Comments about Communities 204

Appendix 2: Localities and Data.....218

Appendix 3: Correlation 243

Appendix 4: Guilds.....287

References.....289

Vita 306

List of Tables

Table 3.1: Lithology of Brownwood units in hand sample and thin section 91

List of Figures

Figure 2.1: Stratigraphic position of the echinoid Lagerstätten in the Winchell Formation section at the Lake Brownwood Spillway 14

Figure 2.2: Location of the Lake Brownwood Spillway locality of the Winchell Formation 15

Figure 2.3: TMM 1967TX100 16

Figure 2.4: Diagram of TMM 1967TX100 17

Figure 2.5: TMM 1967TX101 18

Figure 2.6: Diagram of TMM 1967TX101 19

Figure 2.7: *Archaeocidaris brownwoodensis*, holotype and paratypes 28

Figure 2.8: *Archaeocidaris brownwoodensis*, paratypes 30

Figure 2.9: Sketch of elements from *Archaeocidaris brownwoodensis* 32

Figure 2.10: *Archaeocidaris gracilis* and unnamed echinocystid echinoid 36

Figure 2.11: *Elliptechinus kiwiaster*, holotype and paratypes 43

Figure 2.12: *Elliptechinus kiwiaster*, paratypes 45

Figure 2.13: Sketch of elements from *Elliptechinus kiwiaster* 47

Figure 2.14: Epibionts on *Archaeocidaris* spines 56

Figure 2.15: Number of *Crurithyris planoconvexa* per echinoid size from TMM1967TX101 slab 59

Figure 2.16: Size and number of *Crurithyirys planoconvexa* individuals 60

Figure 2.17: Number of attached fenestellid bryozoan colonies and their diameters (cm) 61

Figure 2.18: Epibiont association with archaeocidarid spines 62

Figure 2.19: Position of epibionts on spine as distance (cm) from base of the spine shaft 63
Figure 2.20: Location of *C. planoconvexa* and fenestellid bryozoan colonies on spines.....64
Figure 3.1: Map of Texas and Midwestern United States Pennsylvanian outcrop belts and localities used in this study.....90
Figure 3.2: Outcrop from the Lake Brownwood Spillway Locality of the Winchell Formation near Brownwood, Texas.....92
Figure 3.3: Outcrop of the Winchell Formation near Perrin, Texas.....94
Figure 3.4: Outcrop of the 1-435 cloverleaf in Kansas City.....95
Figure 3.5: Outcrop showing stratigraphic location of Plattsmouth samples from the Waverley Quarry, southwest of Kansas City.....96
Figure 3.6: Selection of endmembers and axes 105
Figure 3.7: Cluster analysis of all samples using relative abundance data.....110
Figure 3.8: Cluster analysis of all samples using presence-absence data.....112
Figure 3.9: Bray-Curtis ordination of all samples, relative abundance data.....114
Figure 3.10: Bray-Curtis ordination of all samples, presence-absence data.....116
Figure 3.11: Cluster analysis of all samples using relative abundance data, crinoids culled.....120
Figure 3.12: Bray-Curtis ordination of all samples using relative abundance data, crinoids culled. 122
Figure 3.13: Cluster analysis of all samples using relative abundance data, phylloid algae culled. 124

Figure 3.14: Bray-Curtis ordination of all samples using relative abundance data, phylloid algae culled. 126
Figure 3.15: Cluster analysis of all samples using relative abundance data, common taxa (crinoids, echinoids, *Composita,* and *Minilya*) and phylloid algae culled. 128
Figure 3.16: Bray-Curtis ordination of all samples, relative abundance data, common taxa (crinoids, echinoids, *Composita*, and *Minilya*) and phylloid algae culled. 130
Figure 3.17: Cluster analysis of all samples using relative abundance data, brachiopods only. 135
Figure 3.18: Bray-Curtis ordination of all samples, relative abundance data, brachiopods only. 137
Figure 3.19: Cluster analysis of all samples using relative abundance data, bryozoans only. 139
Figure 3.20: Bray-Curtis ordination of all samples, relative abundance data, bryozoans only. 141
Figure 3.21: Cluster analysis of Brownwood samples using relative abundance data. 144
Figure 3.22: Bray-Curtis ordination of Brownwood samples, relative abundance data. 145
Figure 3.23: Cluster analysis of units and localities using relative abundance data. 148
Figure 3.24: Bray-Curtis ordination of Brownwood samples, relative abundance data. 149

Figure 3.25: Cluster analysis of taxa in all samples using relative abundance data. 156
Figure 3.26: Cluster analysis of brachiopods from all samples using relative abundance data. 158
Figure 3.27: Percent of *Minilya* bryozoans and phylloid algae per unit or locality 159
Figure 3.28: Percent of small, attaching brachiopods (*Crurithyris, Punctospirifer,* and *Hustedia*, in blue) and large productids (*Reticulatia, Antiquatonia, Echinaria,* and *Linoproductus*, in maroon) per sample 160
Figure 3.29: Example of lack of depth gradient. 163
Figure 3.30: Ternary arrangement of baffling gradients seen on ordination scatterplots. 166
Figure 4.1: Stratigraphic section of the Pennsylvanian (Missourian) Winchell Formation at the Lake Brownwood Spillway, north of Brownwood, north-central Texas 187
Figure 4.2: Cluster analysis of taxa and guilds in all samples using relative abundance data. 190
Figure 4.3: Crinoid identification per total number of points in point-counts on limestone surfaces 197
Figure 4.4: Number of unidentified brachiopod fragments per total brachiopods in point counts on limestone surfaces 198

Chapter 1: *Community*

"Nomenclature implies a great deal about how we perceive nature to be organized." Springer and Miller, 1990, p. 14.

"Community ecologists have been very sloppy about what they have called communities in the past." Maurer, 1999, p. 48.

The term community is loaded with many connotations and little agreement on precise definition, both in theory and in practice. The idea of community research has proliferated through literature, with holistic, integrated definitions taught in ecology textbooks while researchers use the word community to freely describe any group of organisms being investigated. This review of the word community explores the concept in theory and in practice, examining definitions and factors that influence definitions, followed by the use and practicality of communities in paleoecology.

In theory, communities are defined as all organisms living in a given area, with varying emphasis in any given definition on community structure and organism interaction (for community definitions, see Appendix A). In practice, communities are often studied via limited taxon lists, such as brachiopod or phytoplankton communities. Although an ecologist or paleoecologist might state a more inclusive definition in a text or review paper, the actual research is often carried out on a more limited community according to the researcher's specialty. To explore community dynamics under a more holistic definition would require many specialists and

perhaps involve greater research time than that of a community defined by a limited taxon list (Boucot, 1999a).

INFLUENCES ON COMMUNITY

Extremes in community models include classical Gleasonian individualistic views (Gleason, 1929) and Clementsian superorganism views (Clements, 1926). Modern definitions of the holistic community often fall within these two extremes and range from a simple statement about taxa in any given area (Pianka, 1994) to interacting populations with identifiable structure (Ross, 1981). Most discussions about communities state that interactions between organisms occur, whether or not those interactions determine community existence. Organism interactions have some effect on community processes, even if interactions are something as seemingly minor as determining larval settlement sites.

One agreement in holistic community definitions is the idea that a community is mostly scaleless; that is, no distinct size, area, boundary, nor level of recurrence can be determined as an inherent trait of all communities. Scales can range from microorganisms and epibionts on a shell to geographic regions and millions of years, with boundaries created to split samples into many communities or lump them into only a few. Boundaries that are defined for communities often result in the splitting of an ecological continuum, whether accidentally through faulty analysis or lack of data, or for ease of communication. Additionally, how a community is defined affects the boundaries and/or continua observed within an investigation. In this study (see chapter 3), more community types are identified and gradients are more detailed using all available data than they would be if only the brachiopod community were investigated.

PALEOECOLOGY AND THE COMMUNITY

Fossil community research differs from ecological investigations because of time and preservational factors. In modern communities, geologic time is not a factor during investigation; most questions are concerned with only those processes that occur on very short time scales. Fossil communities occur in deep time, with much information lost to various time-averaging and preservational processes. Because of the time-factor of paleocommunity research, many community definitions in paleontological texts include a statement about community recurrence through time.

Community recurrence most often has been referred to as lacking significant taxonomic change. In one definition of community recurrence, communities are thought to change only when structure and dynamics changes; species turnover is less important to community change (DiMichele and Philips, 1995). This statement is more fitting for a *community type* than for a community; community types are groups of similar communities, whether taxonomically or otherwise designated. Community types, like communities, are scaleless. Community types in chapter 3 occur within one Texas formation and contemporaneous rocks in Kansas. Conversely, Bretsky (1969) has recognized recurring Paleozoic community types. In this dissertation, communities may retain the same taxa while undergoing structural or dynamics changes, and become a radically different community. Also, communities may have a significant taxonomic turnover and also become a radically different community, whether or not structural and dynamics change occurs.

In paleocommunity analysis, a truly holistic community has yet to be preserved, because of loss of contemporaneous soft tissues and skeletal remains of all micro- and macroorganisms, data on interactions, biochemical cycling information, and effects of vagile and pelagic species. Lack of preservation and geologic time factors require careful analysis of fossil and rock data, not only for

study of preserved organisms but also to recover information about unpreserved organisms and processes. Assumptions about time, unpreserved organisms, trophic relationships, and taphonomy are based on these analyses.

A major argument in paleoecology is whether fossil communities contain enough data to permit some level of ecological study or whether time-averaging, taphonomy, and general lack of ecological time scales place too many limitations on community study. Viewpoints tend to fall into one of two categories: either the fossil record is only capable of supporting biodiversity investigations and gross ecological generalizations (e.g., Valentine and Jablonski, 1993), or that community structure and biotic interactions are indeed possible with careful sampling and analysis (e.g., Hickey and Younker, 1981). Those that suggest the impossibility of capturing fossil community structure cite a poor fossil record (e.g., Kauffman and Scott, 1976), whereas others push beyond the paradigm of fossil record limitations to investigate organism interactions (e.g., Hermoyian et. al., 2002). Although the lack of ecological data in fossil communities, such as community structure, is sometimes attributed to a lack of information in the fossil record, other authors (Johnson, 1972, Hickey and Younker, 1981; Leighton, 2001) note that biotic interactions and structure not only may be discernable in the fossil record, but that understanding such processes are critical to answering paleoecological questions, such as why communities recur.

Another statement about fossil communities is that, although structure is ascertainable in the fossil record, "certain structural aspects cannot be detected" (Hickey and Younker, 1981, p.1-2). At this point in time, this statement is true. Unpreserved organisms are difficult to detect, leading to difficulties in physical structure. The importance of vagile organisms and predators (those that do not leave traces) in fossil communities remains difficult to ascertain, and proxies for primary productivity and nutrient cycling are few. However, with continuing work in areas such as organism interaction, nutrient cycling, geochemistry, and proxies for missing organisms such as epibiosis, ecological structure in fossil communities

can be recovered. Fossil community research cannot be applicable to both ecology and paleoecology without reaching beyond biodiversity issues to investigate dynamics such as interactions, spatial distribution, and trophic relationships.

Although statements about the ability to study fossil community structure are diverse, the strongest opinion is that ecological structure in fossil communities cannot be studied without direct analogy to relevant modern communities (Robertson, 1999). Because many fossil communities are very unlike modern communities, ecological structure in the fossil record is therefore unattainable (Robertson, 1999). If this is the case, then most Paleozoic communities can never be studied at any greater depth than biodiversity investigations. However, Paleozoic community dynamics have been studied, albeit not to the detail of modern communities. Because most Paleozoic communities do not have direct analogs to modern communities, and especially because time-averaging is an issue, progress in community aspects beyond biodiversity has been slower than that of Quaternary community study. However, because fossil communities and community types recur, individual samples can be compared, not to modern communities, but to each other to discern recurring structure and dynamics.

This idea of paleocommunity structure, although fairly common in paleocommunity investigations of the 1960's and 1970's (e.g., Walker and Alberstadt, 1975), has been all but lost during the push to explore Phanerozoic marine biodiversity in great detail. Early investigations explored ecological phenomena such as succession (i.e., Walker and Alberstadt, 1975) and three-dimensional structure (Alberstadt et. al., 1974) in communities inclusive of all preserved taxa. Recent paleocommunity research (whether biodiversity- or structually-driven) often focussed on limited taxon lists, such as brachiopods only. In cases where researchers incorporated all taxa, phyla that were difficult to identify, such as sponges, bryozoans, and echinoderms, were lumped into one taxon each, leaving the remaining taxa, such as brachiopods and molluscs, to dominate the analytical results.

The practice of defining communities by limited taxa may result from the time, effort, and number of specialists needed to investigate holistic community questions (Boucot, 1999a). Although limited-taxa communities are utilized in fossil community analysis, a more integrated approach is available to the community paleoecologist. Spatial information, such as clustering and teasing original spatial data from a time-averaged bed, can be determined using various grid and cellular techniques (i.e., Neighbor Proximity Analysis, Leighton, 2001). Biotic interactions, such as overgrowths and epibiosis, are directly observable in calcified taxa, and predation scars often are preserved in shells, allowing interpretation of the nature and frequency of predators. Three-dimensionality in a fossil community can be determined from simple deduction of various tiers, and some unpreserved organisms are indicated by the presence, type, and amount of epibionts as well as by xenomorphs in calcitic surfaces and trace fossils in rock.

A few optimistic viewpoints suggest that use of the word community will eventually come to some sort of consensus (Boucot, 1999b). Other ecologists and paleoecologists suggest that the term community is useless and advocate dropping it altogether, whether from definition problems or other concerns (e.g., Ricklefs, 1973; Underwood and Petraitis, 1993). Still others state that although the holistic definition of community is optimal, it is only an ideal; in practice, a holistic community could never be fully recovered, especially in the fossil record (Kauffman and Scott, 1976; Boucot, 1999a). Given the conflict over the term community, it is unlikely that an unambiguous definition and practical application of community is imminent. Fortunately, disagreement over community definitions and usage does not preclude research into ecological issues, whether from an inclusive definition of community or through limited-taxa datasets.

In this dissertation, community is defined as all of the macroorganisms found in the study area and the biotic interactions and structure associated with them. This definition differs from assemblage, which is a term used only for the

organisms in the study area. Because this dissertation deals with fossil organisms, community simply refers to the fossilized remains of the original live community.

Because of the temporal nature of the fossil record, community constituents need not be directly contemporaneous. Fine-scale environmental and biotic perturbations, such as storm events and annual differences in recruitment, are often lost to time-averaging; therefore, fossilized individuals may have been closely spaced in time, although not necessarily contemporaneous. Therefore, it is assumed, after taphonomic and time-averaging evaluation, that most fossil communities in this study are an average of a temporal continuum of communities undergoing only minor changes, if any.

Chapter 2: Echinoid Lagerstätten from the Pennsylvanian Winchell Formation, Lake Brownwood Spillway, Brownwood, Texas

ECHINOID TAXONOMY

INTRODUCTION

An unusually well preserved echinoderm community from the Lake Brownwood Spillway in north-central Texas contains an exceptional echinoid assemblage. Thousands of a medium-sized, incredibly spiny *Archaeocidaris* were preserved along several bedding planes. Interspersed among the archaeocidarids are three less common echinoid species as well as occasional crinoids, brachiopods, bryozoans, and rarer edrioasteroids and asterozoans. Plant debris, mainly pteridosperms and lycopsid leaves and wood, is abundant throughout these horizons. Some archaeocidarids contain epibionts on their spines, particularly bryozoans and the small brachiopod *Crurithyris*, which in some cases are represented by over 30 individuals on one *Archaeocidaris*.

This locality is unusual in that echinoids are represented by thousands of articulated individuals. Archaeocidarids were most likely aggregating, with other echinoids haphazardly distributed in the horizons. Three smaller, presumably juvenile specimens of these archaeocidarids were also recovered. The sheer number and spectacular preservation of all of these specimens have made the Brownwood echinoids a popular item on the commercial paleontology market and a favorite among collectors.

All recovered echinoids represent four new taxa. The most common of these is one species of *Archaeocidaris*, represented by 79 complete and numerous partial specimens. The second most common echinoid, represented by 19 specimens, is an ellipsoidal lepidocentrid positioned with its long axis upright. Like the archaeocidarids, it appears to be fully epifaunal with a small lantern at the adoral end of its long axis. The echinoid is covered in many thin, short, straight spines, giving it a slightly "fuzzy" appearance, much like a kiwi fruit. Other new echinoid species include four specimens of a straight-spined archaeocidarid and a problematic echinocystid, are described below.

Although complete echinoids from these new taxa are unknown outside of the Lake Brownwood Spillway locality, isolated plates and spines of the two *Archaeocidaris* species were found in other Winchell Formation localities. No specimens of other Paleozoic echinoid genera not described in this study are currently known from this Brownwood locality.

The Lake Brownwood Spillway locality was and still is very popular withamateur and commercial collectors through the past decade. Unfortunately, natural erosion and mining of the shale beneath large limestone overhangs caused the locality to become a dangerous collecting site and resulted in at least one major injury during its collecting history when an overhanging ledge collapsed on a commercial collector. Floods through the Spillway from Lake Brownwood occasionally make collecting easier by undermining and collapsing limestone overhangs, but these events are sporadic in semi-arid north-central Texas.

GEOLOGY AND DEPOSITIONAL ENVIRONMENTS

The Lake Brownwood Spillway exposes the uppermost Cedarton Shale and the entire Winchell Formation of the Missourian Canyon Group in north-central Texas (Figure 2.1). The Winchell Formation was deposited along a northeast-

southwest strike on the Eastern Shelf of the Midland Basin (Figure 2.2). In the northern half of the field area, the Winchell Formation occurs as two phylloidal bank systems and in the south as three to six limestones, some of which are phylloid algal, separated by shales. Northward, in the Brazos River Valley area, the phylloid-dominated Winchell Formation is locally influenced by the Perrin Delta system, separating it from the contemporaneous Chico Ridge Limestone to the northeast. An area of Cretaceous cover, called the Callahan Divide, separates the Winchell Formation outcrops of the Brazos River Valley to the northeast from the outcrops of the Colorado River Valley, which contain multiple limestone units, to the southwest.

The outcrop at the Lake Brownwood Spillway is an excellent exposure of the Winchell Formation in the Colorado River Valley. This locality was greatly influenced by terrigenous siliciclastics (73% of the 32 m Winchell Formation section), containing abundant shales as well as paleosols between the few resistant limestone and marly units (27% of the section). The lower two-thirds of the Winchell Formation is most prominent in this outcrop, with the upper third slumped and mostly covered by vegetation on the ridge just south of and above the Spillway.

The echinoid Lagerstätte occur in a channel-shaped, finely laminated, black shale ranging in thickness from 0.5 m on the edges of the locality to 1.5 m in the middle of the Spillway. This shale is channel-shaped in cross section, ranging from less than 0.5 meters at the lateral edges of the Spillway to over 1.5 meters in the middle of the outcrop. Pteridosperm and lycopsid leaves as well as abundant unidentified carbonized wood fragments are present in some horizons, and leaf debris coats nearly all bedding planes. Abundant leaf fossils, highly abundant leaf and wood debris, high amounts of silt, and laminated structure indicate still water and proximity to the paleoshoreline, such as a protected bay or estuary. Several thin (<1 cm) limestone packstones containing abundant *Composita, Acanthopecten,* crinoids, bryozoans, and limestone nodules occur sporadically in the shale and

comprise approximately 3% of the channel thickness. These are interpreted to be tempestites of abraded fossil debris and weathered limestone nodules washed into the submarine channel.

The black shale conacts a massive, pink, overhanging wackestone; large meandering horizontal burrows weather in relief in the upper 10 cm of the black shale and are prominent on the underside of wackestone slump-blocks. Below, the black shale has an abrupt contact with a sparsely fossiliferous, greenish-gray shale.

Seven horizons of echinoid aggregations, totaling approximately 3% of the channel thickness, occur in the black shale. Several of these horizons also contain at least three genera of crinoids, the edrioasteroid *Parapostibulla*, an unidentified asteroid, occasional clumps of the brachiopods *Parajuresania*, encrusting *Crurithyris,* rare *Composita* and *Linoproductus*, and fenestellid bryozoan fronds.

Most echinoids are preserved as articulated to slightly disarticulated crushed specimens with most or all of the spines still present. The spines make the echinoids more spectacular as display specimens, but unfortunately hide much of the test (especially on the non-archaeocidarids) necessary for identification and comparison with other taxa. The adoral and oral body walls are usually flattened with little or no internal filling, indicating that the echinoids were buried whole and rapidly crushed by collapse of the imbricate interambulacral and ambulacral plates. Most archaeocidarids are oriented with the adoral side down, but a few are oral side up and others are crushed sideways with the large ambital spines unidirectionally aligned. The elongate lepidesthids typically are preserved on their sides with the small spines pointing radially. In most echinoids, spine and plate elements remain closely associated, indicating that spines were still attached to the specimen at death and remained close to their respective tubercles after burial. However, no apical systems have been recovered from the thousands of known museum or privately collected specimens, and no individual apical plates were found in surrounding sediments. It is possible that these areas were missing before burial because of scavenging or predation, or were lost via disruptive gas release during decay of

internal tissues, but no firm conclusions can be drawn for this unusual phenomenon. Very few plates and spines are found loose in the black shale, suggesting that echinoids were not indigenous to the submarine channel.

Crinoids and starfish, although less abundant, also display relatively little disruption from transport or decay. Delicate fossils such as fenestellid bryozoan colonies and spines of the brachiopods *Parajuresania* and *Linoproductus* are complete with no breakage except for that from postburial compression or overabrasion during preparation. Taphonomy in the Lagerstätten indicate repetetive rapid burial events, possibly from freshwater and sediment input with little or no fossil transport.

DISCOVERY, COLLECTION, AND PREPARATION

The occurrence of abundant complete echinoids at the Lake Brownwood Spillway site was recognized at least as early as the late 1960's. Warme and Olson (1971) documented their occurrence in an X-ray photograph of a spinose archaeocidarid still in matrix and noted their occurrence on a measured section of the Lake Brownwood Spillway outcrop. Commercial and private collection has been occurring since the late 1980's and Brownwood echinoids frequently appear in commercial venues such as gem and mineral shows, fossil shows, and on Ebay. Unfortunately, the archaeocidarid-bearing shales readily disaggregate when exposed and wetted. The multi-plated echinoids of the Spillway locality were preserved as slightly disarticulated tests that fused into loosely cemented discs of plates during diagenesis. These specimens fracture and are lost to weathering as the enclosing shales are exposed. Problems with shale and echinoid disaggregation inhibited the collecting of complete specimens until preservatives became available to stabilize freshly collected echinoids in the field. In the lab, the echinoids must be prepared dry, typically by using an air abrasive machine with a soft powder such as sodium

bicarbonate, and further stabilized to prevent disaggregation of sediments and echinoids. Unfortunately, specimens are very susceptible to humidity, which causes mineral growth (mostly halite and gypsum) on the surface of the shale.

Most of the specimens studied here were collected and prepared by Dan Ryder and donated to the University of Texas in 1999 for study and description. Several other specimens were carefully prepared by Danny Harlow and donated to the University as part of this project. Other specimens were collected in the field by the author or donated by amateur collectors to expand morphological data, recovery of disarticulated elements, and petrographic and geochemical analyses.

In addition, two large prepared slabs containing multiple specimens, each approximately one-half square meter in size, were purchased from Dan Ryder as research and display specimens by the Texas Memorial Museum (TMM 1967TX100) and by the Department of Geological Sciences (TMM 1967TX101), University of Texas. The larger TMM 1967TX100 slab contains 27 mostly complete archaeocidarids along with a mostly intact *Delocrinus* crinoid, a *Linoproductus* and four *Composita* brachiopods, and several fenestellid bryozoan fronds (Figures 2.3, 2.4). The slightly smaller TMM 1967TX101 slab from a different layer contains 20 complete archaeocidarids, one of which is a juvenile specimen, and nine oval lepidocentrids (Figure 2.5, 2.6). *Crurithyris* brachiopods are abundant epibionts on the spines of these archaeocidarids, totaling 133 individuals. Several spines also contain bryozoan encrusters, including small, attached fenestellid fronds.

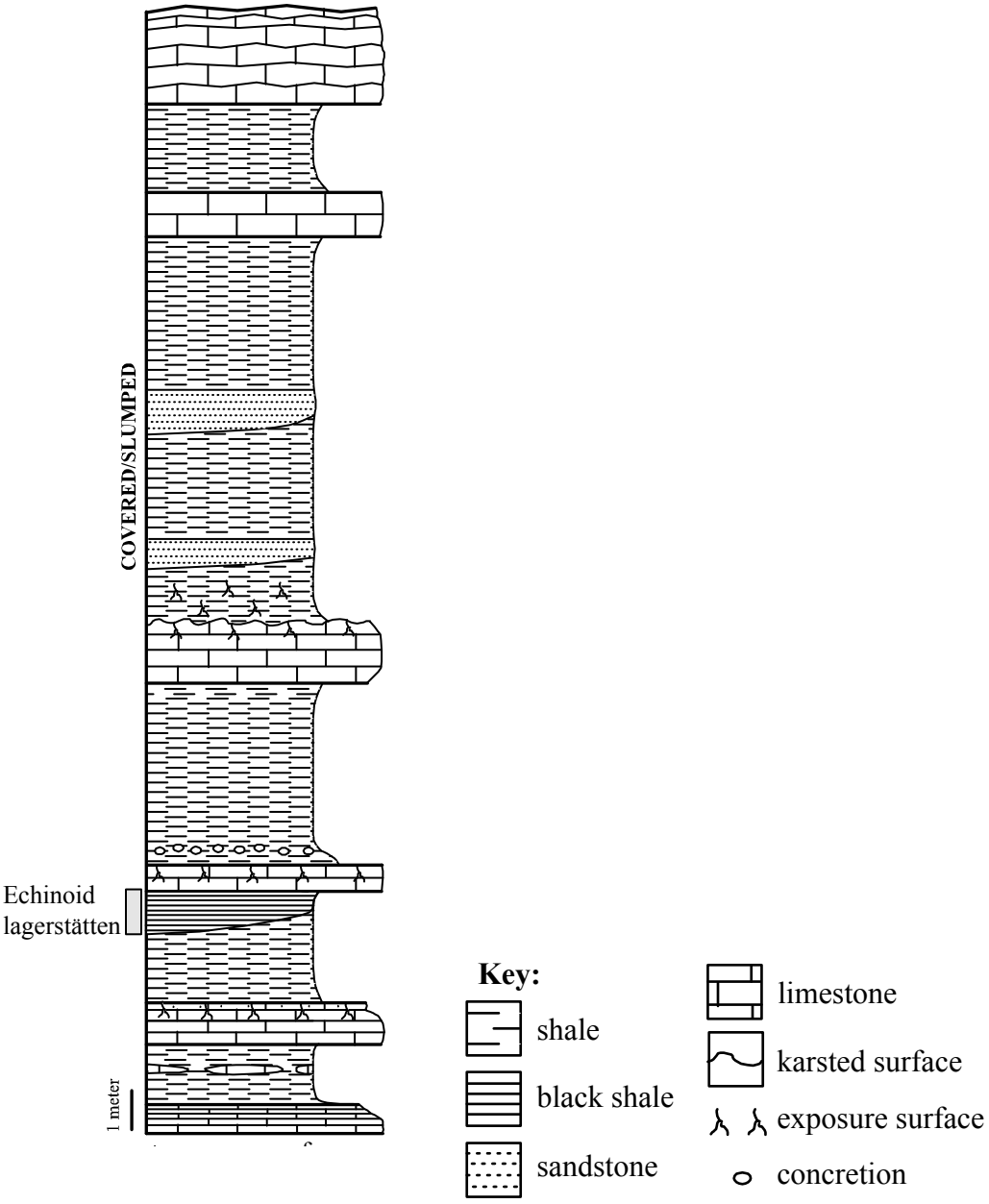


Figure 2.1. Stratigraphic position of the echinoid Lagerstätte in the Winchell Formation section at the Lake Brownwood Spillway.

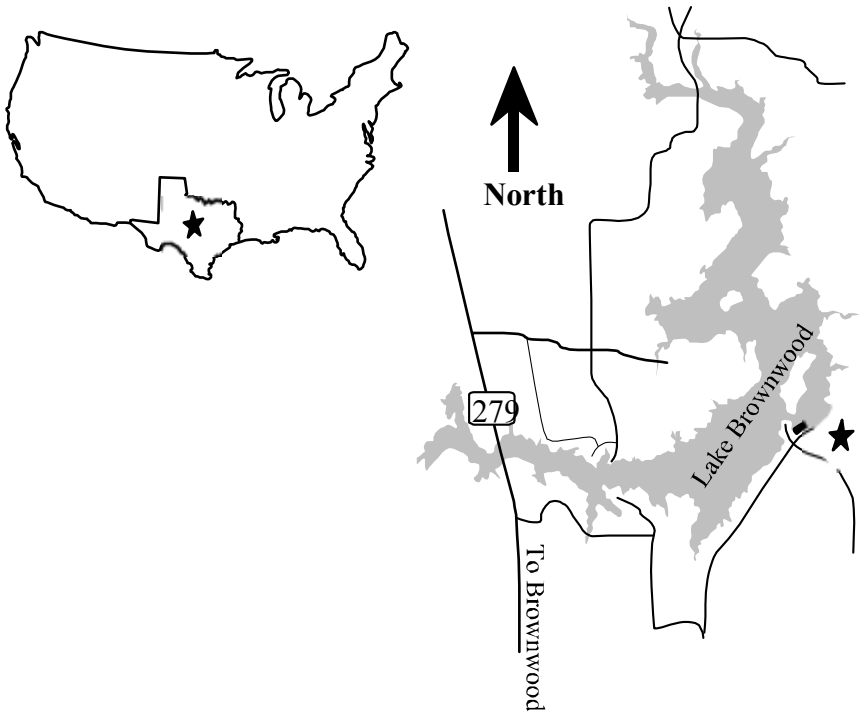


Figure 2.2. Location of the Lake Brownwood Spillway locality of the Winchell Formation.

Figure 2.3. TMM 1967TX100. Slab on display at the Texas Memorial Museum.

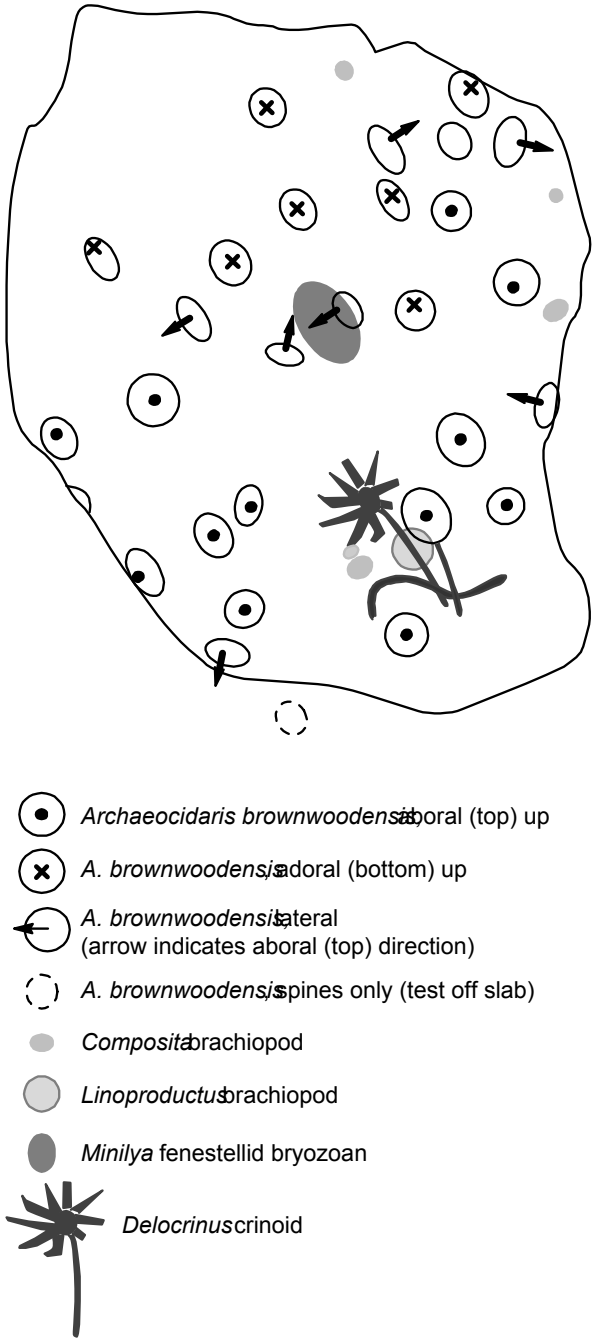


Figure 2.4. Diagram of TMM 1967TX100.

Figure 2.5. TMM 1967TX101. Slab on display at the John A. and Katherine G. Jackson Geological Sciences Building, University of Texas at Austin.

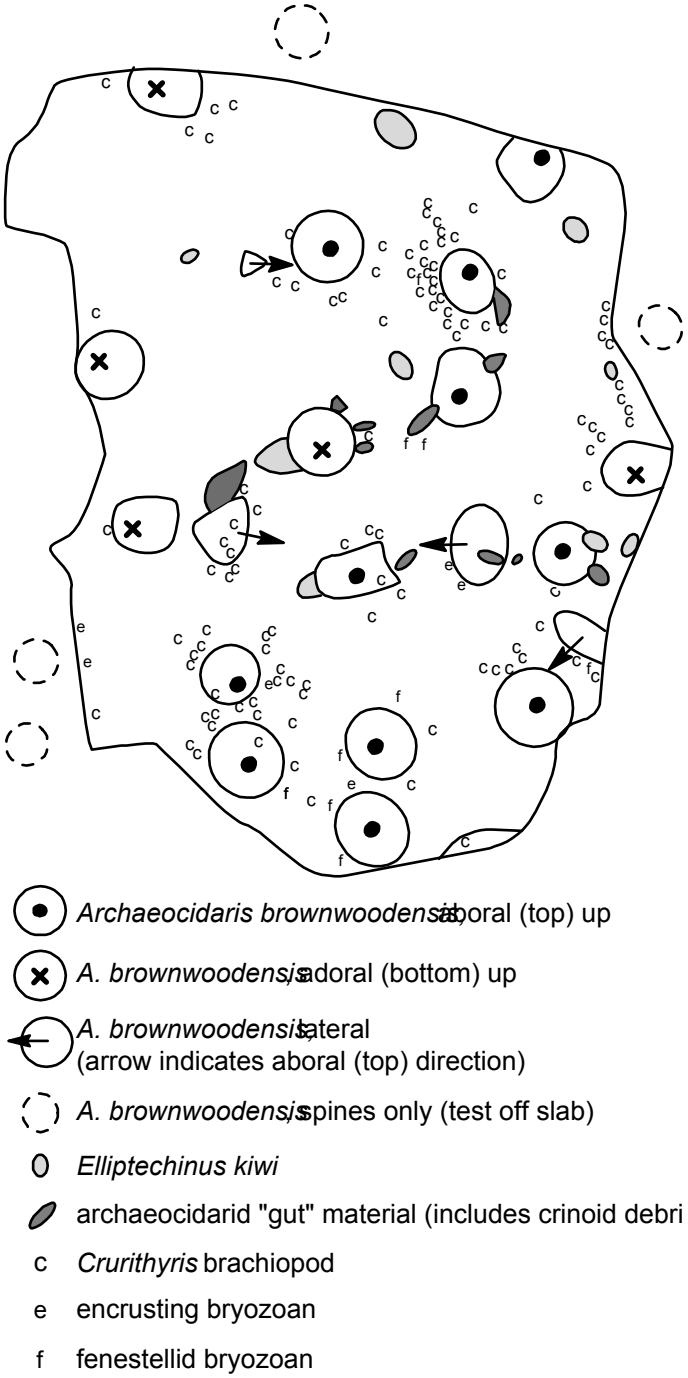


Figure 2.6. Diagram of TMM 1967TX101.

PALEOECOLOGY

Thousands of archaeocidarids apparently were aggregating in this submarine channel. Modern echinoids previously were noted to aggregate for feeding (Rodriguez and Farina, 2001) and spawning (Lamare and Stewart, 1998; Young et al., 1992), and also aggregate in experiments because of density of individuals or predator presence (Hagen and Mann, 1994). However, the Brownwood echinoid spines appear undamaged by predation, and few predators (e.g. sharks or cephalopods) were found in the shale outside the echinoid layers. Although predator and density causes for aggregation of the Brownwood archaeocidarids cannot be discarded, feeding or spawning seem more likely. First, there is abundant plant debris in the locality, and because the lanterns of *Archaeocidaris* are interpreted as optimal for scavenging and herbivory (Smith, 1984), it is possible that this is a feeding aggregation of archaeocidarid echinoids. Second, these horizons represent discrete events, and the extremely high abundance of the archaeocidarids compared to other echinoids might indicate spawning aggregations. The similarity in size of all aggregating archaeocidarids and the rarity of juvenile individuals (only three known specimens found to date) might further suggest a mass-spawning by adults. Several species of modern regular echinoids were reported to migrate into shallow water to form mass spawning aggregations (Durham, 1966); another example is *Evechinus chloroticus* from New Zealand (Lamare and Stewart, 1998). Carbon isotope comparisons of plant material, gut material, and sediment on the TMM1967TX101 slab may shed insight into whether echinoids were consuming terrestrial plants.

Many of the *Archaeocidaris* specimens on the TMM 1967TX101 slab have black sediment (even darker than the matrix) containing white cirrals and other crinoid debris within their tests and oozing out from between their interambulacral plates. This is interpreted as possible gut contents representing the final meals of the echinoids (Schneider, 2001a). Because of its high organic content and the

abundance of plant debris in the surrounding matrix, leaf matter may have been a major part of the diet of these echinoids. Crinoids are less common in the echinoid layers (none are present on this TMM 1967TX101 slab), but submersible observations of living cidaroids and dissected gut contents indicate that some cidaroids prey on deep-sea crinoids (Baumiller et al., 2001). This Pennsylvanian aggregation provides the first evidence of regular echinoids possibly preying on, or at least scavenging, crinoids from the fossil record.

Crurithyris brachiopods and bryozoans are preserved on ambital spines. Epibionts are located on the proximal end of the spines, most within 2 cm of the spine base. These attaching organisms are suggested to have had a commensal relationship with the echinoids, benefiting from the elevated position, mobility of the echinoid, and protection by the spines. Echinoids, conversely, do not appear to have been positively or negatively influenced by epibiont presence (Schneider, 2002; in press).

The black shale unit at the Spillway locality previously was interpreted as a shallow-water submarine channel from a tidal creek (Warme and Olson, 1971). Here it is suggested as a shallow, near shore, low energy, marine environment, such as a bay or estuary, based on fossil taphonomy, sediment, and fine laminations. No evidence of normal wave base structures is known, but tempestites occur in thin, discontinuous packstone horizons. Fossils in these packstones often are fragmented and contain different taxa than the echinoid horizons, including abundant crinoid and fenestellid debris, various brachiopods, rare trilobite fragments, small *Lambeophyllum* corals, broken archaeocidarid spines, and the pecten *Aviculopecten*. The differences between the echinoderm and packstone assemblages suggest that the fossils in the packestones were transported into the black shale from an adjacent area during storm events.

SYSTEMATIC DESCRIPTION

Class ECHINOIDEA Leske, 1778

Order CIDAROIDEA Claus, 1880

Family ARCHAEOCIDARIDAE M'Coy 1844

Genus *Archaeocidaris* M'Coy, 1844

Type species.--*Archaeocidaris (Cidaris) urii* Flemming, 1828, by subsequent designation (Bather, 1907, p. 453).

Diagnosis.--Cidaroid with four interambulacral columns and a slightly flexible test. Test sub-spherical to oval; diameter up to 150 mm. Ambulacra narrow with two columns of plates; pore pairs obliquely or horizontally placed; pores uniserial. Ambulacral triads present but weak. Interambulacral area wide with four columns of slightly imbricate plates, usually hexagonal; primary tubercles perforate and noncrenulate; interambulacral plates imbricate over ambulacral plates at adambulacral sutures.

Occurrence.--Late Devonian to Permian, North America; Carboniferous, Europe.

Discussion.--Several other Paleozoic cidaroids occur within the same temporal range. *Lepidocidaris* is confined to Mississippian-aged rocks of North America, but the interambulacra contain six to eight columns of plates, unlike the four columns of *Archaeocidaris* (Fell, 1966). The ambulacral triad is also more pronounced in *Lepidocidaris*, with every successive third plate being much larger than adjacent plates, rather than the weaker triads of *Archaeocidaris*. Four columns of interambulacral plates also characterize the genus *Nortonechinus*, but the plates are distinctly diamond-shaped, resembling the interambulacral plates of *Lepidocidaris* (Fell, 1966).

Archaeocidaris brownwoodensis new species

Figures 2.3 – 2.9

Diagnosis.--A medium-sized *Archaeocidaris* with large, highly ornamented spines; ambulacra nearly straight; twelve to thirteen ambulacral plates per adambulacral plate; interambulacral plates hexagonal; primary tubercles large; single circle of scrobicular tubercles around edge of interambulacral plate.

Description.--Test oval in cross-section; adult test diameter 35-50 mm. Ambulacra one-ninth the width of interambulacral areas at midzone. Ambulacra slightly sinuous, with columns not alternating to slightly alternating. Ambulacral plates four times wider than high. Pores oblique, with outer pore slightly more adorally situated than inner pore. Outer pore oval; inner pore sub-oval to sub-rectangular. Plates strongly overlap orally and imbricated under adambulacral plates, flange of ambulacral plates extends from suture and slopes upward to meet adambulacral plate. At midzone, 12-13 ambulacral plates per adambulacral plate. Tubercles on ambulacral plates not present or not preserved. Pedicellariae not preserved. Interambulacra with four columns of plates. Columns alternate, creating honeycomb-like pattern of plates. Plates hexagonal, with equal dimensions or slightly wider than high. Adambulacral plates pentagonal, beveled along adambulacral edge, and deeply striated on inner surface of adambulacral suture. Interambulacral plates average range from 6 to 8 mm wide at midzone. Approximately thirty scrobicular tubercles per plate with 4-5 scrobicular tubercles per edge of hexagonal plate at midzone, alternating with tubercles on adjacent plates. No secondary tubercles present on interambulacral plates.

Primary tubercle and boss approximately one-fourth to one-third the diameter of interambulacral plate at midzone, average diameter 2 mm, average height 1.5 mm. Boss approximately two-thirds height of tubercle. Scrobicular tubercles small, undifferentiated and arrayed concentrically around primary tubercle in single row along edge of interambulacral plate. Scrobicular tubercle approximately 0.5 mm in diameter but variable within single plate.

Aristotle's lantern represented by several crushed specimens. Demipyramids smooth with distinct groove. Epiphyses do not meet over foramen

magnum. Foramen magnum deep, teardrop-shaped. Brace wide, deeply furrowed along compass. Teeth relatively wide, serrated with up to 5 prominent serrations.

Primary spines triangular in cross-section and highly ornate with many spinules or thorns. Thorns on main part of spine approximately 60 degrees to axis of spine. Spines straight to very slightly curved. Ambital spines exceed 7 cm in length in large individuals. Adoral spines distinctly more gracile, shorter, thinner, slightly curved. Aboral-most spines undifferentiated, thick, short, without ornament, slightly rough in texture. Spine ornament increases with distance away from the apical system until the ambital zone. Spine neck above base smooth, notably constricted and cylindrical, gradually flattening to a distinctly sub-triangular shape. Flattened area above neck with two to three striations bearing alternating thorns. Small or juvenile specimens and adoral spines with reduced flattening above neck. Distal end of shaft triangular in cross section. Edges of shaft thorny; thorns distally increase in alternation and spacing. Tip of shaft delicate, pointed. Annulus prominent, distinct. Base finely longitudinally striated, increasing by fifty percent from acetabulum to bottom of annulus; height of base equal to outer diameter of acetabulum.

Scrobicular spines small, slightly striated with rounded tips. Spine width variable but length approximately equal to that of interambulacral plate edge. Spines circular to oval in cross section. Base little more than abrupt swelling.

Apical system unknown from all specimens in the collection.

Etymology.--The new species is named for Lake Brownwood Spillway locality, just north of Brownwood, Texas.

Type specimens.--Holotype TMM 1967TX60, disarticulated specimen with aboral and adoral areas displayed, with partial ambulacra, interambulacral plates, primary and secondary spines, partial peristome, slightly crushed Aristotle's lantern; paratypes TMM 1967TX1, disarticulated specimen similar to holotype; TMM 1967TX3, three disarticulated specimens similar to holotype; unfigured specimens TMM 1967TX2, 4-6, disarticulated specimens similar to holotype; TMM 1967TX7,

inner surface of partial ambulacrum and interambulacral areas; TMM 1967TX16, two disarticulated, presumably juvenile specimens; TMM 1967TX35, disarticulated specimen similar to holotype, with *Composita* brachiopod, edrioasteroid, and *Septopora* bryozoan; TMM 1967TX62, laterally crushed disarticulated specimen; TMM 1967TX99, disarticulated specimen with peristome; TMM 1967TX61, disarticulated specimen with well preserved fenestellid epibionts; TMM 1967TX101, with 27 total individuals complete specimens similar to holotype; TMM 1967TX100, with 20 total individuals, complete specimens similar to holotype.

Occurrence.--Middle Pennsylvanian, middle Missourian Stage, Winchell Formation, Canyon Group, Lake Brownwood Spillway near Brownwood, Brown County, north-central Texas.

Discussion.--Several thousand mostly complete but slightly disarticulated echinoids are known from the type locality. *Archaeocidaris brownwoodensis* is, by far, the most abundant of all echinoid species found in the Spillway channel. Although all of the *A. brownwoodensis* specimens are disarticulated, most plates and spines remain in close association, with ambulacra often disintigrated, interambulacral plates slightly disturbed with bases of primary spines lying close to their respective tubercles, and lanterns articulated but crushed. Pedicellariae and apical systems are not yet known for these echinoids. Sediment surrounding the specimens is not strongly lithified, and unless measures are taken to stabilize specimens in the field, individual archaeocidarids disaggregate very quickly as the shale dries out or becomes saturated. Almost all of the multitude of known specimens are presumed adults; very few small, assumed juvenile individuals have been recovered from the Spillway.

This species most closely resembles two other upper Paleozoic *Archaeocidaris* species. The species *Archaeocidaris immanis* (Kier, 1958) from the Pennsylvanian Dewey Limestone of Oklahoma is similar in its hexagonal interambulacral plates and scrobicular tubercles, but the resemblance is superficial.

Interambulacral plates of *A. immanis* are significantly longer than wide, with adambulacral plates retaining a hexagonal shape. The ambulacra are also markedly more sinuous than that of *A. brownwoodensis* and contains a much higher ratio of ambulacral to adambulacral plates. Pore pairs of *A. immanis* are horizontal rather than oblique.

A lower Permian archaeocidarid, *A. cowleyi* (Boos, 1929), resembles the small specimens of *A. brownwoodensis*, ranging from 10-30 mm in diameter. Spines of *A. cowleyi* differ mainly in being more delicate with a blunt rather than pointed tip and a smaller, narrower tubercle on the interambulacral plates. Spine bases of *A. cowleyi* are proportionally wider and shorter and are undifferentiated from the annulus. Interambulacral plates are more delicate and proportionally smaller than *A. brownwoodensis*.

Small size is also a major differentiating factor between *A. brownwoodensis* and several other species, which are only one-half to one-third of the size of *A. brownwoodensis*. Although there are other significant differences, none of the other species has strongly hexagonal plates. *Archaeocidaris aliquantula* (Kier, 1958) and *A. blairi* (Miller, 1891) are older Mississippian archaeocidarids from the United States. *Archaeocidaris aliquantula* spines are unadorned and slightly curved, very different from the extravagant spines of *A. brownwoodensis*. Primary tubercles of *A. blairi* are much taller and narrower than those of *A. brownwoodensis*, and in both Mississippian species, scrobicular tubercle distribution differs greatly from that of the Brownwood archaeocidarid in that the scrobicular area is much wider in *A. aliquantula* and much reduced in *A. blairi.* *Archaeocidaris hemispinifera* (Chesnut and Ettensohn, 1988), also Mississippian in age, is distinct from *A. brownwoodensis* in having primary spines only on the oral hemisphere of the test. It may also have more than four rows of interambulacral plates, but like the Brownwood archaeocidarid, has non-sinuous ambulacra. Another small Carboniferous echinoid from Russia, *A. rossica* (von Buch, 1842), has hexagonal plates similiar to those of

A. brownwoodensis, but the ambulacra are very sinuous. Spines also appear to be much more delicate on the Russian archaeocidarid.

Archaeocidaris brownwoodensis is distinct from *Archaeocidaris gracilis* (described below) in the Lake Brownwood Spillway locality in its highly ornate spines. However, it is the immense quantity of specimens recovered from the Lake Brownwood Spillway locality that makes *A. brownwoodensis* the most distinctive echinoid from the echinoderm community.

Overall, spine ornamentation is great on all specimens, but slight differences in spine ornament occur between specimens. Some specimens have spines with a slightly greater angle between the shaft and thorns, often with longer thorns, giving the animal a greater defensive appearance. Others appear to have more gracile spines, both in slightly reduced thickness of the shaft and decreased angle between the shaft and thorns, causing the spines of those specimens to appear more fragile. Spine lengths at ambitus are commonly up to 1.5 times the diameter of the test, although echinoids recovered from the lowest horizon contain spines that are proportionally shorter, approximately 1.3 times test diameter.

With the thousands of echinoids recovered from this locality, the only significant size differences occur in the rare, small, possibly juvenile individuals (< 15 mm, containing only the thin, gracile, lightly ornamented adoral spines of larger specimens), such as TMM 1967TX16. The large specimens, presumed fully adult, range from 39 to 60 mm in test diameter. It is likely that some variability in test size resulted from disarticulation and compaction.

Archaeocidaris brownwoodensis is distinguished from the other Winchell archaeocidarid species by its spine morphology. Outside of the black shale, *A. brownwoodensis* echinoids are most abundant in the limestones of the Lake Brownwood Spillway locality, but also occur in the shales. In other Winchell Formation localities, *A. bronwoodensis* is less common, occurring in shales with another fairly abundant, undescribed *Archaeocidaris* species and occasionally with the even less common *A. gracilis,* described below.

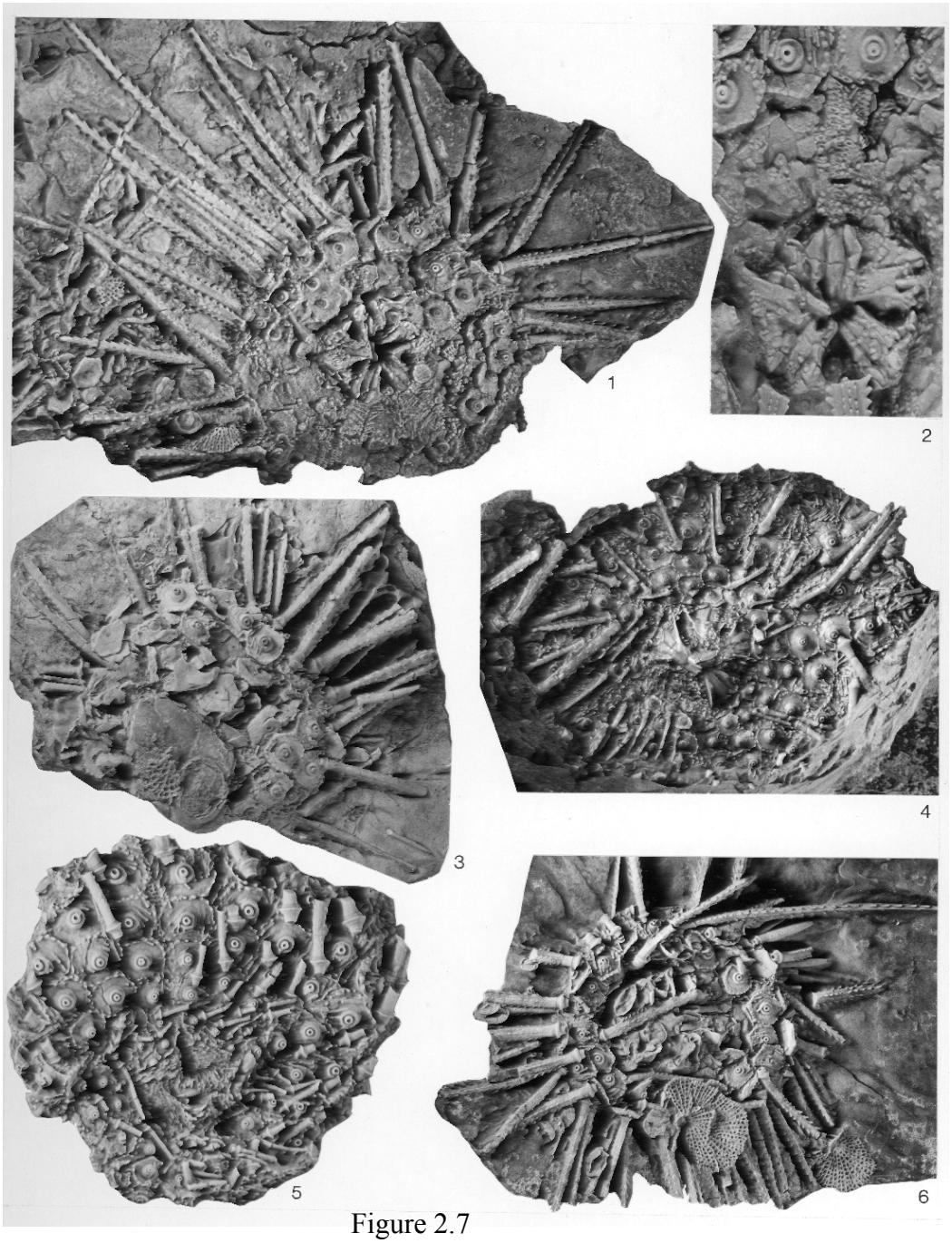


Figure 2.7

Figure 2.7. *Archaeocidaris brownwoodensis*, holotype and paratypes. Specimens 1 (apical view), 4 (oral view) are TMM 1967TX60, holotype, magnification X0.9. Specimen 2 (apical view) is TMM 1967TX1, magnification X2. Specimen 3 (apical view) is TMM 1967TX35, magnification X1.2. Specimen 5 (oral view) is TMM 1967TX99, magnification X1. Specimen 6 is TMM 1967TX61, magnification X1.

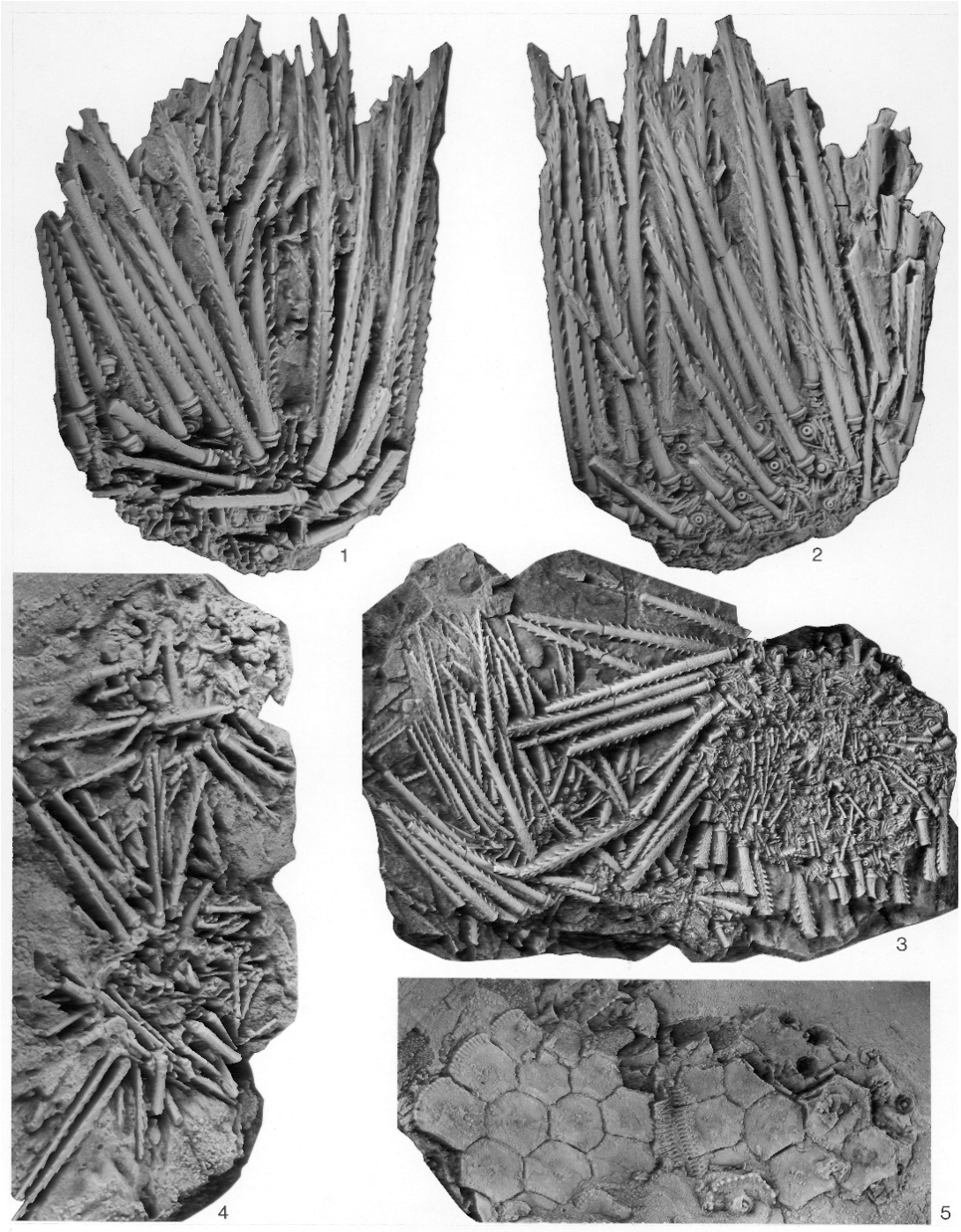
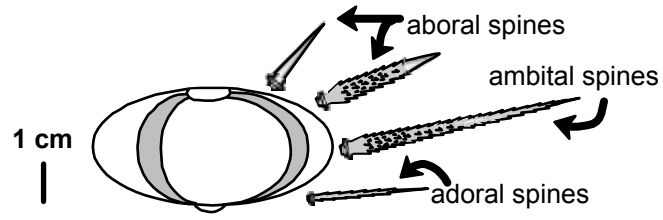


Figure 2.8

Figure 2.8. *Archaeocidaris brownwoodensis*, paratypes. Specimens 1, 2 (lateral views) are TMM 1967TX62, magnification X1. Specimen 3 (oral view) is TMM1967TX3, magnification X0.8. Specimen 4 (apical view, top specimen; oral view, bottom specimen) is TMM 1967TX16, magnification 2.9. Specimen 5 (lateral view, internal) is TMM 1967TX7, magnification X0.8.



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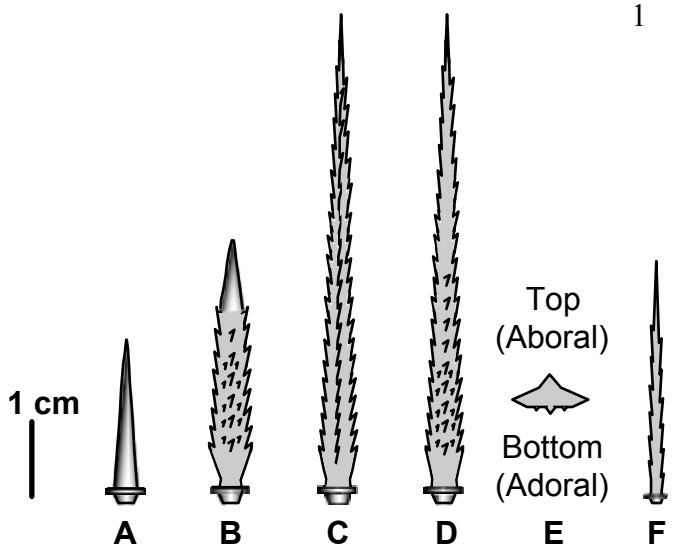

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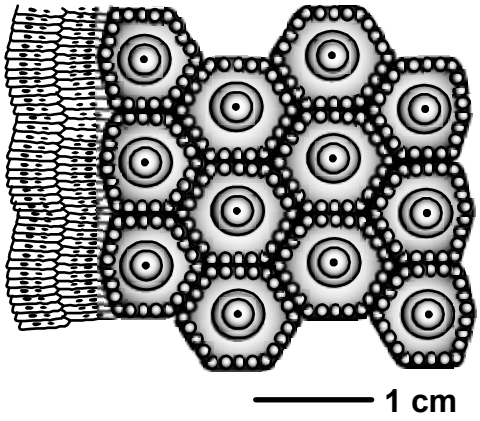

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Figure 2.9

Figure 2.9. Sketch of elements from *Archaeocidaris brownwoodensis*. (1) Placement of spine types relative to test. (2) Growth series of spines, youngest to oldest. (A) and (B) are young, aboral spines; (C) is front, back, and cross-section through ambital spines respectively, and (D) is an adoral spine. (3) Sketch of ambulacral and interambulacral segment.

Archaeocidaris gracilis, new species
Figure 2.10 (1-4)

Diagnosis.—An *Archaeocidaris* species with hollow, smooth spines; test with four columns of hexagonal interambulacral plates and two columns of subrectangular interambulacral plates with fewer scrobicular tubercles than *A. bronwoodensis*. Interambulacral tubercles prominant and high with elliptical perforations.
Description.--Test disarticulated, but probably oval to round in cross section. Ambulacral plates not preserved articulated. Plates subrectangular, pore pairs oval and parallel.

Interambulacra with four columns of hexagonal plates. Plates slightly wider than high with central tubercle covering much of surface. Twelve scrobicular tubercles surround central tubercle. One scrobicular tubercle located on each corner of plate plus one more in the center of the margin between corners. Primary tubercles deeply perforate, high, often with slightly elliptical mammelon. Perforation elliptical. Top of boss striated. Areole only slightly raised from plate surface.

Primary spines straight, smooth, finely striated. Base is truncated cone with bottom of base approximately two-thirds that of top below annulus. Height of base slightly longer than maximum width. Acetabulum elliptical. Bottom of base striated. Annulus distinct and well striated. Shaft slightly sinuous, curving for short distance from base before straightening into hollow spine. Tip sharp, gradually decreasing from shaft.

No lantern elements noted and apical system unknown.
Etymology .—Latin *gracilis* for its delicate, long, unornamented spines.
Type specimens.--Holotype TMM 1967TX20, small disarticulated specimen with many interambulacral plates in association, a few ambulacral plates, and radiating spines. Paratypes TMM 1967TX17, TMM 1967TX18, small disarticulated

specimens with some plates and numerous spines; TMM 1967TX55, large disarticulated specimen covered by *Echinelliptus kiwiaster* (n. sp.).

Occurrence .--Middle Pennsylvanian, middle Missourian stage, Winchell Formation, Canyon Group, Lake Brownwood Spillway near Brownwood, north-central Texas.

Discussion.–Only four specimens of this species are known from the Brownwood locality. One large (45 mm) and three small (test diameter 10 to 15 mm) specimens were recovered from the Lake Brownwood Spillway locality. Other spines similar to those of this species were found in a thin shale from a Winchell Formation outcrop near Perrin, TX, but were a very rare component of the fauna. In the Lake Brownwood Spillway, only one isolated, partial spine was found outside of the black shale in a limestone float block.

Spine morphology is the greatest difference between *A. gracilis* and *A. brownwoodensis*. Without exception, spines of *A. gracilis* are smooth, hollow, and finely striated; these are very distinct from the highly ornate spines of *A. brownwoodensis.*

This species also differs from all other *Archaeocidaris* in its interambulacral plates. Compared to other archaeocidarids, it contains a reduced number of scrobicular tubercles. Other than *A. brownwoodensis*, only *A. immanis, A. antiquantula,* and *A. rossica* have hexagonal plates similar in outline to this species, but each of these archaeocidarids contains many more scrobicular tubercles on their interambulacral plates.

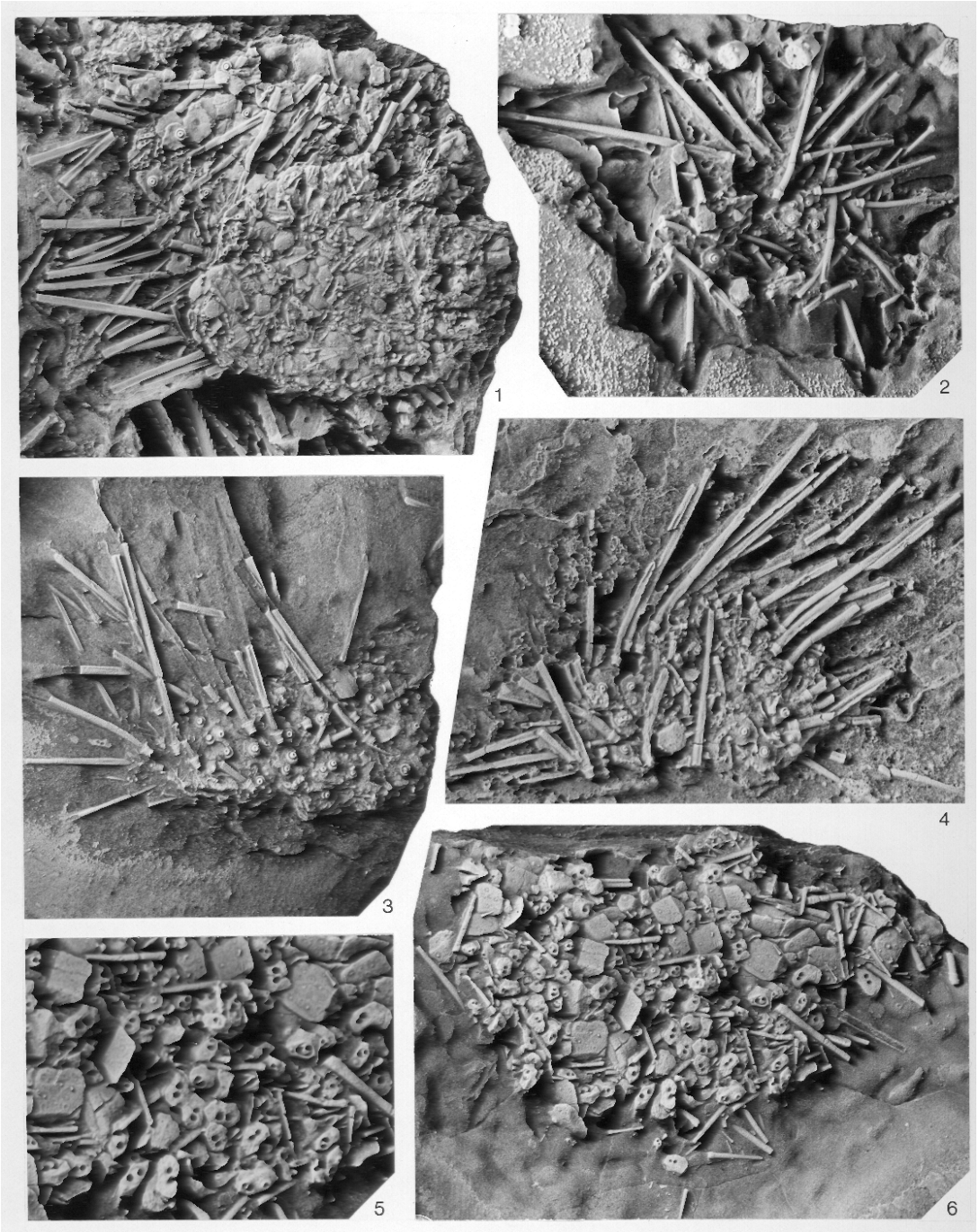


Figure 2.10

Figure 2.10. *Archaeocidaris gracilis* and unnamed echinocystid echinoid. Specimen 1 is TMM 1967TX55, *Archaeocidaris gracilis* (n. sp., apical view?) covered by *Elliptechinus kiwiaster* (n. sp., lateral view), magnification X1. Specimen 2 (apical view) is TMM 1967TX18, magnification X3. Specimen 3 (lateral view) is TMM 1967TX20, holotype, magnification X2.6. Specimen 4 (lateral view) is TMM 1967TX17, magnification X4; Specimens 5, 6 (oral views?) are TMM 1967TX24, magnification X2.5 and X3.3 respectively.

ORDER Perischoechinoidea

FAMILY Lepidocentridae

Elliptechinus, new genus

Type species.--Elliptechinus kiwiaster, new species; Missourian, north-central Texas, USA.

Diagnosis.—Lepidocentrid with 5-7 interambulacral columns and 2 rows of ambulacral plates comprised of hourglass-shaped primary and eye-shaped secondary plates. Ambulacra narrow, strait, with tubercles situated perradially. Interambulacra wide, plates irregular in shape but with consistent morphology within columns; central column imbricates over adjacent columns. Tubercles small, simple; primary spines approximately 1 cm, thin, striated.

Etymology.—Genus name *Elliptechinus,* Latin meaning spiny ellipse.

Occurrence.—Pennsylvanian (Missourian), Winchell Formation, Canyon Group, Lake Brownwood Spillway, north-central Texas, USA.

Elliptechinus kiwiaster, new species

Figures 2.5, 2.6, 2.11 - 2.13

Diagnosis.–Same as genus.

Description.–Test oval in vertical cross-section with maximum measurements of 68 mm tall by 45 mm wide. Ambulacra straight, bicolumnar, relatively narrow. Two distinct types of plates alternate, each plate containing one pore pair; pore pairs located adradially. Plates either primary hourglass-shaped, constricted between perradial tubercle and pore pair, or secondary eye-shaped, constricted on either side of pore pair with smaller perradial tubercle. Hourglass-shaped plates with large spine tubercle against perradial suture and pore pair against adradial suture. Plate is

wasp-waisted, with variable constriction in middle of plate. Plate fully in contact with perradial and adradial sutures. Secondary eye-shaped plates may appear occluded, but actually contact adradial suture beneath primary hourglass-shaped plates, sometimes appearing on surface of test in thin space between hourglass-shaped plates. Partial peripodium, appearing as a semicircular groove, located adorally beneath pore pair. Eye-shaped plates nested between constrictions of adjacent hourglass-shaped plates. Every other eye-shaped plate contains smaller tubercle. Tubercle of secondary plate approximately 2/3 size (in larger plates) or 1/3 size (in smaller plates) of that on adjacent primary plate. Because of alternation of primary and secondary plates, pore pairs appear biserial, with secondary pore pairs closer to perradial suture than those of primary plates. Outer, adradially situated pore of secondary plate longitudinally overlaps inner, perradially situated pore of primary plate. Pores subtriangular to oval in shape. Perradial suture not distinct; tubercles from primary and secondary plates contact and alternate vertically along the suture. Approximately 3-4 ambulacral plates per adambulacral plate.

Interambulacra wide with up to seven columns of plates. Plates subhexagonal and imbricate strongly from central column towards ambulacra and less strongly down column. Central column of interambulacral plates, column 4 (in the case of 7 columns) or column 3 (in the case of 5 columns), imbricates over neighboring columns. Adambulacral plates imbricate over ambulacra. Columns alternate, causing plates to line up in diagonal rows, creating a chevron-pattern with central column as point on chevron. One primary tubercle located aborally, two secondary tubercles located adorally, the entire triad triangular in arrangement. Tubercles low, little more than swelling in middle of barely visible areole. Largest plates in center of interambulacra with decreasing plate size away from center column.

Spines on interambulacral plates slightly longer and thicker than ambulacral spines. Spines finely striated. Stereom distinct on spine striae, creating minute ridges as well as striae. Tips rounded. Spine bases on interambulacral spines equal

in width and height. Milled ring striated and distinct when preserved but not large. Primary and secondary spines not distinctly differentiated in size on interambulacral plates even though tubercles differentiated in size.

Aristotle's lantern present but crushed on several specimens. Lantern high, narrow. Peristome not preserved on specimens.

Etymology.–Species name *kiwi*, because with spines preserved, these echinoids resemble kiwi fruit; Latin *aster,* resemblance or like.

Type specimens.–Holotype TMM 1967TX23, slab containing three well-preserved specimens with spines, collected and prepared by Danny Harlow. Paratypes TMM 1967TX21, large partial specimen; TMM 1967TX22, half of an articulated echinoid without spines; TMM 1967TX25, small articulated specimen missing many spines; TMM 1967TX26, partial articulated echinoid without spines prepared so both sides of test showing; TMM 1967TX27, small specimen; TMM 1967TX58, disarticulated specimen; TMM 1967TX98, slightly disarticulated specimen; TMM 1967TX101, large slab with many *Archaeocidaris brownwoodensis* (n. sp.) and 9 specimens of *Elliptechinus* in various conditions, most lacking spines.

Occurrence.--Middle Pennsylvanian, middle Missourian stage, Winchell Formation, Canyon Group, Lake Brownwood Spillway near Brownwood, Brown County, north-central Texas.

Discussion. – This species is the second most common echinoid in the black shale of the Lake Brownwood Spillway locality, represented by 19 specimens. *Elliptechinus kiwiaster* is more variable than its more abundant *Archaeocidaris brownwoodensis* (n. sp.) neighbors in size and number of interambulacral columns.

Elliptechinus specimens often were better articulated than the large archaeocidarids. One slab contained three fully articulated specimens complete with spines attached to or touching their respective tubercles. Other specimens were prepared so spines were abraded off, displaying plate sutures and other test features.

Because lanterns are located at one end of the elliptical echinoid test, this echinoid is interpreted to have lived upright as epibenthos, with the long axis

perpendicular to the substrate. In shape, *Elliptechinus kiwiaster* resembles elliptical lepidocentrids described by Kier (1958) from Mississippian rocks in the Midwest.

The ambulacra of *Maccoya* Pomel, 1869 and those of this species are very similar. Both contain primary centrally constricted plates and secondary end-constricted plates. However, interambulacral plates differ significantly. In *Maccoya*, plates are distinctly hexagonal and thick, with numerous tubercles on each plate, giving the test a rugose appearance. Although seven columns of interambulacral plates occur in *Maccoya*, the plates do not imbricate. Instead, they abut each other along all sutures. In *E. kiwiaster*, interambulacral plates contain one primary tubercle and two, slightly smaller, secondary tubercles, and lack the multiple tubercles of *Maccoya.* More importantly, plates imbricate strongly in this Brownwood lepidocentrid, unlike the *Maccoya* palaechinid. Other palaechinids, particularly species of *Palaechinus*, resemble *E. kiwiaster* in a few interambulacral features, but lack the distinctive ambulacral plating. For example, the Mississippian echinoid *P. canadensis* Kier, 1953 contains a similar ambulacral to interambulacral width ratio and a similar number of interambulacral plates, but each of those plates contains approximately 30 secondary tubercles and numerous scrobicular tubercles.

Despite the similarity in ambulacra between *Maccoya* and *E. kiwiaster*, it is unlikely that *E. kiwiaster* can be placed within the Palaechinidae. Ambulacral traits, particularly in the distinctive primary and secondary plates, may be a case of convergent evolution. Because of strong imbrication in all plate types, *E. kiwiaster* is better placed in the Lepidocentridae.

In lepidocentrids, there is superfical resemblance in test shape and interambulacral areas. The youngest previously described lepidocentrids are Mississippian in age from Belgium (Jackson, 1929), Great Britain (Hawkins, 1935) and North America (Kier, 1958, 1965). *Lepidechinus cooperi* (Kier, 1958) does not greatly resemble *E. kiwiaster* in shape or single elements, except for hexagonal interambulacral plates. In *L. iowensis* Jackson, 1912, ambulacral areas contain 7 columns of plates, but variability in ambulacral plates is limited to an enlargement

of every third plate, rather than the arrangement of primary and secondary plates of *E. kiwiaster.*

Elliptechinus kiwiaster is variable in ambulacral and interambulacral plate shapes. Other than size of specimens, the most distinctive variability occurs in the amount and length of constriction in primary ambulacral plates. Smaller specimens have less constriction, but this is not constant in all the specimens observed. Interambulacral plates are subhexagonal, but each specimen differs slightly in the outline of its plates. In larger specimens, additional spine bases are observed; either spines are added with increased growth or spine bases were not well preserved on smaller specimens. Otherwise, location of the primary and secondary tubercles on interambulacral plates of smaller specimens is consistant between specimens, as is the relative sizes of these tubercles.

Elliptechinus kiwiaster does not add all ambulacra columns proximal to the apical system; rather, extra plates are added between columns further down the test to increase width as the animal grows. One unusual specimen, TMM 1967TX26, contains one interambulacrum of 7 columns in which column 5 is the central column, imbricating over columns 4 and 6, while all other interambulacra on this specimen and on other specimens follow the general rule described above.

This species also occurs in the Spillway limestones, often as distinct isolated ambulacral plates and spines or less commonly as interambulacral plates. However, these elements are a very rare component in other Winchell Formation communities, and occur primarily in the limestones upsection from the black shale.

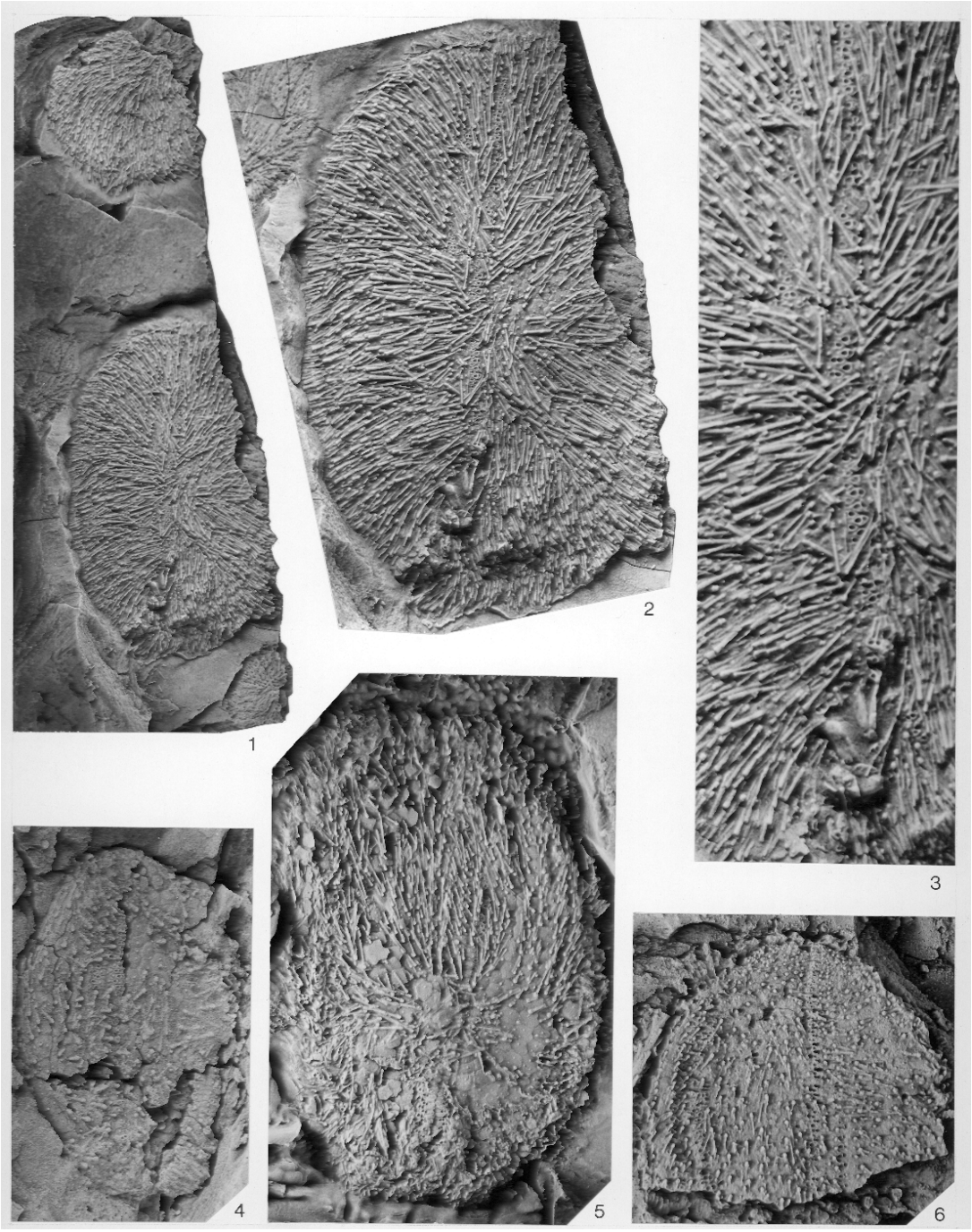


Figure 2.11

Figure 2.11. *Elliptechinus kiwiaster*, holotype and paratypes. Specimens 1-3 (lateral views) are TMM 1967TX23, holotype, magnification X0.7, X1.2, and X1.6 respectively. Specimen 4 (lateral view) is TMM 1967TX25, magnification X2.3. Specimen 5 (oral-lateral view) is TMM 1967TX98, magnification X1. Specimen 6 (lateral view) is TMM 1967TX22, magnification X2.

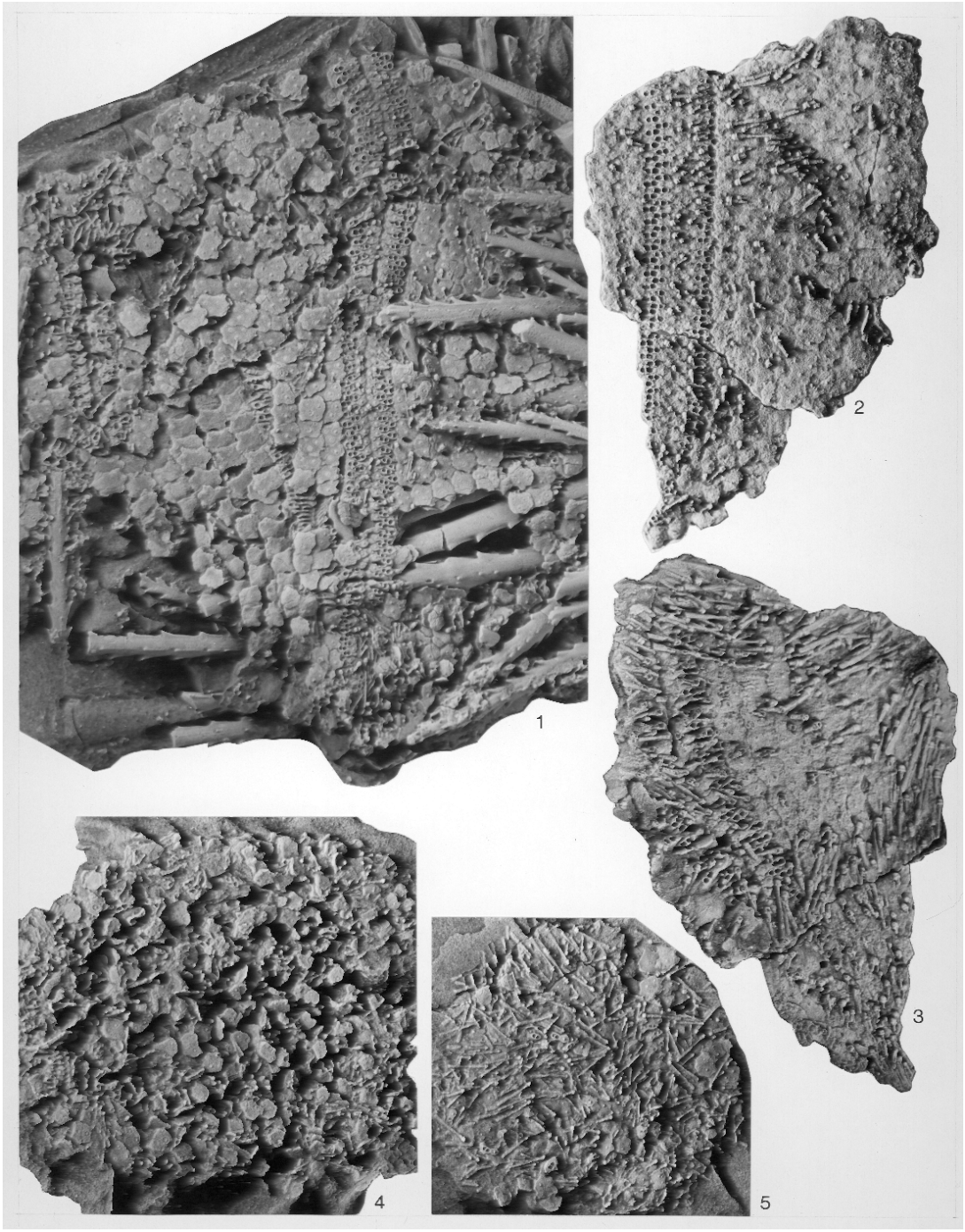


Figure 2.12

Figure 2.12. *Elliptechinus kiwiaster*, paratypes. Specimen 1 (lateral view) is TMM 1967TX21, magnification X0.8. Specimens 2, 3 (lateral views) are flip sides of TMM 1967TX26, magnification X2. Specimen 4 (? view) is TMM 1967TX58, magnification X1.5. Specimen 5 (apical view?) is TMM 1967TX27, magnification X2.8.

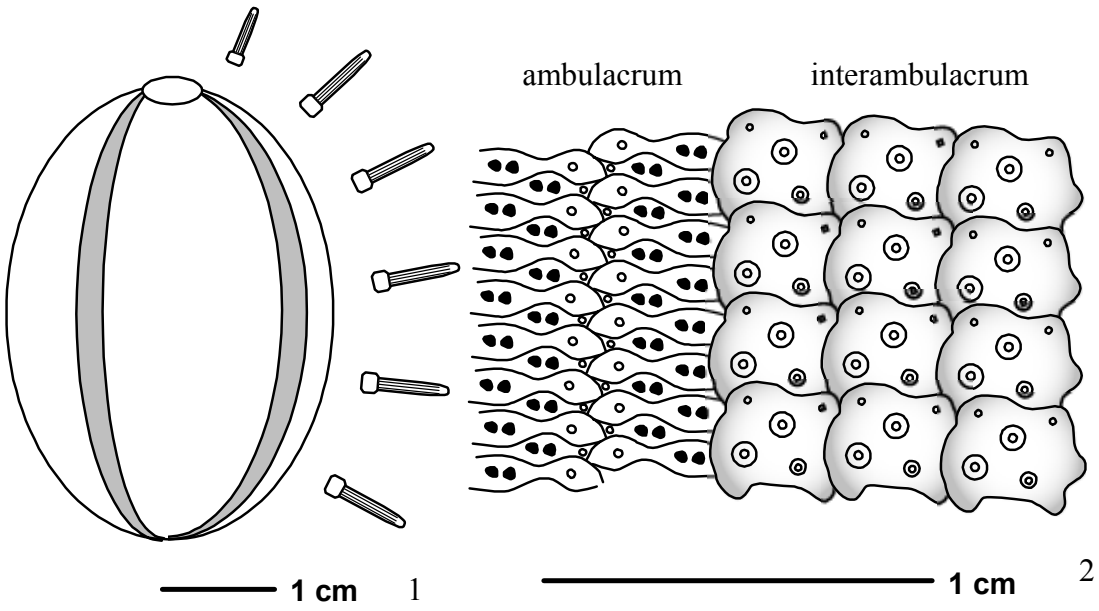


Figure 2.13. Sketch of elements from *Elliptechinus kiwiaster*. (1) Placement of spine types relative to test; and (2) sketch of ambulacral and interambulacral segments.

Family Echinocystidae?

Unnamed new species

Figure 2.10 (4, 5)

Diagnosis.—Small Echinocystidae echinoid with 4 or more rows of variable ambulacral plates, two rows of diamond-shaped interambulacral plates.

Description.—Based on one disarticulated specimen. Disarticulated test 22 mm by 32 mm; ambulacral plates abundant, fewer interambulacral plates present. Ambulacral plates variable in shape, but fit into three major shapes: subtriangular (smallest, without tubercles), subpentagonal (largest, without tubercles), and subhexagonal (with tubercle) plates. Subtriangular and subhexagonal plates elliptical or rounded. All plates bevelled for imbrication, with strongest overlap over pointed end of subpentagonal plates. Pore pairs oval, parallel, surrounded by peripodia as a distinct circular groove contacting outer lateral edges of pore pair. Tubercles distinct, perforated, unornamented areole and mammelon. Specimen interpreted to have at least four columns per ambulacra.

Interambulacral plates few, probably only two columns per interambulacra. Plates smooth to slightly pustulate, diamond-shaped, slightly taller than wide. Minute tubercles imperforate, little more than tiny boss and suggestion of areole. Five tubercles per plate arranged centerally and towards corners.

Ambulacral spines finely striated, tapering, 3-6 mm in length. Spine base little more than rounded swelling at bottom of spine. Interambulacral spines less than 1 mm in length, and approximately 0.1 mm wide. Spine base little more than slight swelling at bottom of spine.

Lantern elements and apical system not seen.

Figured specimen.—TMM 1967TX24, disarticulated specimen with well-preserved ambulacral and interambulacral plates, some spines.

Occurrence.--Middle Pennsylvanian, middle Missourian stage, Winchell Formation, Lake Brownwood Spillway near Brownwood, Brown County, north-central Texas.
Discussion.—This specimen is the most unusual of the Brownwood echinoids because it is the only echinocystid recovered from the site. It most closely resembles the aboral side of the Permian genus *Pronechinus* from Turkey (Kier, 1965). In both taxa, ambulacral plates are variable in shape and size and pore pairs are surrounded by distinct peripodium. However, pore pairs are variable in *P. anatoliensis*, whereas they are consistent from plate to plate in the Brownwood echinocystid. Tubercles on ambulacral plates are more distinct in the Brownwood echinocystid. Interambulacral plates are similar between the two echinoids in shape and proportion, but plates of *P. anatoliensis* are covered in secondary tubercles, causing the surface to appear rugose. Tubercles are few and only barely suggested on the interambulacral plates of the Brownwood echinocystid.

There are also similarities to the adoral side of the North American Carboniferous echinocystid genera *Proterocidaris* and *Eupholidocidaris* in their many rows of ambulacral plates. However, the interambulacral plates of the Brownwood echinocystid are very consistent in their diamond shape, lack of major tubercles, and few interambulacral columns.

It is impossible to tell whether the ambulacra of this echinocystid are prominant over the entire test or if it is enlarged only adorally as in *Pronechinus*. The Brownwood echinocystid also bears some resemblance to the lepidesthid *Meekechinus elegans* Jackson, 1912. *Meekechinus* contains numerous interambulacral plates, but every plate contains one distinct tubercle, unlike the plates in the Brownwood echinocystid. The interambulacrum of *Meekechinus* contains only three columns of plates, which is more similar than the aboral side of *Pronechinus* to the interpretation interambulacrum of the Brownwood echinocystid.

One distinctive feature of the Brownwood specimen is the difference in thickness between ambulacral and interambulacral plates. Ambulacral plates are as

much as three times thicker than the very thin interambulacral plates, with great variability in plate shapes.

Although this echinoid is only represented by one jumbled specimen in the black shale Lagerstätte, this echinoid is the second most common echinoid in the rest of the Spillway locality. Several disarticulated specimens were noted in the limestones above the black shale and isolated ambulacral plates occur in most Brownwood limestones. No isolated elements are known from any of the other shales.

EPIBIONTS ON *ARCHAEOCIDARIS*: PALEOECOLOGICAL INTERACTIONS

INTRODUCTION

Epibiont assemblages on live hosts are common in modern ecosystems and are now increasingly investigated in the fossil record (e.g., Key et al., 1996; Lescinsky, 1997). Well-attached organisms, such as encrusting bryozoans, are common in marine fossil assemblages, but soft-tissue attachers, such as pedunculate brachiopods and macroalgae, though spectacular when found intact with their host, are more rarely preserved. Most fossil assemblages are time averaged, and biotic interactions, such as predation and competition, often can be assessed only indirectly. When hosts and attaching organisms can be shown to be contemporaneous, epibiosis provides a unique opportunity for direct study of biotic interactions between epibionts and their hosts, as well as interactions among epibionts.

The majority of preserved epibiont-host associations contain skeletal remains of sessile hosts with cemented epibiont organisms. Common hosts include brachiopods (Alexander and Scharpf, 1990; Bordeaux and Brett, 1990), crinoids (Grant, 1963; Powers and Ausich, 1990; Peters and Bork, 1998), bryozoans (Watkins, 1981; Sandy, 1996; Zampi et al., 1997), sponges (Carerra, 2000), and others, as basibionts to brachiopods (Richards, 1972; Sandy, 1996), crinoids (Powers and Ausich, 1990; Taylor and Brett, 1996), bryozoans (Alvarez and Taylor, 1987; Lescinsky, 1997), sponges (Molineux, 1994), annelids (Hurst, 1974; Peters and Bork, 1998), and various others. Soft-bodied epibionts also are preserved as traces on the host or in xenomorphs (Evans and Todd, 1997). Fossilized vagile

organisms with epibionts are less common; examples include trilobites (Brandt, 1996; Taylor and Brett, 1996) and cephalopods (Seilacher, 1968; Baird et al., 1989).

Echinoids can utilize organisms and objects as camouflage via actively collecting them with tube feet or by providing substrate for settling organisms. Several species of modern echinoids are known to utilize objects as camouflage by holding them aloft over their tests with tube feet (Smith, 1984). These coverings are ephemeral and need to be recollected and repositioned every time the echinoid drops its camouflaging organism or object. These types of temporary relationships between echinoids and their kidnapped organisms or objects are not known in the fossil record, though Smith (1984) postulated this type of anti-predatory behavior for Paleozoic lepidesthids.

More permanent associations in the form of epibionts are known from modern cidaroids, which lack a soft-tissue covering on the spines, creating a very habitable spot for various attaching organisms (Smith, 1984; Nebelsick, 1999). These relationships, until now, were unknown from the Paleozoic fossil record, although Smith (1984) suggested that the highly ornate spines of archaeocidarids may have been a favorable substrate for attaching organisms.

A fossil locality near Brownwood, Texas is known for an unusually well-preserved echinoderm assemblage (Schneider, 2000, 2001a). This locality contains several horizons of thousands of aggregating *Archaeocidaris* echinoids and preserves a record of *Crurithyris planoconvexa* and bryozoan epibionts on archaeocidarid spines. This locality contains the earliest incidence of contemporaneous echinoid-epibiont association, including attaching organisms not usually preserved on hosts. Additionally, because early cidaroids such as *Archaeocidaris* are the sister taxon to all later echinoids (Smith, 1984), this occurrence has significant implications for early epibiont attraction facilitated by specialized echinoid spine ornamentation.

MATERIALS AND METHODS

Echinoids were recovered, mainly by amateur and commercial collectors, from several horizons in a channel-shaped, shallow-water, estuarine-influenced black shale in the Pennsylvanian (Missourian) Winchell Formation near Brownwood, Texas (Figures 2.1, 2.2). This Lagerstätte may have formed from repeated, rapid freshwater and sediment input, catastrophically killing and rapidly burying the fauna (Schneider, 2000, 2001a). All faunal specimens are completely to nearly completely articulated, and epibiont associations with hosts remain intact, implying rapid burial. Minor transport of echinoids is evidenced by inverted echinoid specimens, suggesting that a current disturbing the aggregation was strong enough to disrupt the aggregation pattern but not intense enough to cause extensive damage. Terrestrial plant fossils, including complete leaves and pieces of wood, are abundant throughout the black shale and indicate close proximity to the paleoshoreline. Among the 4 to 5 cm-diameter aggregating *Archaeocidaris* echinoids are three other species of echinoids, several crinoids, asterozoans, edrioasteroids, several species of brachiopods, and occasional shark teeth. Fenestellid and encrusting bryozoans, as well as *Crurithyris planoconvexa* brachiopods, are found only on the spines of the aggregating *Archaeocidaris*; no other echinoids, including one other small archaeocidarid species, host epibionts. Several edrioasteroids were recovered on *Composita* brachiopods (Sumrall et al., 2000; Schneider, 2000), but no epibionts were noted on other brachiopods. Large fenestellid fronds were collected from the lower horizons, but no other epibionts were found loose in the Lagerstätte horizons.

Over sixty specimens from the echinoderm Lagerstätte were donated to the University of Texas at Austin for the purpose of studying the taxonomy and ecology of these echinoids. In addition, two large 0.5 m^2 slabs containing at least 25 echinoids each were acquired by the Texas Memorial Museum (TMM 1967TX100) and the Department of Geological Sciences (TMM 1967TX101) at the University of

Texas at Austin. Epibionts occur on solitary echinoid specimens as well as on the TMM 1967TX101 slab; no epibionts were found on the TMM 1967TX100 slab. The collection contains 79 individual *Archaeocidaris* echinoids (27 of these from the TMM 1967TX100 slab and 20 from the TMM 1967TX101 slab). All measurements of echinoids and epibionts were made with a clear ruler to the nearest 0.1 cm, with a margin of error of approximately 0.1 cm.

Spines on these archaeocidarids are -triangular in cross section with the widest, flatter side adorally situated (Figure 2.9(2)). Thorns occur on each edge of the spine, set at an angle to the spine shaft and alternating down the length of the spine. On the underside of each spine, up to three rows of smaller thorns cover at least the lower third of the spine length. Spines are widest near the base and gradually taper to a sharp point at a maximum of 7.2 cm in length. Adoral spines are diminutive and gracile, whereas the top two rows of aboral young spines are short, somewhat squat, and contain no ornament. Spines located between the adoral and aboral zones are highly ornate and elongate, with the longest spines located at the ambitus of the test. In instances where spine tips were absent, spine length was estimated by comparing type and spacing of ornament with ornament of complete spines on the same echinoid.

Crurithyris planoconvexa occurs in the black shale only in association with echinoid spines in the archaeocidarid horizons (Figure 2.14 (1-3)). Although pedicles were not fossilized, most specimens are preserved touching or in very close association with individual spines. Location of each *C. planoconvexa* with respect to the spine base was measured from the contact of the brachiopod beak with the spine. Occasionally, *C. planoconvexa* individuals are dissociated from the spines or are situated such that it was impossible to discern which spine was the original substrate, though all are well contained within the spine halo. Several specimens were associated with other *C. planoconvexa* in a clumping fashion, with 3 or more individuals overlapping. Width was measured for each well-preserved brachiopod, but in cases of moderately crushed individuals, maximum dimension was used as a

proxy for width. In many cases where brachiopods were too crushed for accurate measurement, a relative rank of small, medium, and large was established. For analysis of the entire assemblage, small individuals were considered to be 0.4 cm or less; medium, 0.5 to 0.7 cm; and large, 0.8 to 1.0 cm.

Bryozoans are represented by small fenestellid bryozoans or *Fistulopora*-like encrusters around the entire spine (Figure 2.14 (3, 4)). Fenestellid colonies were measured as maximum diameter of the colony and distance of holdfast from the spine base. Encrusting bryozoan colonies were measured as length of spine covered and proximal edge of the colony from the spine base. Most colonies are well preserved, but in some cases, fenestellid colonies had traces of fragmentation on the edges. More often, spines of encrusting bryozoans were broken or covered, impeding measurement. All fragmentation and breakage likely occurred during recovery of specimens from the shale or during air abrasion; specimens in the field and those carefully prepared contain complete colonies. In two instances, fenestellids occurred with *C. planoconvexa*, with one fenestellid shading a *C. planoconvexa* and in the second specimen, the fenestellid growing around two small (0.3-0.4 cm) brachiopods. The latter specimen also contains an encrusting bryozoan in the same location.

Two phenomena were investigated: the location of epibionts on spines and the interactions between echinoids and their epibionts. These were intended to evaluate possible patterns and preferences of epibiont settling, as well as any relationships between the epibionts and their host echinoids. Measurements for epibiont and host organisms were analyzed using Pearson's correlation, chi-square, and T-tests.

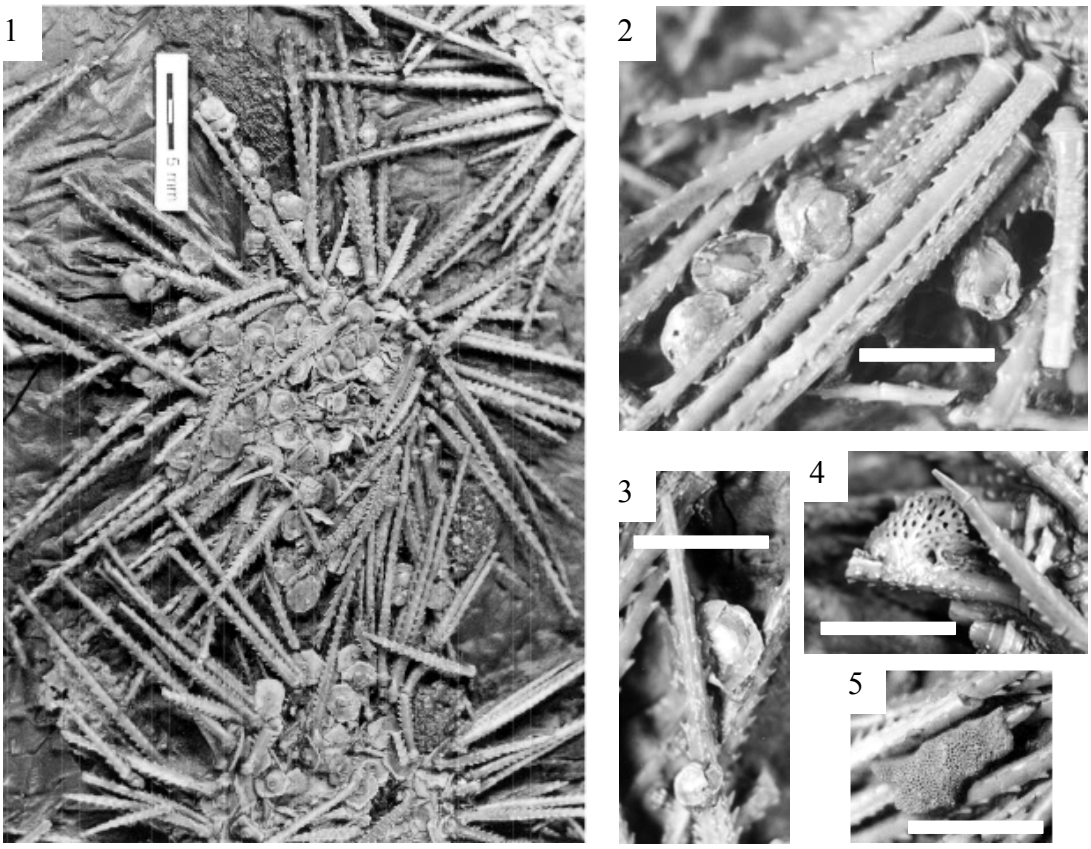


Figure 2.14. Epibionts on *Archaeocidaris* spines from specimen TMM 1967TX101. (1, 2, 3) *Crurithyris planoconvexa* articulated on spines. (4) Fenestellid bryozoan frond on spine. (5) Encrusting tubuliporate bryozoan on spine.

RESULTS

Of the 79 total echinoids used in this study, 39 contain at least one epibiont. Preserved epibionts per echinoid range from one to over 30, with a mean of 7.73.

The TMM 1967TX101 slab was chosen for analysis of echinoid size and epibiont occurrence because it represents a single-event sample of 20 individuals with and without epibionts. One echinoid, approximately 1 cm in diameter and presumably juvenile, did not contain the highly ornate spines of larger adult echinoids and lacked epibionts, so it was not included in the study. Diameters of adult echinoids with and without epibionts do not differ significantly, nor do number of epibionts appear to affect echinoid size (Pearson's $r = -0.42$, $p > 0.07$; t-test = -0.67, 18 df, $p > 0.25$; Figure 2.15). In fact, both the largest and smallest of the presumably adult echinoids on the TMM 1967TX101 slab contain epibionts.

All encrusted echinoids were included in epibiont size analysis. *Crurithyris planoconvexa* brachiopods are 0.1 to 1.0 cm wide, with a mean of 0.56 cm and a standard deviation of 0.24 cm. Most *C. planoconvexa* fall into the medium size range, 0.5-0.7 cm (Figure 2.16). Small *C. planoconvexa*, though less common, are present and fairly evenly distributed among the echinoids except in one case. On one echinoid, six of eight brachiopods are smaller *C. planoconvexa* specimens in the 0.3 to 0.5 cm range. Another unusual echinoid contained all of the 0.1 cm brachiopods, with 13 of the 14 recorded individuals occurring on one spine.

Fenestellid bryozoan colonies ranged from 0.4 to 2.2 cm in diameter with a mean of 0.86 cm and a standard deviation of 0.49 cm (Figure 2.17). One fenestellid colony, represented only by a holdfast, was not counted in size analysis. Most fenestellid colonies are oval, with the long axis perpendicular to spine length.

Most encrusting bryozoan colonies were on partially covered or broken spines; consequently few accurate measurements could be made. The largest intact

colony enveloped 3.3 cm of a 5.0 to 6.0 cm broken spine, and the smallest intact colony covered only 0.4 cm of the spine. Except for the thickest colony, which measured approximately 0.05 cm thick, encrusting bryozoan colonies were thin and unmeasured.

All epibionts are located on the longer spines (3.0 to 7.2 cm) near the middle of the echinoid (Figure 2.18). However, there is no significant correlation between epibiont occurrence and length of echinoid spines (Pearson's $r = 0.094$, $p > 0.05$). Epibionts were found on any spine between the aboral and adoral spine zones.

Placement of epizoans relative to the spine base differs between taxa (Figure 2.19). *Crurithyris planoconvexa* showed a strong preference for proximal placement on the spine, though most fall within an area between 0.5 and 2.0 cm on the spine regardless of spine length (11 $\leq$ 0.5 cm; 108, 0.6 to 2.0 cm; 31 > 2.0 cm; $\chi^2 = 51.63$). Bases of most fenestellid colonies occur within 1.0 cm of the spine base (11 colonies occur $\leq$ 1.0 cm from spine base, 2 colonies occur > 1.0 cm from spine base, $\chi^2 = 6.23$). The lower, test-proximal edges of encrusting bryozoan colonies fall significantly within 1.5 cm from the spine base, regardless of spine length (19 colonies occur $\leq$ 1.0 cm from spine base, 3 colonies occur > 1.0 cm from spine base, $\chi^2 = 11.64$). Using Pearson's correlation, in each of taxa, epibiont location with respect to spine base was highly significant (*C. planoconvexa*: $r = -0.39$; fenestellids: $r = -0.47$; encrusting bryozoans: $r = -0.54$).

Settlement of *C. planoconvexa* and fenestellids primarily occurred on the upper and lateral surfaces of the spines (Figure 2.20). Encrusting bryozoan colonies encircled spines, so settlement site could not be determined. Overall, there was no distinction between choosing one lateral edge of the spine or another, but several individual echinoids contained a *C. planoconvexa* assemblage with a distinct preference for a left or right side relative to the articulation to the test.

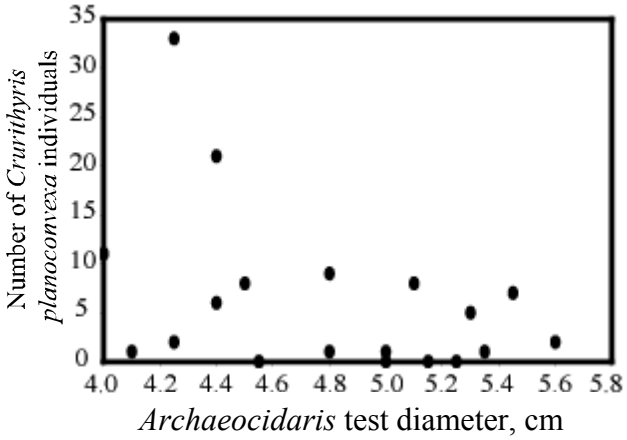


Figure 2.15. Number of *Crurithyris planoconvexa* per echinoid size from TMM 1967TX101 slab. *C. planoconvexa* measured as diameter (cm) in the horizontal direction. Only echinoids with complete tests were included.

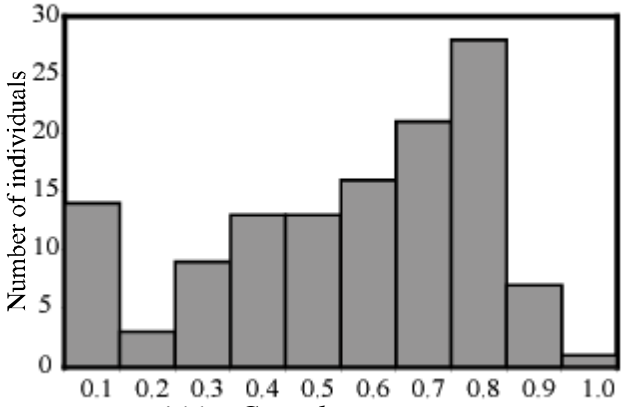


Figure 2.16. Size and number of *Crurithyris planoconvexa* individuals. (1) Number of individuals per width (cm) of *C. planoconvexa*. In some cases, brachiopods were crushed; because *C. planoconvexa* is wider than long, the longest axis of the crushed specimens was measured. (2) Relative sizes of *C. planoconvexa*. Many *C. planoconvexa* were crushed beyond accurate measurement, and were therefore categorized as small, medium, or large. Included in this chart are the measured *C. planoconvexa*, with small = crushed and uncrushed individuals 0.1 to 0.4 cm; medium = crushed and uncrushed individuals 0.5 to 0.7 cm; and large = crushed and uncrushed individuals + 0.8 to 1.0.

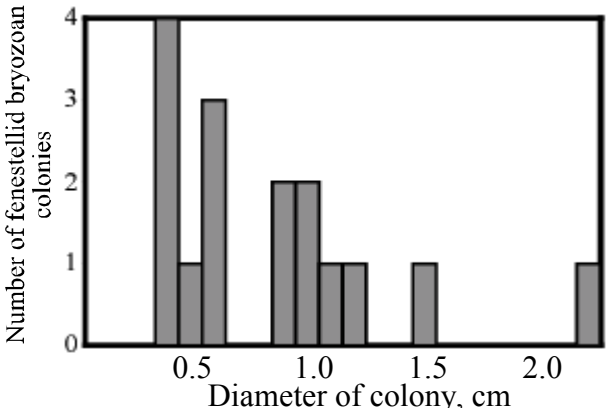
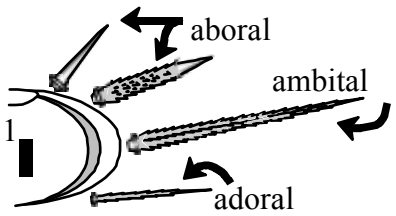
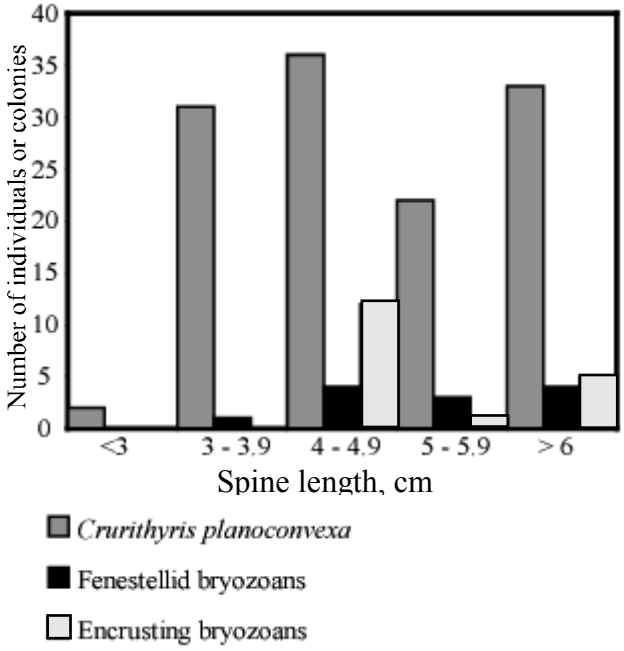


Figure 2.17. Number of attached fenestellid bryozoan colonies and their diameters (cm).



1



2

Figure 2.18. Epibiont association with archaeocidarid spines. **(**1) Sketch of partial echinoid test in life position portraying placement and morphology of spine types of *Archaeocidaris* sp. from the Winchell Formation of Brownwood, Texas. Adoral and aboral spines contained no epibionts; ambital spines, in this study, refer to all fully developed, large spines between the adoral and aboral spine zones. (2) Number of epibionts per length category of spines.

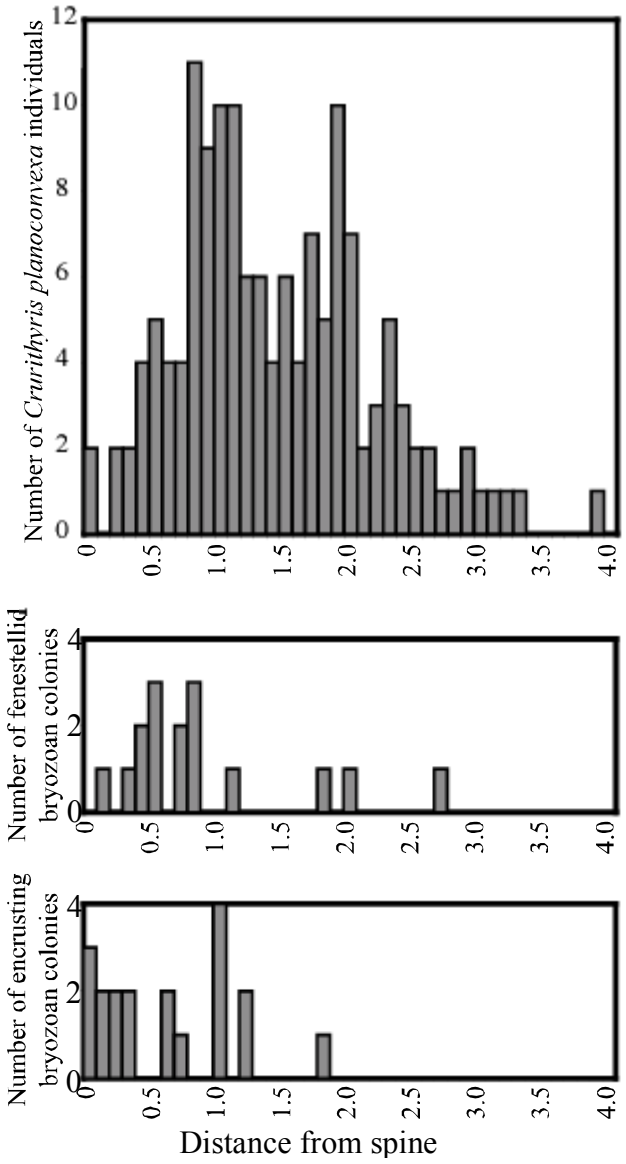


Figure 2.19. Position of epibionts on spine as distance (cm) from base of the spine shaft. Only those epibionts in contact with or closely associated with distinct spines are reported here.

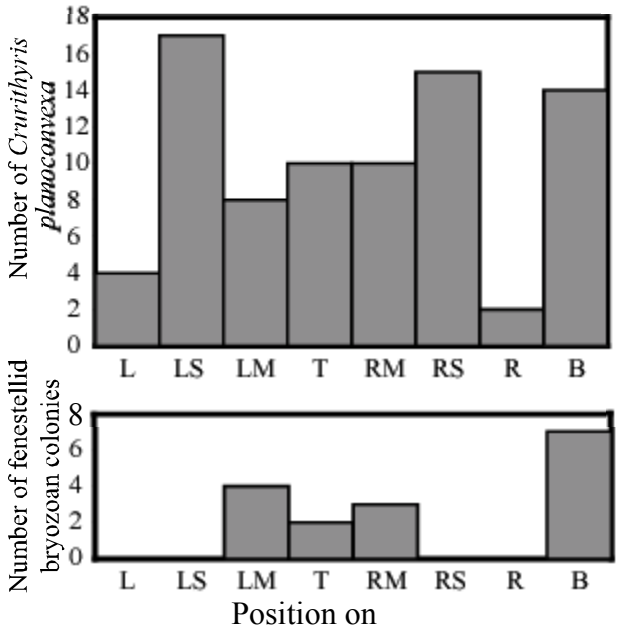


Figure 2.20. Location of *C. planoconvexa* and fenestellid bryozoan colonies on spines. Encrusting bryozoan colonies are not represented because colonies encircle the entire spine. Key: T = Top spine edge, RM/LM = Right/Left Middle of the spine; RS/LS = Right/Left Spine edge; R/L = to the right or left of the top spine edge, but more precise position undeterminable; B = bottom.

DISCUSSION

Epibiont Assemblage

Location of the epibionts on the spines is statistically significant, and therefore cannot be attributed to random placement. Three mechanisms can be invoked for this pattern: active host action to epibiont settling (antifouling behavior), passive host action to epibiont settling (accidental mechanical antifouling), or active preferences of larval epibionts.

Active antifouling behavior is known in many organisms. Crustaceans regularly moult shells, which serves as a means of removing epibionts that settle on the carapace (Abello and Corbera, 1996; Patil and Anil, 2000). Life habits, such as burial or sediment cover, also can inhibit epibiosis (Bordeaux and Brett, 1990; Negreiros-Fransozo et al., 1995). Ornament, though sometimes conducive to epibiont settling (Feifarek, 1987), also can deter settlement, such as in spines on *Platystrophia* brachiopods (Richards, 1972). These archaeocidarid spines, obviously, did not deter organisms from settling on them, though the echinoids may have used other means to limit the amount of encrustation. Paleozoic archaeocidarids, like their modern cidaroid relatives, had pedicellariae, which, if similar to their modern counterparts, contained toxins that may have been utilized in removing pests. However, pedicellariae on most extant echinoids are short, small, and less mobile than other appendages, and are mainly used in clearing the test of debris and pests (Smith, 1984). It is possible that larvae, which may venture near the test before settling, could be eliminated via pedicellariae, leaving fewer organisms to settle on the spines. However, this does not account for the significant proportion of epibionts located proximal to the test, which may have been in range of attacking pedicellariae.

Accidental, mechanical antifouling via abrasive action may be responsible for the removal of more distally located epibionts. Abrasion is used, whether intended or not, by modern organisms to remove epibionts (Patil and Anil, 2000). Echinoid spines are mobile, rotating on articular surfaces between the spine base and tubercle, much like a ball-and-socket joint with an internal medial ligament. As the *Archaeocidaris* spines moved, they likely touched or hit other objects, including other spines on the same organism. Epibionts located distally likely would have experienced more of these abrasive movements than those located proximally. Therefore, the decreasing incidence of epibionts on *Archaeocidaris* with increasing distance from the spine base may simply be a function of increased distal abrasion from spine movement. Unfortunately, without experimental testing, this phenomenon can only be one of several possible explanations.

Alternatively, the seemingly preferential, non-random location of epibionts on the spines may simply be the result of epibiont larvae preferentially settling on specific sites on the echinoid spines. Modern epibionts show similar preferences on their live host substrates (Schmitt et al., 1983; Barnes and Clarke, 1995; Abello and Corbera, 1996; Key and Barnes, 1999; Key et al., 1999). Some fossil epibionts also seem to prefer certain placements on skeletal material or orientations with respect to host orientation (Alexander and Scharpf, 1990; Powers and Ausich, 1990). It is possible that, like other bryozoan epibionts, these encrusting and fenestellid bryozoans on the archaeocidarid spines preferentially settled close to the test. *Crurithyris planoconvexa* brachiopods also may have settled preferentially proximal to the test, although similar settlement patterns of other fossil brachiopods are rare (Alexander and Scharpf, 1990).

Epibiont occurrence is limited to the ambital, or middle, non-aboral and non-adoral spine zones on the test. Adoral spines are gracile, sparsely ornamented, and located on the bottom of the test. Although these spines were formed during early growth of the echinoid and moved adorally with introduction of new plates and spines, they may not have been settled by epibiont larvae because of uninhabitable

spine morphology or, later in the echinoid's life, proximity to the sediment. Aboral, or top, spines are newly formed and are either entirely smooth or are ornate only proximal to the test. It is possible that these spines either are too young to have encountered settling epibiont larvae or have insufficient ornament for attachment sites. Ambital spines, however, are large and highly ornate, and may have facilitated epibiosis by providing ample suitable settlement sites for epibiont larvae.

It is also possible that a combination of mechanisms can be invoked to explain epibiont distribution. The preferential settling of epibiont larvae, the abrasion of juvenile epibionts from distal ends of spines, and echinoid clearing of larval epibionts by pedicellariae all could simultaneously apply to a given assemblage. Epibiont larvae may settle preferentially, though larvae and juveniles may be less able to handle increased current and abrasive stresses on more distal portions of the spine, so any distally-settling juveniles will be lost. Bryozoans may be less tolerant to distally located stresses caused by spine movement than *C. planoconvexa* brachiopods, which may be reflected in the greater distal range of the brachiopods. Pedicellariae may not actively rid the echinoid of all epibionts (particularly those never approaching the reach of pedicellariae) and pedicellariae cleaning may occasionally mistake an acceptable epibiont for a less-desirable object.

Crurithyris planoconvexa brachiopods from 0.1 to 1.0 cm wide are preserved on echinoid spines, although medium-sized specimens are more numerous. This epibiont size bias may occur for several reasons. First, smaller *C. planoconvexa* individuals may be detached from the host during life or dissolved during diagenesis. *Crurithyris planoconvexa* specimens of any size range are among those dissociated with the echinoids in the Lagerstätte horizons, indicating that all *C. planoconvexa* remained in contact with their host archaeocidarid echinoids after death and detatched during decay. It is possible that smaller brachiopods had lower preservation potentials, though no dissolution or partial specimens were noted among the smaller individuals. Also, one unusual specimen

contained thirteen 0.1 cm *C. planoconvexa* brachiopods on one spine with several larger specimens located on other spines, indicating that the preservation potential for tiny *C. planoconvexa* individuals is high. Therefore, it is likely that most fouled echinoids were not in range of later spatfalls of *C. planoconvexa* larvae, and contained larger individuals from earlier spatfalls.

It is fair to assume that all *C. planoconvexa* brachiopods were alive just prior to or at the time of death of the echinoids, since all individuals remain in contact with echinoid spines or are closely associated with them. This life assemblage not only provides insight into epibiosis of *C. planoconvexa*, but also is a window into the population dynamics of these brachiopods. The wide range of *C. planoconvexa* sizes indicates no distinct episodes of recruitment. This is in accordance with other reported distributions of attached fossil brachiopod size ranges (Cate and Evans, 1992).

Interactions between Epibionts and Archaeocidarids

Interactions between mobile hosts and epibionts are more readily observed in modern systems where living relationships can be studied and experiments can be carried out between hosts, epibionts, and predators. In fossil systems, relationships between hosts and epibionts are not always obvious, though several authors previously noted significant interactions (e.g., Baumiller, 1990). Likewise, without the ability to observe these echinoids and their epibionts in life, it is impossible to know the full nature of their associations. However, by analyzing the relationships of echinoids and their attaching organisms within the context of costs and benefits of epibiosis, it is possible to gain further insight into these biotic interactions.

Epibiosis has both costs and benefits to the hosts and attaching organisms, often with greater benefits to the epibionts (Wahl, 1989; Key et al., 1997; Olabarria, 2000). Directly, epibionts can create turbulence (Richards, 1972), increase weight

and drag (Wahl, 1989; Olabarria, 2000), interfere with soft-tissue function (Wahl, 1989; Key et al., 1995; Key et al., 1996), and disrupt growth (Wahl, 1996; Buschbaum, 2000; Carrera, 2000) of the host. Most encrusting bryozoan colonies are small and thinly cover the *Archaeocidaris* echinoid spine, so most likely had little effect on spine movement. Conversely, fenestellid colonies and *C. planoconvexa* brachiopods, which were extended at an angle from the spines, likely increased drag and weight significantly on the spine. Because most epibionts are located proximally on the *Archaeocidaris* spine, effects from weight and drag may be minimized on the echinoid spine. Furthermore, in most cases, few epibionts occur on any one echinoid, decreasing any effect on the echinoid host. No epibionts were found on the test of any echinoid in this study, suggesting that epibionts were not present on plates covered with an epidermis. The presence of soft tissues and pedicellariae would deter epibiont settling on the test (Smith, 1984).

Growth effects in the contemporaneous archaeocidarids on the TMM 1967TX101 slab, as noted above, were statistically insignificant; therefore, epibionts may have had little effect on echinoid growth. Two echinoids with the largest number of epibionts are among the smaller represented individuals; it is possible that these two individuals may have experienced decreased growth rates. However, excluding these two specimens, any correlation between epibiont abundance and echinoid size is weaker still. Epibiont influence on echinoid growth cannot be completely discounted, because the single sample used in the analysis contains only 25 individuals. More conclusive results must await future slabs of many *Archaeocidaris* or other localities of aggregating echinoids with epibionts.

Competition between epibionts and their hosts is often postulated and sometimes experimentally shown to be detrimental to fouled organisms (e.g., Wahl, 1989; Key et al., 1996; Olabarria, 2000). However, because archaeocidarid echinoid feeding mechanisms differ greatly from their suspension-feeding epibionts, competition for food resources is unlikely.

Epibionts can significantly influence predation on their host organisms. Through camouflage, epibionts can mask the host's chemical and visual signals (Feifarek, 1987; Wahl, 1989; Patil and Anil, 2000). In this way, epibionts may inhibit predators from attacking the host organism. Conversely, epibiosis may attract predators in the sense that one type of epibiont may be more acceptable to a predator than another or actually slow down the host, making it more available to the predator (Schmitt et al., 1983; Wahl and Hay, 1995; Laudien and Wahl, 1999). Epibionts may also attract their own predators, which may damage the host (Wahl, 1989; Wahl et al., 1997; Laudien and Wahl, 1999). The only predator remains recovered from the Brownwood Lagerstätte sediments are occasional shark teeth, and sharks may or may not have preyed on echinoids.

The number of preserved epibionts per echinoid ranges from one to over 30, with a mean of 7.73. Unless unpreserved soft-bodied organisms also were attaching to echinoid spines, it is unlikely that these epibionts created significant visual camouflage. Chemical camouflage can neither be discounted nor strongly suggested, since 43 of 79 total echinoids in the study do not contain epibionts. Therefore, it is difficult to discern the nature of the effects of epibionts on predation of echinoids from this study alone.

Highly ornamented spines in upper Paleozoic archaeocidarids, assuming that spines are antipredatory, might indicate an increase of predation on echinoids. Predation would be difficult to discern because most Paleozoic echinoids are represented only by isolated plates and spines. A preliminary study by the author (Schneider, 2002 and unpublished data), based on Pennsylvanian and lower Permian archaeocidarids, suggests an increase in spine ornament through time as well as an increase in epibiont diversity, abundance, and spine coverage. Because of this increase, predation pressures could be inferred to be significant for the archaeocidarid, because of energy spent to make and maintain highly ornamented spines and to tolerate abundant epibionts.

Epibionts, in turn, receive a variety of benefits from settling on a host organism. Hosts that contain ornament will either attract (Feifarek, 1987; Olabarria, 2000) or repel (Richards, 1972; Bordeaux and Brett, 1990) epibionts, depending on the nature of the ornamentation. Several modern and fossil organisms with spines and other ornament have positive or negative effects on epibiont settlement. Modern spondylid oysters with spines (Feifarek, 1987), spinose brachiopods (Hurst, 1974; Alvarez and Taylor, 1987), and ornate neogastropods (Olabarria, 2000) previously were noted to contain abundant and occasionally diverse epibiont assemblages, suggesting that some kinds of ornament encouraged epibiont presence. Spines are thought to actively attract attaching organisms to settle (Feifarek, 1987) and highly ornate and sculpted surfaces provide increased surface area for settling, decreased contacts with other epibionts, and refuges from predators (Wahl, 1989; Olabarria, 2000). Therefore, spines that serve as a substrate for epibiosis double as protective devices for both the host and any epibionts that may settle on them. Sharing the defenses of the host organism, or associational defense, is common in epibiosis (Wahl, 1989). Ornate archaeocidarid spines, as mentioned above, previously were proposed as ideal spots for epibiosis (Smith, 1984). Echinoid spines attracted epibionts, and in turn were a source of extrinsic defense for the attaching organisms.

Secondary tiering on skeletal material is an effective means of becoming elevated above the substrate (Bottjer and Ausich, 1986). Situated some distance above the sediment, epibionts can often experience favorable conditions, such as increased currents, increased food intake and exudate removal, and decreased sediment fouling (Feifarek, 1987; Wahl, 1989; Key et al., 1995; Key et al., 1996). In mobile organisms, additional currents are created from the host's movement, which may further increase food gathering and carry exudates away from the epibiont (Taylor and Brett, 1996; Olabarria, 2000). In this manner, the hitchhiking *C. planoconvexa* brachiopods and bryozoans on the Brownwood echinoids were able to elevate themselves within the benthic boundary layer, increasing food supply

and water currents through a combination of height above the substrate, echinoid wandering, and spine movement.

In some systems, epibionts settle on live skeletal material simply for lack of other inert hard substrate; in other words, hard substrates for attachment are a limiting resource (Key et al., 1995; Carrera, 2000). Wahl (1989, p. 184) stated that "all unprotected, apparent (sensu Feeny, 1976) solid surfaces in the sea sooner or later become fouled." Another explanation for exploitation of a living host is that it is an unoccupied substrate where interactions with other attached organisms will be minimal (Olabarria, 2000). In other cases, host species create a favorable environment for epibionts either via physical morphology of the shell or chemical signals from other epibiont organisms, which encourages larvae to settle (Wahl, 1989). In any event, epibionts are known to increase community diversity through exploitation of these surfaces (Taylor and Brett, 1996; Gutt and Schickan, 1998). If Smith (1984) was correct about ornate archaeocidarid spines facilitating epibiosis, then one use of echinoid spines – the attraction of epibionts – may have been maintained in archaeocidarid and cidaroid echinoids. It is possible that the echinoids in this study are an early stage in active epibiont recruitment in cidaroids, but further work is needed.

In mobile organisms, epibionts are exposed to currents created by the movement of the host organism and may even increase their biogeographical range by being carried along during host dispersal (Wahl, 1989; Key et al., 1995; Olabarria, 2000). Vagile hosts also may serve as a mobile refuge from potential predators of epibionts (Ozolinsh and Kupriyanova, 2000). Conversely, the epibiont is subject to several disadvantages when attached to a mobile host. Epibionts may be carried into unfavorable and stressful environments with the movement of the host. In the case of the archaeocidarid echinoids, this is an unlikely problem for their epibionts because echinoderms are generally intolerant of hypo- or hypersaline conditions. Extant New Zealand *Evechinus* echinoids are known to aggregate in the bottom saline layer of very shallow estuarine environments during breeding for

short periods (Lamare and Stewart, 1998) and so may be tolerant of short-term stresses. Fossil archaeocidarids from Brownwood aggregated in shallow-marine conditions, possibly in an estuarine environment that was normally saline, with several aggregations possibly perishing from freshwater runoff (Schneider, 2000, 2001a). Epibionts occur in these Lagerstätte horizons only in association with the echinoids. It is probable that these *Archaeocidaris* aggregations were ephemeral phenomena, occurring only for short times in this locality for food gathering or spawning, because salinity and oxygen conditions, as in many modern estuaries, may have fluctuated on short to long time periods. Therefore, epibionts may have settled on spines elsewhere and were carried by the echinoids into the locality. This interpretation is supported by the lack of isolated *C. planoconvexa* brachiopods in the surrounding sediment or on other potential hosts, such as *Composita* brachiopods or on the few crinoids.

Crurithyris planoconvexa and other small attaching brachiopods are only found as loose brachiopods in other Winchell Formation localities. Fenestellids, as in many other Pennsylvanian localities, are very common, and small sheets of encrusting bryozoan colonies are readily collected in some units. Most *C. planoconvexa* brachiopods are found in environments with prime habitats for epibiosis, particularly in archaeocidarid debris-rich units or phylloid algal mounds. It is likely that many loose brachiopods once were attached to archaeocidarid spines as well as to other substrates as secondary tiering organisms.

Competition between epibionts, when it occurs, is a significant cost to epibiosis (Alexander and Scharpf, 1990; Lescinsky, 1997). Some epibionts actively compete with others for space, such as bryozoan overgrowth of other attaching organisms (Alvarez and Taylor, 1987; Lescinsky, 1997). In the Brownwood archaeocidarid Lagerstätte, no evidence of spatial competition exists among preserved epibionts. Considering the numerous echinoid spines and the fact that most spines contained no epibionts, space was not a limiting resource and competition for attachment sites can be inferred to be minimal.

Host relationships with their epibionts have been described as parasitic, commensal, mutualistic, or accidental. Most often, the majority of the benefits fall to the epibionts, with costs to the host usually greater than any possible benefits (Key et al., 1997; Olabarria, 2000). Some potential hosts discourage epibiosis via mechanical (i.e., abrasion), physical (i.e., skeletal features), or chemical means (Wahl, 1989). These antifouling mechanisms are not readily apparent in fossil organisms, though some animals, such as punctate brachiopods, are rarely fouled by encrusting organisms (Alexander and Scharpf, 1990; Bordeaux and Brett, 1990). In some studies, preferences of host substrates and epibiotic organisms are apparent. One smooth Ordovician sponge species was encrusted preferentially by bryozoans, indicating a possible affinity of the sponge for potential bryozoan settlers (Carrera 2000). In the case of the Brownwood archaeocidarid echinoids, no apparent antifouling mechanisms are noted, though the possibilities of abrasion through spine movement and attack with pedicellariae are possible (Wahl, 1989).

In this study, majority of the benefits fell to the brachiopods and bryozoans attached to the echinoids, because specimens without epibionts were apparently as successful as those with them. Therefore, the relationship between epibionts and the *Archaeocidaris* echinoids cannot be called mutualistic or parasitic, and is accidental, or more likely commensal, in association. In mutualism, both species benefit from the epibiosis; however, benefits from the epibionts to the echinoids are unclear at best. Parasitism also does not explain the association, because parasites have a detrimental effect on their host. Epibionts at the Brownwood locality do not appear to have affected negatively their echinoid hosts in any significant way. Accidental associations are those in which a cosmopolitan encrusting organism lands on a substrate that may be less favorable, such as a bryozoan colony on a sea snake (Key et al., 1995). An accidental association is essentially neutralism, where an epibiont settles on a substrate simply because it is available, with no notable benefits other than open substrate. Benefits to the epibionts in the present study may be significant, so it is more likely that the relationship between the epibionts and the

host echinoids is commensal, whether or not the epibiont larvae preferentially settled on the spines.

CONCLUSIONS, CHAPTER 2

Four new echinoid species, *Archaeocidaris brownwoodensis, Archaeocidaris gracilis, Elliptechinus kiwiaster,* and an unnamed echinocystid species occur in a recurring *A. brownwoodensis* aggregation in a black shale in the Lake Brownwood Spillway locality of the Pennsylvanian (Missourian) Winchell Formation near Brownwood, Texas. The presence of *Elliptechinus kiwiaster* is the youngest occurrence of lepidocystids, previously known only as late as the Mississippian Period.

Archaeocidaris brownwoodensis echinoids contain abundant attached *Crurithyris planoconvexa* brachiopods representing a range of sizes from 0.1 to 1.0 cm. Much rarer, small fenestellid and encrusting bryozoan colonies are present. These epibionts are located on spines closer to the middle of the test than adorally and aborally located spines and are more often situated on the lower, test-proximal half of the spine. Patterns of settlement on proximal ends of the spine may result from antifouling behavior of the echinoid, accidental antifouling from abrasion, larval epibiont preference, or a combination of these.

Epibiont effects on echinoids were probably minimal. Weight and drag effects were minimal because of size and sparsity of epibionts. Because there is no significant difference in diameters of echinoids with and without attaching organisms, epibionts apparently had no effect on growth of echinoids preserved in the Lagerstätte. However, this is based on one sample of 25 contemporaneous fouled and unfouled echinoids from the TMM 1967TX101 slab.

Potential benefits are greater for the epibionts, including associational defense, transport into different environments and away from predators, increased

water currents from echinoid and spine movement, and open habitats for settlement with consequent decreased competition with other epibionts. Costs to these epibionts would primarily occur as mortality from echinoid predators and transport into stressful environments, though the latter is unlikely given presumed echinoderm intolerance to extremes of salinity stress. Echinoids may have experienced increase weight and water drag from epibionts, though this may have been minimized by placement of epibionts on the spines. Epibionts can aid in camouflage, but it is unlikely these epibionts played a significant role in defense. Size and sparsity of coverage of epibionts likely created little visual camouflage for the echinoid; chemical effects on camouflage by *C. planoconvexa* and bryozoans are unknown. Therefore, relationships between the host echinoids and their epibionts are most likely commensal, with most of the benefits falling to the epibionts.

This study supports the hypothesis that highly ornate archaeocidarid spines were ideal habitats for epibiosis (Smith, 1984). Furthermore, ornate, soft-tissue-free spines in the archaeocidarid-cidaroid lineage are here hypothesized to have evolved for active epibiont recruitment.

Chapter 3: Community Paleoecology of the Winchell Formation near Brownwood, Texas and Other Contemporaneous Localities

INTRODUCTION

Ecological questions, especially with regard to temporal patterns and the processes that cause them, are "uniquely answerable" using the fossil record (DiMichele, 1994, p. 89). Although fossil communities are often time-averaged and rarely represent the entire live assemblage (Staff et al., 1986), time-averaging can have benefits to paleoecological study. Time-averaging smoothes out minor perturbations and annual cyclicity, such as fluctuations in recruitment, resource-poor periods, and seasonality (Olszewski, 1999); although such detailed information is lost to the paleoecologist, large-scale patterns and processes are available through appropriate use of data. For example, with loss of ecologic-time noise, patterns of change can be revealed in communities as they respond to changing environments resulting from tectonism, plate movement, sea-level rise and fall, and long-term succession (Walker and Alberstadt, 1975; Sanchez et al., 2002). Additionally, fossil ecosystems are unique in that ecological processes can be discerned and tested through the observation and analysis of temporally repetitive communities, a variable that is not available to the modern ecologist.

The fossil record has often been accused of being inadequate to answer fine-scale ecological questions. Many researchers, paleontologists and ecologists alike, maintain that only large-scale patterns and some processes are possible through fossil data (i.e., Valentine and Jablonski, 1993; see chapter 1 for others). Other researchers are more optimistic about the fossil record, suggesting that fossil data is adequate for ecological-scale questions (i.e., Hickey and Younker, 1981).

Furthermore, research into organism interactions, such as predation and competition, is becoming more common in paleoecology as new techniques are developed to deal with the time-averaging and temporal factors unique to paleontology. With these new and growing fields of paleoecological interactions, it may be possible to investigate more than simple large-scale patterns in community paleoecology and begin to ask questions about community structure and processes behind change at multiple scales.

In investigating processes behind community patterns through time, it is crucial that appropriate scales and data be used. If questions are whole-community in nature, and detailed insights into community structure are desired, then data collection also must be detailed and include the entire taxonomic assemblage. Although single- or few-taxon studies are valuable for certain questions, such as brachiopod- or coral- assemblage data to investigate environmental versus biotic controls on those taxa through time, they cannot characterize the nature of whole communities outside very large-scale patterns. Limited-taxon assemblages, such as brachiopods- or trilobites-only, can say nothing about the importance of bryozoans in community structure. Although the use of indicator taxa showed that a single-taxon analysis can represent a single large-scale, whole-community pattern (Peters and Bork, 1999), parallels between all-data and limited-taxon lists are often broad in nature and cannot begin to reproduce the intricate, diverse patterns and processes of entire communities.

This study will examine recurring patterns in communities and will investigate in what detail community recurrence and structure can be revealed through fine-scaled analysis using all fossil data. For example, large-scale community patterns such as those typical in onshore-offshore gradients (Olszewski and Patzkowski, 2001) can be attained through limited faunal lists, but details into community dynamics beyond this large-scale pattern can only be gained through finer-scaled investigation. Use of all fossil data may define other patterns and

causes, such as organisms that mediate and change environments and interactions between organisms.

Definition of Community

The definition of community is seemingly almost as diverse as the number of papers on the subject. Communities are rarely discreet entities; they are spatially and temporally gradational, and boundaries are arbitrarily placed by researchers (e. g., Johnson, 1972; Bennington and Bambach, 1996). A community can range from an assemblage of organisms within one taxon – for example, the brachiopod or crinoid community – to encompassing the entire flora and fauna of the study in question. Likewise, community can also mean the macrofaunal or microfaunal assemblage, depending again on the nature of the study. Therefore, community must be defined within the scope of the research being presented.

In deep-time paleontology, the definition of community and associated words, such as megacommunity or community type, usually revolves around the notion of recurrence. Although DiMichele (1994) defined communities simply as multispecies assemblages, other community definitions (e. g., Hickey and Younker, 1981; Raup and Stanley, 1978; Rollins et al., 1979) contained an emphasis on recurrence. Bennington and Bambach (1996) expanded the idea of community recurrence with regard to the investigation of coordinated stasis. In their use, communities referred to individual samples and recur only if they were statistically indistinguishable; community types, conversely, recurred if the samples are statistically distinct but otherwise similar.

In this study, "community" simply refers to the fossilized remains (including animals, plants, and traces) of the original live community. Because of the temporal nature of the fossil record, community constituents need not be directly contemporaneous. Fine-scale environmental and biotic perturbations, such as storm

events and annual differences in recruitment, are usually lost to time-averaging; therefore, fossilized individuals may have been closely spaced in time, although not necessarily contemporaneous. Additionally, community refers to both the single community and the recurring community, based on analytical results, at fine scales. Groupings of similar communities into larger scale patterns will be referred to as community types, and indicate collections of fossils that are essentially similar but of variable taxonomic and abundance composition.

Classic extremist models of Gleasonian (communities as a superorganism; Gleason, 1929) and Clementsian (communities comprised of independently responding organisms; Clements, 1926) communities have led to investigations into the degree of organism interaction versus environmental controls on species assemblages. Although the extremist views stress biotic or environmental controls, it is entirely possible to have both paleoenvironment and species interactions influencing the same fossil community. In his crinoid study, Holterhoff (1996) emphasized the importance of scale on these two community controls: at local scales and individual samples, interactions were important in shaping community structure. At a larger, regional scale, environmental processes influencing recruitment and the species pool were dominant; processes acting at the local community scale were lost in the overall pattern of community recurrence. DiMichele (1994) and Peters and Bork (1999) noted individualistic responses of species to environment on short time scales, but strong, more tightly integrated organizational patterns of recurring communities were apparent on longer time scales. It is this long-time-scale pattern of community recurrence that led to the highly debated idea of coordinated stasis of Brett and Baird (1995) and whether or not communities recur in tight associations at fine taxonomic scales and similar relative abundances (Bennington and Bambach, 1996; Bonuso et al., 2002).

Overall, much attention has been paid to environmental mediation of community recurrence. Most deep-time paleocommunity studies, whether accomplished using all data or limited assemblages of taxa, result in environmental

justification of recurrence patterns. For example, in the brachiopod and bivalve comparisons of Olszewski and Patzkowski (2001), oxygenation and onshore-offshore gradients were interpreted to be the environmental factors that determined brachiopod- or bivalve-dominated communities. As an example of a study using more inclusive taxa, Webber (2002) investigated the causes behind cyclicity in Ordovician faunal patterns of the type Cincinnatian Series. In this case, environmental change was assumed *a priori* to cause community change as well as lithologic cyclicity; his results indicated that, rather than eustacy, faunal changes through the section were more likely the result of storm events.

In all scales of community work, and whether the question is environment- or biotic interaction-driven, the researcher must remember that communities, at the finest scale, contain individuals from different and usually disparate taxa. These individuals must be recruited, interact with other individuals whether directly (i.e., host substrate for epibionts) or indirectly (i.e., predator choice of a neighbor), respond to environmental perturbations, and die to be preserved as part of the fossil community or lost to consumption, decay, and dissolution. These processes, as pointed out by Holterhoff (1996), are important in local communities. When using all fossil data collected at fine scales, local community processes may provide deeper insight into community structure and the processes controlling recurrence.

The boundaries and limits for community recurrence also must be defined. Boucot (1981) used dominant taxa to define community recurrence. This can be limiting in the sense that highly abundant taxa may be dominant in different communities, with the remaining community compositions very distinct (such as phylloid algae-dominated communities in this study). Brett and Baird (1995) used set percentages of holdover and carryover taxa to define recurrence. This method of recurrence recognition assigns a minimum relative abundance for each taxon; if that number is met, the community recurs. This method arbitrarily places boundaries on community recurrence, regardless of variations in the live assemblage or in taphonomy and preservation. For example, in this study, one recurring community

is characterized by abundant fenestellids, but samples from the shale above Brownwood limestone 2 fall within this category except that they contain abundant *Neochonetes*, a brachiopod not present or rare in other samples. The presence of thin-shelled, abundant *Neochonetes* may result from preservational differences, may have had high recruitment success, or may have experienced optimal conditions in the live community. However, the remainder of the faunal list is very similar to those of other fenestellid-rich shale samples, placing it in the fenestellid-dominated recurring community, regardless of high numerical abundances of *Neochonetes*. As noted above, Bennington and Bambach (1996) used statistical tests to determine recurrence between samples for coordinated stasis; however, this is limited to very fine scales, and also sets strict boundaries for community recurrences, regardless of variations in taphonomy or species recruitment. Conversely, using their definition, community type would then be defined as recurrence at any scale, from several very similar samples along one bedding plane to large-scale, unit or locality-based assemblages recurring in several basins through long time periods.

Recurrence in this study is recognized after analysis; samples or units that are closely associated in cluster, ordination, and correlation at the given scale of analysis (samples versus units or localities) are considered to recur. Although this method does not place a numerical limit on recurrence, it allows for variability between samples in a highly detailed dataset. In this sense, communities recur when taxon lists, dominance patterns, and relative abundances generally agree.

Rahel (1990) showed that recurrence is, in part, biased by the sampling method used. If recurrence is based on absolute abundances, then recurring communities are rarely seen because of variability between samples. Conversely, if presence-absence data are used, communities tend to recur more readily because abundance variability is obscured. In this study, presence/absence and relative abundance data are used together to define recurrence as well as to check for fidelity of relative abundance-based analyses. Because most analyses were performed using

both relative abundance and presence/absence of taxa, a stronger argument for community recurrence can be made when both methods of data analysis agree.

This study investigates three phenomena: community recurrence upsection in one outcrop compared to recurrence between outcrops at variable distances; the use of whole faunal analysis versus brachiopod- or bryozoa-dominated analysis; and the impact of scale on interpretations of community recurrence.

GEOLOGY AND BACKGROUND

The strikingly cyclic nature of Carboniferous rocks have been long realized; Moore (1931) described alternating limestone-shale sequences in Middle and Upper Pennsylvanian strata of Midcontinent outcrops, long after the repetitive nature of Carboniferous strata from the United Kingdom was realized by William Smith in the nineteenth century (see Winchester, 2001). Wanless and Weller (1932) proposed the word cyclothem for repeating sequences of rock types in the Illinois Basin. Shortly thereafter, this term was applied ton other Midcontinent strata (Moore, 1936).

Early work by Weller (1930) attributed the alternating packages of limestones and shales to periodic tectonism. Wanless and Shepherd (1936) instead suggested that changes in global eustacy, caused by the waxing and waning of Gondwanan ice sheets, controlled the apparent cyclicity in Midwestern rocks. However, the investigation into autocyclicity of Midcontinent rocks did not cease. In some studies, shifting deltaic sedimentation was considered to be the primary, or occasionally sole, reason for cyclic Carboniferous sediments and was applied to Appalachian (Ferm, 1970), Texas (Galloway and Brown, 1973), and Illinois (Merrill, 1975) rocks.

Heckel (1977, 1980) examined the allocyclicity of Carboniferous rocks of the Midwest in great detail and restated the idea of marine transgressive-regressive

sequences in regard to glacial eustacy. He proposed a model for a typical Kansas cyclothem, consisting of:

1) middle (offshore, transgressive) limestone, which was thinly bedded, skeletal in nature, and dense;

2) core (offshore, maximum flooding) shale, a gray to black, phosphatic, dysoxic to anoxic, sediment-starved facies that contained a characteristic conodont fauna and occasionally dysaerobic-adapted macrofauna of specific crinoids and brachiopod taxa;

3) upper (regressive) limestone, usually thick, skeletal, and shallowing upwards, often including ooid shoal, lagoonal, and peritidal carbonates and occasional subaerial exposure at the top; and

4) outside (nearshore) shale, a gray-green shale or red paleosol, usually sandy and sparsely fossiliferous, with occasional coals overlying these.

Conodont faunas were stratigraphically and regionally used to characterize nearshore and offshore facies in Carboniferous rocks (Heckel and Baesemann, 1975; Swade, 1985). Boardman and others (1984) complimented these conodont studies with a macrofaunal model for onshore-offshore facies, and included a nearshore, eurytrophic molluscan fauna, followed by a diverse, stenotrophic crinoid, brachiopod, coral, and fusulinid fauna, and finally followed by an offshore gastropod, bivalve, ammonite, and conulariid fauna.

Discrepancies in the Kansas cyclothem model were explained by Heckel (1989) as five possible divergences from modeled facies preservation:

1) marine inundation too fast, resulting in the lack of a transgressive limestone (equivalent to the Illinois cyclothem);

2) sea level rise not of significant magnitude to form the core shale;

3) regression too fast for upper limestone to form;

4) sea level drop not far enough to form a complete regressive sequence; and

5) regression occurred during a time of overwhelming siliciclastic influx, resulting in decrease or loss of carbonate facies.

The fifth discrepancy, overwhelming siliciclastic influx, was used to describe the problematic cyclic sedimentation in north-central Texas (Boardman and Heckel, 1989; Heckel, 1989). Although repetitive limestone- or shale-dominant formations can be observed the Strawn, Canyon, and Cisco Groups, the more clearly defined (albeit debatable) nature of Kansas or Illinois cyclothems is difficult to discern in rocks of north-central Texas. This is, in part, caused by the differences between basins, outcrops, and paleogeography of Texas and Kansas.

Outcrops in north-central Texas occur on a shallow, narrow shelf of the Midland Basin, contrary to the extensive shelf north of the Arkoma-Anadarko basin of central Oklahoma. Moreover, Texas outcrops occur in narrow, parallel-to-shore bands, with younger units to the west and older unites to the east. This has made shoreward and basinward facies migration based on surface stratigraphy difficult to see; instead, surficial facies repetition is assumed from lithology (Heckel, 1984) and fossil content (Boardman et al., 1984; Boardman and Heckel, 1989), as well as an underlying assumption that cyclicity should be similar to Midcontinent strata. Paleosol repetition was recognized and deemed cyclic by Harrison (1973), and based on isotopic data, exposure surfaces on Texas limestones were also ascribed to cyclicity (Brown, 1982). Onshore-offshore trends of fossil assemblage zones were utilized by Boardman et al. (1984) to recognize cyclicity in outcrops where lateral surface observations were impossible.

Subsurface analyses provide only slightly more distinct patterns of repetition in Pennsylvanian stratigraphy of north-central Texas. Brown (1969) demonstrated several repetitive sequences in north-central Texas Virgilian and Wolfcampian formations, but attributed the apparent cyclicity to shifting deltaic input on a slowly subsiding shelf, resulting in complex regional stratigraphy. Cleaves and Erxleben (1982) examined older Desmoinsian and Missourian subsurface stratigraphy in the Brazos River Valley and determined that cyclicity in the area was highly influenced by deltaic sequences. Missourian cyclicity was least apparent in Brazos River Valley non-deltaic sequences because a double-bank system including a massive,

outer bank on the subsiding hinge line of the shelf and a smaller inner bank closer to shore.

In subsurface and outcropping Texas rocks, cyclicity at the level of Kansas and Illinois cyclothems is lacking. This is caused mainly by high amounts of siliciclastic input from the Ouachita orogenic belt in the form of delta shifting and fluctuating amounts of terrigenous sedimentation onto an easily overwhelmed narrow shelf. Galloway and Brown (1973) demonstrated the importance of deltas and terrigenous sediment in Pennsylvanian facies of north-central Texas, and although they did not disclaim any possibility of glacial eustatic control, any global sea-level change would have been overprinted by deltaic influence. Boardman and others (1984) and Boardman and Heckel (1989) acknowledged the increased delta input into north-central Texas facies as an explanation for the modification of Texas cyclothems via Heckel's fifth cyclothem discrepancy, the overprinting of cycles by high siliciclastic input.

Core shales were recognized by Boardman et al. (1984) and Boardman and Heckel (1989) based on conodont and other fossil biostratigraphy as well as the presence of phosphatic nodules. In discordance with Kansas core shales, Texas dark-shale fossils were more readily preserved, a fact mainly attributed by Heckel and others to the high amounts of sedimentation. Molineux (1997), however, pointed out the proximity of these dark shales to overlying and underlying obviously nearshore facies, including algal limestones. Although such enigmas were previously attributed to rapid sea level rise or fall and the lack of intervening facies (Boardman and Heckel, 1989, and references therein), Molineux used isotopic, fossil, and plant data to show that such dark shales were not deep-water facies. Instead of the drastic sea level drop required of Heckel's (1989) Kansas cyclothem model, Molineux proposed that eustatic falls were not on the order of magnitude as those in Kansas, and suggested that sea-level oscillations occurred during dark shale deposition. This idea plus the repetition of sizable paleosols and frequent exposure surfaces noted by Harrison (1973) and Brown (1982) would be in accord with the

nature of the Midland Basin shelf; not only was it a narrow shelf, but also relatively shallow during Missourian and later stages. Any high-magnitude sea-level fall could result in off-shelf shoreline migration.

As stated in previous studies (i.e., Holterhoff, 1996), highly cyclic Carboniferous facies are ideal settings for community recurrence study. Additionally, such rocks are highly conducive to investigating different scales of repetition of fossil assemblages.

This Study

Most samples were taken from the Winchell Formation of the Missourian Canyon Group at the Lake Brownwood Spillway near Brownwood, north-central Texas. Other samples, from two other Texas Winchell Formation localities and from the Farley Member of the Wyandotte Limestone (Missourian, Kansas City Group), Merriam, Hickory Creek, and Spring Hill Members of the Plattsburg Limestone (Missourian, Lansing Group) and the Plattsmouth Member of the Oread Limestone (Virgilian, Shawnee Group) near Kansas City, Kansas, were used as additional data for comparison to the Brownwood locality and for investigation into spatial patterns of community recurrence (Figure 3.1).

The Winchell Formation is a limestone-dominated formation of the Canyon Group, occurring in the Upper Pennsylvanian Missourian Stage in north-central Texas. Based on conodont biostratigraphy and global sea level curves, Heckel correlated the Winchell to the Wyandotte, Plattsburg, and Stanton Formations in Kansas (Heckel, 1986; Boardman and Heckel, 1989). The Winchell Formation is characterized by carbonates with intervening shale beds, bounded below by the Wolf Mountain Shale (Brazos River Valley) and Cedarton Shale (Colorado River Valley) and above by the Placid Shale.

The Winchell Formation crops out along a northeast-southwest trending belt in north-central Texas. The Callahan Divide, a Cretaceous cover separating the northern Brazos River Valley from the southern Colorado River Valley in the outcrop belt, made early correlations somewhat difficult. Outcrops in the Brazos River Valley are primarily comprised of two parallel phylloid algal banks, whereas Colorado River Valley outcrops contain several extensive, often phylloid algal limestones separated by shales. The northernmost extent of the Winchell Formation is truncated by the Perrin Delta system, whereas the southernmost Winchell Formation limestones thin out near the central Texas Llano Uplift. Siliciclastic sediments are most common near the Perrin Delta and in the northern part of the Colorado River Valley (Roepke, 1970; Cleaves and Erxleben, 1982).

The Winchell Formation at the Lake Brownwood Spillway (referred to as Brownwood in the text or B in samples and analyses) in the Colorado River Valley contains six distinct and easily recognizable limestones separated by shales and paleosols (Table 3.1; Figure 3.2). The entire Winchell Formation is exposed in the Spillway, including the top several meters of the Cedarton Shale below the Winchell Formation. None of the limestone and shale units are officially named; here the limestones are informally designated in stratigraphic order from bottom to top (limestone (LS) 1) and shales are defined by their nature (black shale (blk)) or by their position in the section (i.e., Brownwood shale 1/2 (Bsh12) refers to the shale between LS1 and LS2; shLS2 refers to the shale directly on top of LS2). Coquinas are treated similarly and are named for the shale where they occur (i.e., coq1/2 or Bcoq12).

To the south of the Lake Brownwood Spillway within the Colorado River Valley, locality RP1 (RP or R; Roepke, 1970) contains two lowermost limestones and one shale of the Winchell Formation. Both limestones are phylloid algal, with the lower limestone containing a less diverse fauna and being less argillaceous than the upper limestone. Repeated visits and surface scouring of the outcrop has determined that the intervening shale is unfossiliferous.

An outcrop near Perrin, TX (Perrin or P) in the Brazos River Valley is a northern outcrop of the Winchell Formation (Figure 3.3). This outcrop is a phylloid algal bank that was heavily influenced by siliciclastics from the Perrin Delta. Most of the limestones are argillaceous and separated by shales varying from less than one cm to over 10 cm thick. Most of the section is fossiliferous, but phylloid algae and crinoids increase upsection as diversity decreases (Schneider, 2001b).

Kansas outcrops were collected by Lindsey Leighton and Peter Kaplan as part of a joint Kansas – Texas research project by Leighton, Kaplan, and Schneider. Care was taken to maintain the same sampling techniques as those used at the Brownwood localities. All outcrops occur in or near Kansas City, Kansas, and are part of the Missourian Lansing and Kansas City Groups, and in one case, from the Virgilian Shawnee Group. The Merriam Limestone, Hickory Creek Shale, and Spring Hill Limestone members of the Plattsburg Limestone of the Lansing Group and the Farley Limestone Member of the underlying Wyandotte Limestone of the Kansas City Group were sampled for fossils at the I-435 and I-70 cloverleaf in Kansas City (Figure 3.4). Samples from the Plattsmouth Limestone Member of the Oread Limestone of the Shawnee Group were taken from an inactive quarry near Waverly, Kansas, northeast of the intersection of I-35 and County-31 (Figure 3.5).

According to bio- and lithostratigraphy of Boardman and Heckel (1989), the Wyandotte Limestone is correlated to the middle Winchell intermediate cyclothem and the Plattsburg Limestone to the upper Winchell major cyclothem; the Oread Limestone is correlated to the Virgilian Finis Shale, significantly upsection from the Winchell Formation. Boardman and Heckel (1989) separated the Winchell into three cyclothems in the Brazos River Valley based on three separate limestone units, defining minor-intermediate-major cyclothems based on areal extent of each unit. No attempt was made to incorporate the more extensive Colorado River Valley outcrops because of significantly less work done in that area. However, assessment of their correlations is beyond the scope of this paper, and for the purposes of this study, and they are assumed valid.

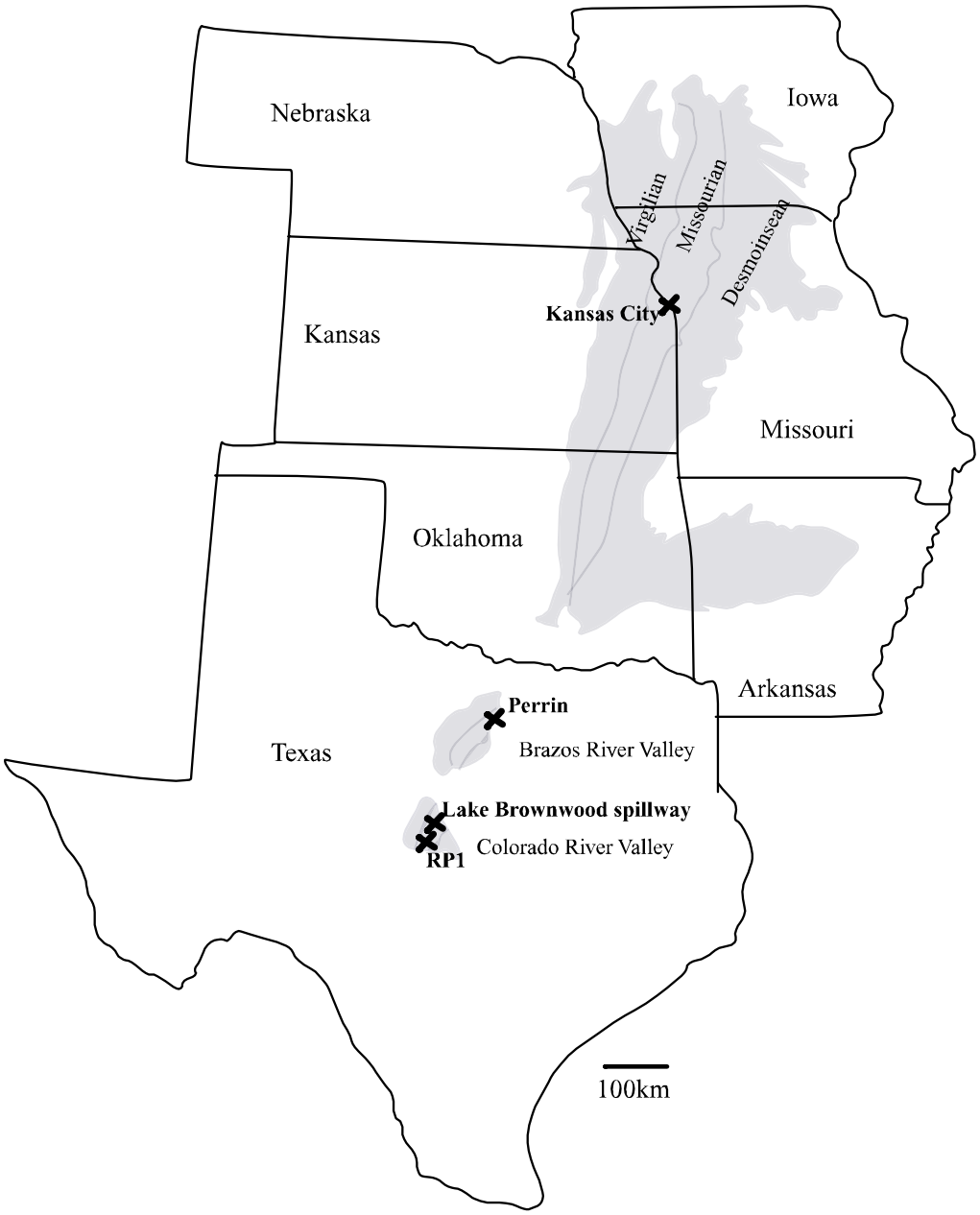
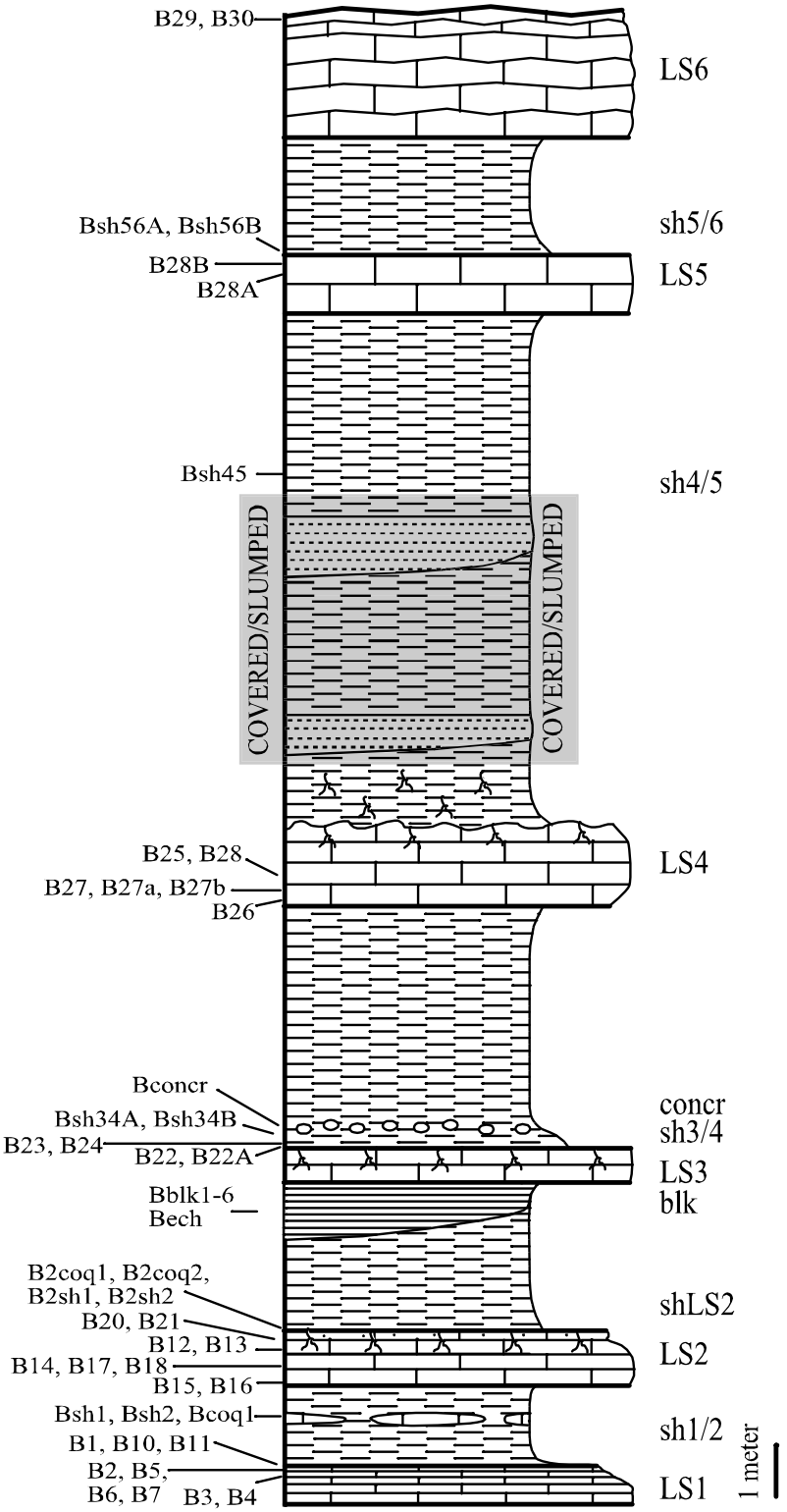


Figure 3.1. Map of Texas and Midwestern United States Pennsylvanian outcrop belts (shaded) and localities (noted with an X) used in this study. Modified from Boardman and Heckel, 1989.

	Thickness(m)	Hand sample	Thin Section
LS6	2.0	Fine-grained, medium-gray, wavy-bedded algal wackestone	Micritic wackestone, with rare brachiopod and crinoid debris. Phylloid blades replaced by blocky cement and occasional geopetals
Sh 5/6	2.0	Brown shale with carbonate nodules, highly fossiliferous in a horizon above LS5.	
LS5	0.8	Dark brown-gray massive packstone to grainstone with few whole fossils	Grainstone with some mud between abraded, mostly echinoderm and fusulinid debris
Sh 4/5	10.5	Medium gray, fossiliferous in one horizon, fluvial sandstones	
LS4	1.5	Brown-gray with hematite partings, fine-grained massive wackestone. Top surface is highly karsted	Micritic wackestone with blocky spar in fractures. Top surface porous grainstone with 10% quartz, fossils abraded and some micritized
Con Sh 3/4	4.5	Medium gray unfossiliferous shale except for concretions and fossil layer at bottom	
LS3	0.6	Red-brown, massive, pack- to grainstone	Abraded, occasionally micritized fossil grains with <20 micrite
Blk	0.5-1.5	Black, silty shale with abundant plant debris and coquina horizons	
LS sh2	1.5	Gray shale with discontinuous coquina and fossil horizons	
LS2	1.0	Massive, argillaceous, gray to light green wacke- to packstone, beds thin towards top	Wacke to packestone, with increasing mud upsection
Sh 1/2	1.8	Gray shale with thin, fossiliferous horizons and thin, discontinuous coquinas.	
LS1	0.3-0.8	Argillaceous, gray wacke- to packstone, beds thin and become more argillaceous upwards	Wacke to packestone, with increasing mud upsection

Table 3.1. Lithology of Brownwood units in hand sample and thin section.

Figure 3.2


B29, B30
LS6
Bsh56A, Bsh56B
sh5/6
B28B
B28A
LS5
Bsh45
sh4/5
COVERED/SLUMPED
COVERED/SLUMPED
B25, B28
B27, B27a, B27b
B26
LS4
Bconcr
Bsh34A, Bsh34B
B23, B24
B22, B22A
concr
sh3/4
LS3
Bblk1-6
Bech
blk
B2coq1, B2coq2,
B2sh1, B2sh2
B20, B21
B12, B13
B14, B17, B18
B15, B16
shLS2
LS2
Bsh1, Bsh2, Bcoq1
B1, B10, B11
B2, B5,
B6, B7
B3, B4
sh1/2
LS1
1 meter

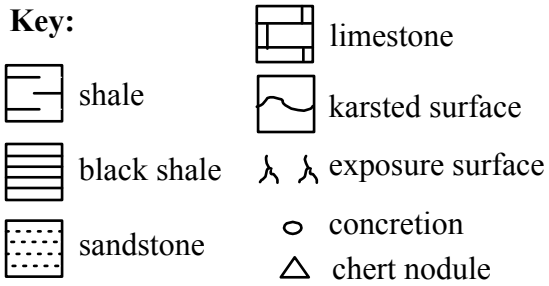


Figure 3.2. Outcrop from the Lake Brownwood Spillway locality of the Winchell Formation near Brownwood, Texas. Sample locations in the section are noted on the left margin of the section; abbreviations for informal unit names used in this study are to the right of the column. Covered part of section reconstructed from Warme and Olson, 1971.

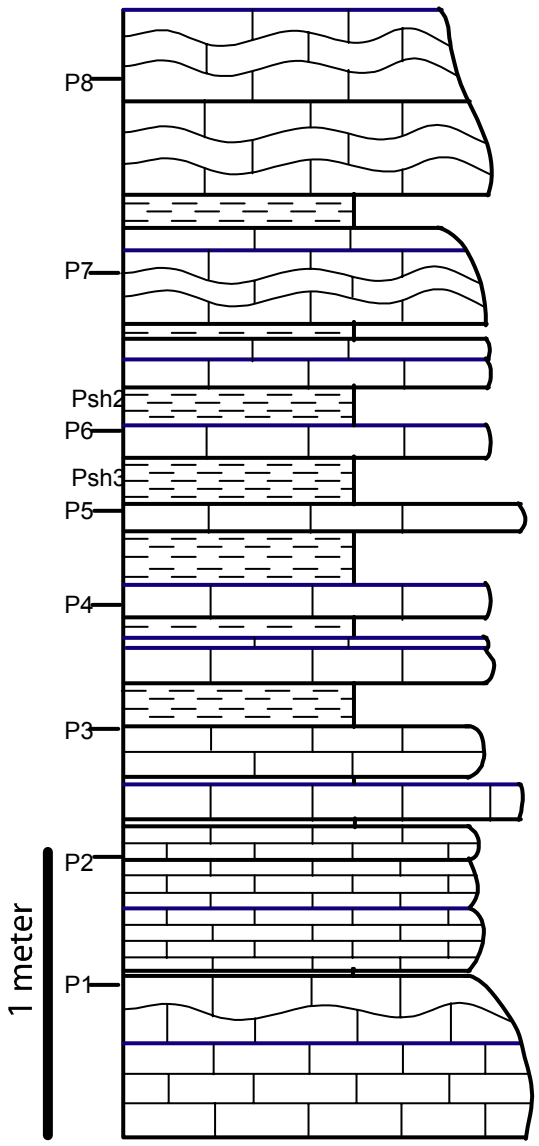


Figure 3.3. Outcrop of the Winchell Formation near Perrin, Texas. See key in figure 3.2. Samples are indicated on the left.

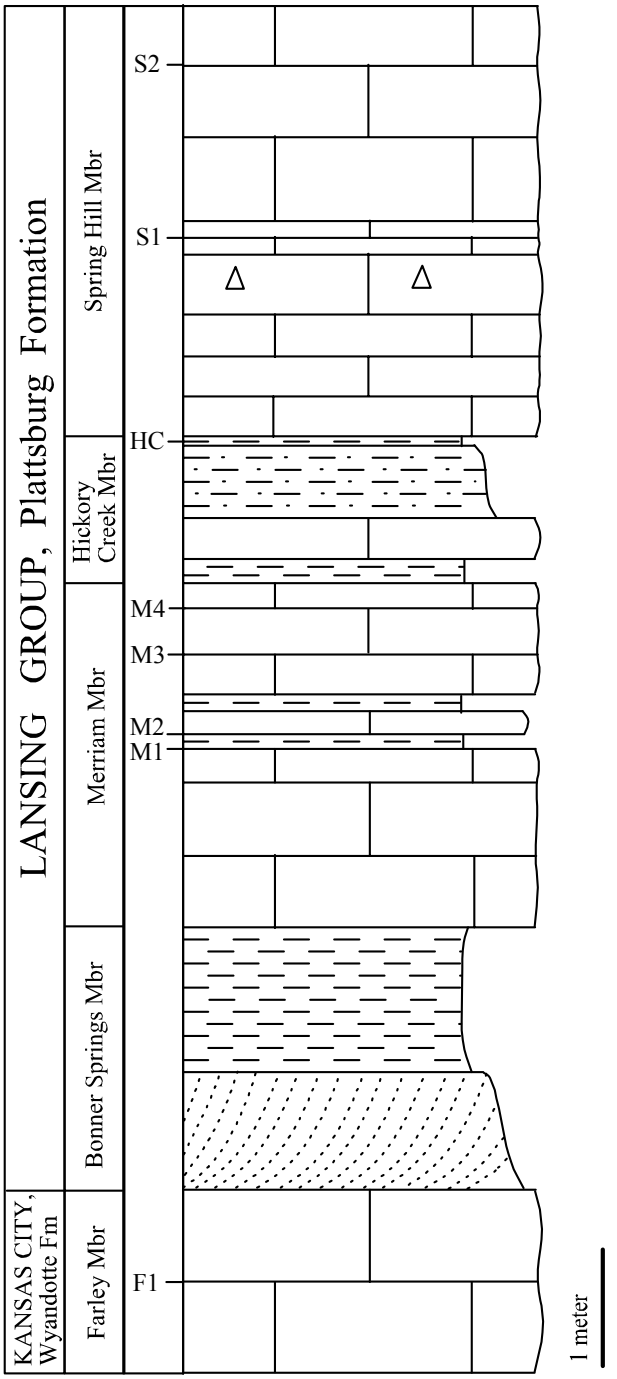


Figure 3.4. Outcrop of the I-435 cloverleaf in Kansas City. Sampled horizons are noted on the left. See key in figure 3.2.

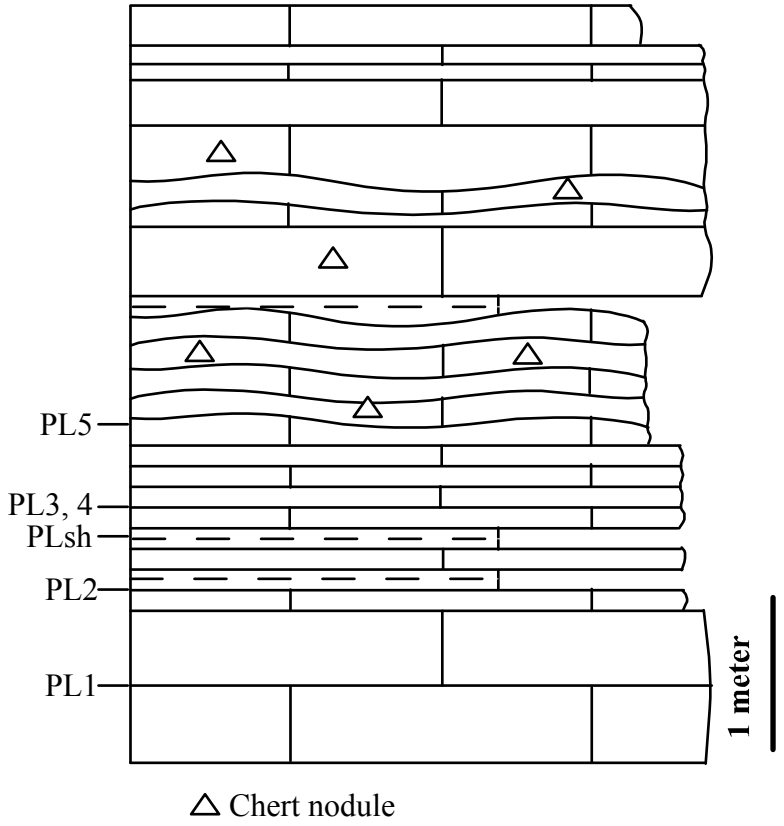


Figure 3.5. Outcrop showing stratigraphic location of Plattsmouth samples from the Waverly Quarry, southwest of Kansas City. See key in figure 3.2. Sample locations are indicated on the left.

TAPHONOMY

Fossil preservation in the outcrops used in this study was often good to excellent. In the Brownwood Spillway locality, all limestones except 3 and 5 contained complete, although often crushed, articulated brachiopods; fragments were much less common than whole specimens. Limestone 6 specimens usually occurred in cross-section on a weathered surface. Whole echinoid spines and crinoid pleuricolumnals represented disarticulated taxa, and fenestellid colonies often occurred as large fragments. In limestone 4, echinoid plates and spines displayed a slightly higher degree of articulation than other limestones, often with several plates and spines in close association. These taphofacies, according to Brett and Baird (1986), indicate low to moderate energy coupled with intermediate sedimentation rates.

Limestones 3 and 5 had a much higher degree of fossil fragmentation, with a higher proportion of small brachiopod fragments and isolated elements from disarticulated specimens, such as crinoid columnals. Echinoid spines, when present, were much more poorly preserved in these limestones, often showing signs of abrasion and breakage. Both of these limestones are interpreted as fairly high-energy environments, which agrees with Brett and Baird's (1986) taphofacies model.

Fenestellid-rich shales (sh1/2, shLS2, sh3/4) contained fairly well-preserved specimens. Brachiopods were often crushed, although rarely disarticulated. Fenestellid colonies increased in completeness upsection at Brownwood, with best preservation in sh3/4. Also in this shale, brachiopods were the least crushed, indicating significantly less compaction.

Communities in the black shale– those in the echinoid Lagerstätte and the packstones – contained the extremes of preservation. The echinoid community

contained nearly articulated echinoderm specimens; the only disruption of articulation occurred with decay after burial as plates collapsed inwards. Brachiopod and fenestellid epibionts remain attached to echinoid spines, and productid brachiopods – *Parajuresania* and *Linoproductus* – retain complete, although occasionally slightly crushed, spines. Black shale packstones, conversely, contained few complete specimens or multi-element pleuricolumnals; most specimens are fragments of complete brachiopods and pectens. The only fossils occurring as complete specimens in communities preserved in the black shale packstones are occasional whole *Punctospirifer* valves and small *Acanthopecten* valves. Although *Parapostibulla* edrioasteroids and *Lophophyllidium* rugose corals were noted in float, none occurred in packstone slabs used in this study.

In concretions from Brownwood shale 3/4, the bivalve-rich community is well preserved with many articulated specimens either closed shut or preserved agape in reddish concretions. In some cases, shell material is preserved on *Myalina* and *Acanthopecten* specimens. *Parajuresania* brachiopods do not contain spines, but spine bases are well preserved. Although not seen in this study, previous collecting resulted in rare conulariids in concretions, all of which were complete specimens. Fenestellid colonies appear to be unfragmented, so far as the individual concretions preserved them.

Brownwood shale 4/5 contained significant amounts of bioerosion and bryozoan encrustation on the shell material. Almost all bivalved animals were represented by disarticulated and/or fragmented skeletal elements, with some of the more robust taxa such as *Myalina* and *Derbyia* containing multiple barnacle borings and encrusting tubuliporate bryozoans. The community in Brownwood shale 4/5 is not interpreted as living in a necessarily high energy environment; rather the nature of fragmentation, frequent borings, and patchy but frequent encrustation suggests much time spent in the taphonomically active zone and/or above the sediment/water interface.

Brownwood shale 5/6 is noted for its abundant *Neospirifer texana*, a very distinctive but readily disarticulated brachiopod. Other brachiopods, including small marginiferiformes, *Punctospirifer,* and *Crurithyris*, are also disarticulated and often crushed. Productids in general tend to be represented by fragments, often with the cardinal process and associated muscle scars as the best preserved part of the brachiopod. Encrustation by tubuliporate bryozoans is uncommon and rarely covers the entire organism. All gastropod and cephalopod material is represented by steinkerns, many of which are incomplete and/or crushed.

Perrin fossils, for the most part, show a higher degree of fragmentation in the limestones than at Brownwood, but are highly variable. Lower and middle Perrin samples tend to contain whole or nearly whole brachiopod valves and occasional whole specimens. Pleuricolumnals are frequent, and one mostly articulated crinoid was recovered from an unsampled horizon. Upsection, in the topmost two samples, specimens are mainly fragments of phylloid algae and single columnals, indicating a higher energy environment than downsection. However, shales contain multiple and sometimes long pleuricolumnals as well as occasional basal circlets from crinoids.

Fossils at RP1 were mostly represented by fragments of phylloid algae and fusulinids, but pleuricolumnals and whole brachiopod valves are also common. The lower of the two limestones at this locality, RP limestone1, contains whole, uncrushed *Composita* that occasionally can be seen in cross section or weathering slightly out of the outcrop. Upsection, limestone 2 contains a more diverse assemblage, but specimens appear to be slightly more crushed and disarticulated than those in the lower limestone.

In Kansas, most Farley fossils are whole, with brachiopods retaining both valves. Good preservation of fossil material continues upsection into the Merriam Limestone, where large productids are complete but lack spines. Spine bases on these brachiopods are well preserved, as is the shell material. In some cases, crushing is minimal, and even large productids are preserved three-dimensionally.

Hickory Creek shales also contain well-preserved material, with either articulated small brachiopods or single valves. Oddly, *Crurithyris* brachiopods, when disarticulated, often split vertically down the middle of the valve, resulting in a collection of left and right sides of valves. In the Plattsburg Limestone, Spring Hill fossils contain a fair amount of spar. The Plattsmouth Limestone of the Oread Formation contains many whole fossil brachiopods with abundant echinoid and trilobite fragments. Some secondary spar is present.

METHODS

Samples were chosen from limestone surfaces and shale beds based on fossil presence. Readily accessible fossiliferous limestone beds were sampled in the field and fossiliferous shales were bulk-collected and screened. Occasional shale samples were also taken from other, seemingly non-fossiliferous shales and screened to be certain that macrofossils were absent. Only macrofossils seen with a 10X hand lens and larger were sampled. Terrestrial plant fossils, although used in paleoenvironmental reconstructions, were not considered in marine community analyses. In most cases, taxa were identified to genus level, because most genera were monospecific. Only in one non-monospecific genus, *Neospirifer*, were taxa identified to species level. Trilobites, sharks, and crinoids were recorded as such because of difficulties with identifying disarticulated taxa on limestone surfaces in the field.

Limestones were point-counted on the outcrop surface in grids or transects of 2 and 5 cm, as judged appropriate for the size of the fossils and available surface of the outcrop. Grid counts were performed for a minimum of 200 points or, when size constrained, for the entire surface exposed. Transects were done on bedding planes where a grid layout was impossible, and the maximum length of surface was counted. Under points of the grid or transect, all material seen in the 10X hand lens was counted, including occasional identifiable fragments. Material, such as whole

brachiopods, pleuricolumnals, and clusters of echinoid spines, that occurred between points were noted during the point count but not included in the final tally of fossils for this study. As often as possible, duplicate samples were taken from elsewhere on the limestone surface to account for spatial variability.

Point-counting in the field was used instead of absolute counts and relative abundance estimates on limestone surfaces to control for the sampling error of fossil miscounts. Wilson (1982) used many point-counted samples in community analyses as proxies for relative abundance in the Pennsylvanian Bird Springs Formation. Watkins (1996) showed that point counts on limestone surfaces in the field approximated biomass. Spatially separate counts, large grids over 200 points, replicate samples, and field comparisons with estimated abundances were used to justify using relative abundances in point-counted samples.

Shales were collected in 2-gallon bags, including duplicate samples where possible, and later screen-washed to isolate fossil material. Although care was taken to not break fragile fossils, such as fenestellid fronds and delicate brachiopods, some fragmentation occurred as a part of the normal screening process. All material was sorted and identified, but only the minimum number of individuals and colonies was considered for analysis. Diagnostic parts of brachiopods, such as cardinal processes, pedicle valves, or right sides of hinge lines were counted. Centimeter-square or -long samples of bryozoans (mostly fenestellids, *Rhombopora,* and encrusting tubuliporates), were weighed to calculate the total square centimeter area or length of each bryozoan taxon. In coquinas and packstones associated with shale units, maximum colony size for each taxon was measured for the total area covered, and these sizes were used to calculate minimum number of colonies for each taxon in the shale. Final tally of minimum number of individuals or colonies from the shales were deemed proportionate to abundances seen in associated coquinas and packstones, and therefore used in comparison to limestone abundances.

All echinoid material was placed in the taxon grouping of echinoids to account for differences between Texas and Kansas samples. In almost all cases,

samples were of *Archaeocidaris* plates and spines, with extremely rare material from lepidocentrid and echinocystid echinoids occurring in Brownwood limestones 3 and 5. Based on spine morphology, *Archaeocidaris* species differ between Brownwood and Perrin; Kansas echinoids are represented by *Archaeocidaris immanus* plates and spines.

Crinoids were the only major taxonomic problem between shale and limestone samples. In limestones, crinoid plates and pleuricolumnals were readily recognizable but identification of distinct taxa was usually difficult or impossible. In bulk-sampled and screened shales, crinoid parts can be sorted into taxa and columnal morphologies, and minimum number of individuals can be determined by counting radials and dividing by 5. Because of these problems, crinoid material is counted as one group in comparisons between limestones and shales. Analyses using relative abundance data were compared to those crinoid-culled and presence-absence analyses to determine whether the different methods of crinoid sampling caused significant discrepancies between limestone and shale samples.

A taxon-sample matrix was set up with 81 samples and 65 taxa. In the case of outcrop RP1, samples were consistently small, and samples from each of the two limestone units were combined into composite samples R1 and R2. For larger-scale comparison, localities also were combined, except in the case of Lake Brownwood Spillway, which was extensively sampled from very different lithologies. The Spillway locality was instead grouped into the respective limestone and shale subunits. When analyses were run using all samples, taxa occurring in fewer than three samples in the entire data set were culled to reduce problems with rare taxa and sampling inconsistencies among the large number of samples (i.e., sponges). All other analyses were run using all occurring taxa.

Sampling differences in limestones and shales are a major problem in analyses, especially in using relative abundance data. To investigate the validity of using both types of data together, analyses were run using both relative abundance and presence/absence data. Rahel (1990) observed the ease of community

recurrence using presence/absence data. In this study, if relative abundance analysis generally agrees with the presence absence data, then relative abundance data is considered valid and the problems encountered in shale and limestone sampling differences are minimal.

Bray-Curtis (polar) ordination in PC-ORD version 4 (McCune and Mefford, 1999) was used to distinguish possible gradients in communities and to ascertain patterns in the samples and units. In Bray-Curtis ordination, the first axis is determined by first selecting endpoints and then using a distance matrix to distribute all other data points relative to the endpoints along one axis. Using variance-regression endpoint selection method (Beals, 1984), the first endpoint is selected because of its greatest variance from all other points; the second point is determined, using linear regression, as the most distant point in the main cloud of data points from the first endpoint (Figure 3.6). Unlike the original Bray-Curtis method, this method of endpoint selection ignores outliers in the dataset (McCune and Mefford, 1999). The second axis is then determined based on the two points of greatest variability that form an orthogonal axis to the first; later axes are similarly determined. This particular Bray-Curtis ordination was chosen because the method looks for the greatest variability between two endmembers, ignores outliers and therefore decreases over-ordinating of the dataset, and can be used for both relative abundance and presence/absence data. However, greatest variability between endpoints does not necessarily mean greatest variability between all points; therefore, other tests, such as correlation, are also used to compare to patterns determined in the ordination plots.

Cluster analyses using PC-ORD Bray-Curtis distance measure (Czekanowski, 1913; Bray and Curtis, 1957) and group average (Unweighted, pair Group/Mathematical Average, or UPGMA) group linkage (Sokal and Michener, 1958) were performed on samples to identify general recurring associations between samples, lithologies, and units/localities. Cluster analysis groups samples or species into a hierarchical dendrogram based on similarities. Bray-Curtis distance measure

allows for heterogeneity between samples and is less sensitive to outliers in the data than other methods. This distance measure only considers those species that are present, as opposed to those that are lacking between two compared samples. The Bray-Curtis equation, which has the form "2W/(A+B)", where W is shared taxa, and A and B are the taxa only in A or only in B. This measure was originally created for presence-absence data, but is also applicable to abundance data; in this study, Relative Sorenson (Bray-Curtis) was used for relative abundance comparisons between samples to account for different sample sizes.

In cluster and ordination analyses, several levels of data inclusiveness were used for sample and unit analyses: all taxa, all taxa minus crinoids, all taxa minus phylloid algae, all taxa minus common taxa (crinoid, echinoid, *Composita*, and *Minilya*) plus phylloid algae, brachiopods only, and bryozoans only. Crinoids were culled in some analyses because of differences between limestone and shale samples. Common taxa and phylloid algae were often the major components of the first three axes, and so were culled to compare adjusted ordinations to all-taxa ordinations, and to distinguish any underlying patterns within the data. Brachiopods and bryozoans were run separately to determine if these larger groups were driving the ordinations and clusters as well as to compare results with community analysis inclusive of all taxa.

Pearson's correlation was performed on relative abundance data only for samples, units, and taxa. Because percentage data is expected to autocorrelate to some extent, a Bonferroni correction was used to adjust significance levels (Leighton, pers. comm.). Additionally, relative abundance data for taxa was graphed to visually examine patterns of covariance and possible environmental, lithologic, and biological causes such as energy, sediment, and degree and type of bafflers.

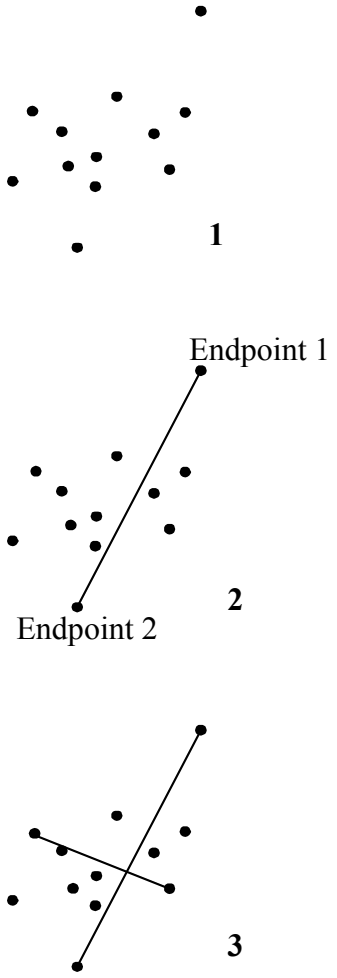


Figure 3.6. Selection of endmembers and axes. (1) Points in n-dimensional space, distances between points determined by variance (demonstrated in 2 dimensions). (2) Axis 1 is set up by choosing endpoint with greatest variance (Endpoint 1) and then finding the point with greatest variance from the original point (Endpoint 2). (3) Axis 2 is determined by the two points with the greatest variance that are orthogonal to the first axes. All subsequent axes in n-dimensional space are similarly chosen and are orthogonal to previous axes.

RESULTS

Cluster and Ordination Analyses

Relative Abundance and Presence-Absence Data

In cluster and ordination analyses, localities and Brownwood units generally tended to group together more strongly than lithologies, except for phylloid-algal limestones. Results from relative abundance data were fairly similar to that of presence-absence data.

In cluster analyses, Brownwood limestones, fenestellid-rich shales, small-brachiopod-rich shales, and some Perrin, Plattsmouth, and Merriam samples clustered in similar manners when using both relative abundance and presence-absence data (Figures 3.7, 3.8). Major differences appeared in arrangement of individual samples, in the splitting of some localities and units, and in phylloidal samples. In presence-absence analysis, phylloidal samples are dispersed throughout the dendrogram, most clustering with other samples from their respective localities, as opposed to the tight cluster in relative abundance analysis. Particularly noticeable is the split of RP samples between Perrin and Brownwood clusters when using presence-absence data; when relative abundance data is used, RP clusters with other phylloid algal samples (including some Perrin samples) and lower Plattsmouth samples.

The three relative-abundance-based clusters of the Brownwood black shale packstones, Brownwood limestones 1(top), 2(top), 3(top), and 4(bottom), and Brownwood limestone 1 and 4, which are primarily driven by *Composita*

abundances, remain clustered in presence/absence analysis but also cluster with fenestellid-rich and Perrin samples. *Composita*, present in nearly every sample, is of lesser importance in determining clusters than in relative abundance analyses, where abundance data of the brachiopod is highly variable. Instead of taxa abundances, presence-absence cluster analysis appears to be affected by diversity.

In presence-absence cluster analysis, more samples are unpaired with other samples at the bottom of the dendrogram. This is in part an effect of the cluster analysis itself; for example, B30 distance matrix indicates a closest similarity to B5. Sample B5 is clustered away from B30 because of lower distance values with other samples in the distance matrix. Dissimilarity between B30 and samples clustered with B5 excludes B30 from the cluster. Additionally, samples that are excluded from clusters are generally of low diversity. Although these samples are similar in their low diversities, they are dissimilar in their taxon lists, and so generally do not cluster.

Bray-Curtis ordination of relative abundance and presence/absence analyses contained limestone-shale patterns (not gradational in siliciclastics or proximity to shoreline; figures 3.9, 3.10). Limestone/shale patterns of each ordination were different, with a left-right pattern on axes 1 and 2 and axes 1 and 3 of relative abundance data and a top-bottom pattern on axes 1 and 2 of presence/absence analysis. Axes 1 and 3 of presence/absence ordination contained a trendline of decreasing siliciclastics with one phylloid limestone sample from Brownwood LS6 as an outlier.

One unusual ternary arrangement of fenestellid-baffled, phylloid algae-baffled, and unbaffled samples occurred in axes 1 and 2 of relative abundance

ordination. This ternary arrangement of samples represents a series of overlapping gradients, indicating the importance of baffling organisms in some samples. Phylloidal samples are mostly isolated in the upper region of the scatterplot, but are gradational with fenestellid-rich samples, which occur on the right side of the scatterplot. Samples that did not contain preserved baffling organisms are located on the left side of the scatterplot, but the gradient between these samples and the phylloidal samples is not as strong as between fenestellid-rich and phylloidal samples, because of decreased proximity between unbaffled and phylloidal samples. Centrally located samples contained variable amounts of fenestellid bryozoans.

Ordination of relative abundance data reflected patterns seen in cluster analyses. Brownwood limestones 1 and 4 were grouped on all three axes, driven by abundant *Composita, Antiquatonia*, and echinoids. Phylloid algae remained a strong group on axes 1 and 2, but were scattered with other limestone samples along axis 3. Presence/absence data cluster and ordination analyses did not agree with each other as well as those of relative abundance data. For example, fenestellid-rich shales, although clustered in the presence-absence dendrogram, are split between several groups in ordination scatterplots.

Grouped samples in relative abundance ordinations were much more tightly aggregated than in that of presence-absence data. Presence-absence samples tended to be distributed as very small aggregations or as individual samples, making large, diffuse groups in all but group 3 of figure 3.10.

Presence-absence data often ordinated on low-diversity endmembers, whereas relative abundance endmembers were often those samples containing high abundances of one common taxon, such as *Composita* or phylloid algae. Those

low-diversity endmembers of presence/absence ordination analyses were isolated and usually unclustered at the bottom of dendrogram in presence/absence cluster analysis. Relative abundance ordination endmembers were not isolated from other samples in cluster analysis, and instead occurred in tight clusters with similar samples, even though they may be somewhat isolated in ordination scatterplots.

Figure 3.7

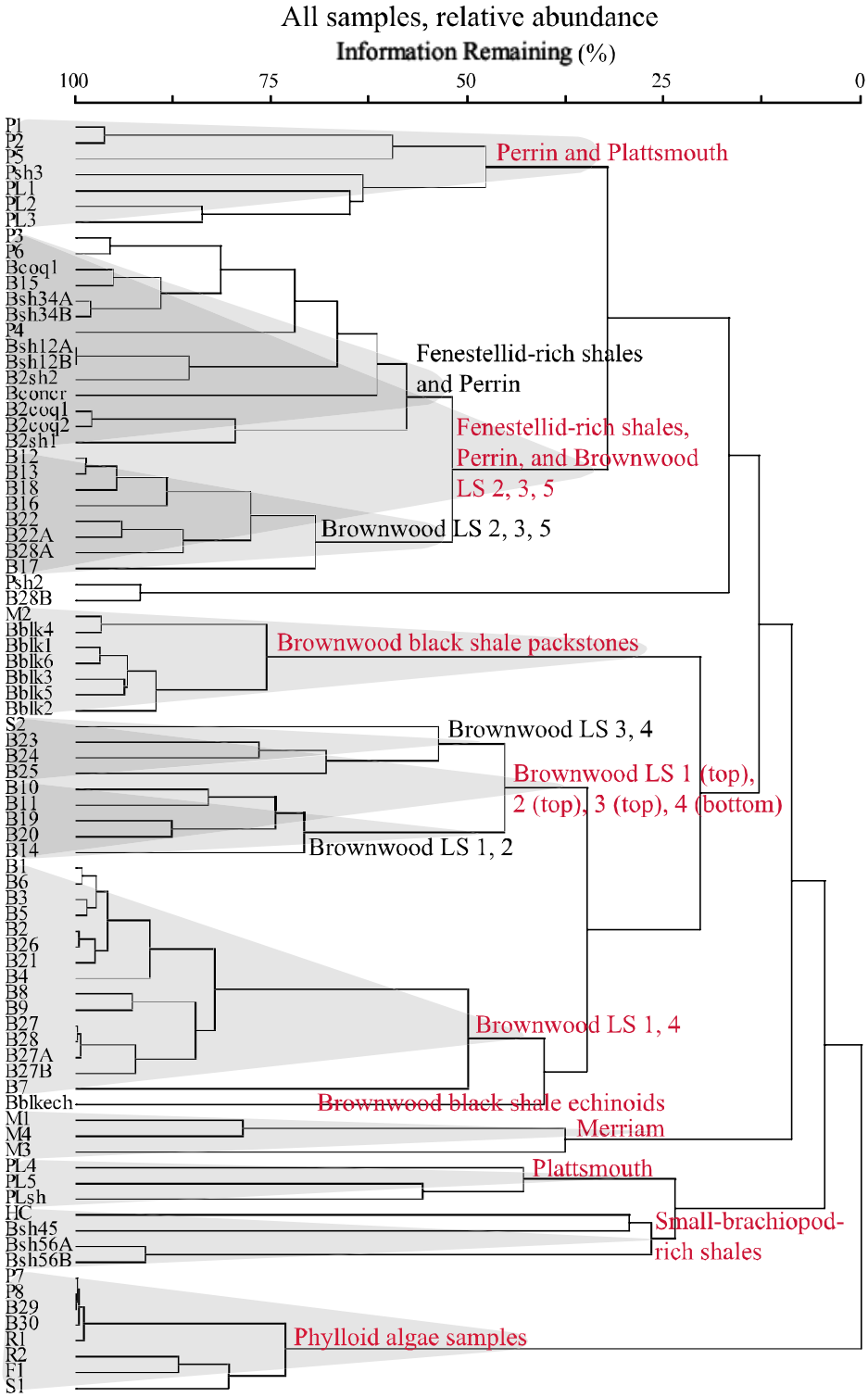

All samples, relative abundance
Information Remaining (%)
100
75
50
25
0
Perrin and Plattsmouth
Fenestellid-rich shales and Perrin
Fenestellid-rich shales, Perrin, and Brownwood LS 2, 3, 5
Brownwood LS 2, 3, 5
Brownwood black shale packstones
Brownwood LS 3, 4
Brownwood LS 1 (top), 2 (top), 3 (top), 4 (bottom)
Brownwood LS 1, 2
Brownwood LS 1, 4
Brownwood black shale echinoids
Merriam
Plattsmouth
Small-brachiopod-rich shales
Phylloid algae samples

Figure 3.7. Cluster analysis of all samples using relative abundance data. Relative Sorenson distance measure and UPGMA linkage were used. Clusters were arbitrarily determined at 50% data remaining and less.

Figure 3.8

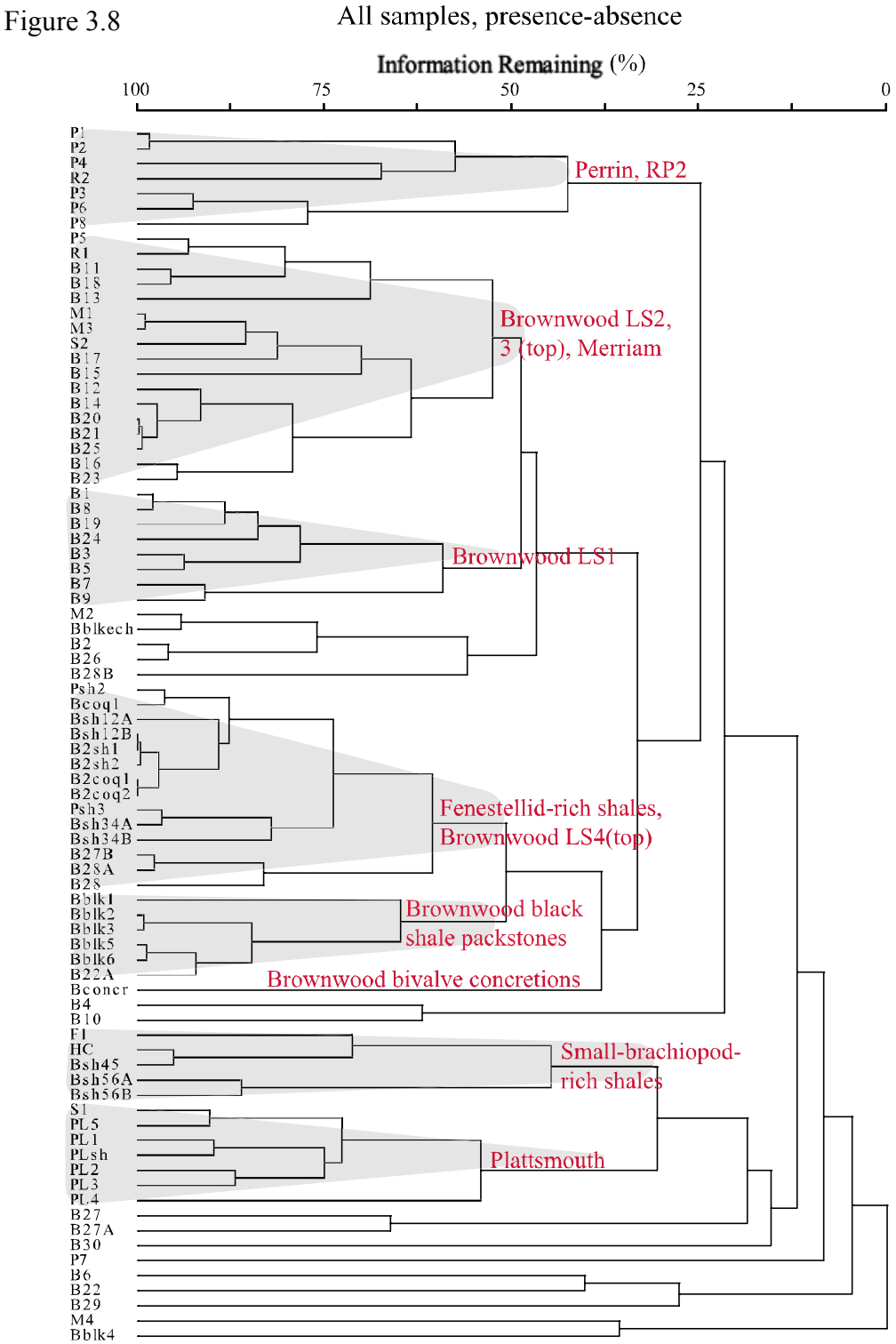

All samples, presence-absence
Information Remaining (%)
100
75
50
25
0
P1
P2
P4
R2
P3
P6
P8
P5
R1
B11
B18
B13
M1
M3
S2
B17
B15
B12
B14
B20
B21
B25
B16
B23
B1
B8
B19
B24
B3
B5
B7
B9
M2
Bblkech
B2
B26
B28B
Psh2
Bcoq1
Bsh12A
Bsh12B
B2sh1
B2sh2
B2coq1
B2coq2
Psh3
Bsh34A
Bsh34B
B27B
B28A
B28
Bblk1
Bblk2
Bblk3
Bblk5
Bblk6
B22A
Bconcr
B4
B10
F1
HC
Bsh45
Bsh56A
Bsh56B
S1
PL5
PL1
PLsh
PL2
PL3
PL4
B27
B27A
B30
P7
B6
B22
B29
M4
Bblk4
Perrin, RP2
Brownwood LS2,
3 (top), Merriam
Brownwood LS1
Fenestellid-rich shales,
Brownwood LS4(top)
Brownwood black
shale packstones
Brownwood bivalve concretions
Small-brachiopod-
rich shales
Plattsmouth

Figure 3.8. Cluster analysis of all samples using presence-absence data. Sorenson distance measure and UPGMA linkage were used. Clusters were arbitrarily determined at 50% data remaining and less. Most samples clustered; those not clustered with larger groups, found at the base of the dendrogram, are samples with low diversity. One cluster of many disparate samples, between the Brownwood LS 1 cluster and the fenestellid-rich shales + Brownwood LS 4 (top) cluster, is unnamed because samples belong to different unit and localities.

Figure 3.9

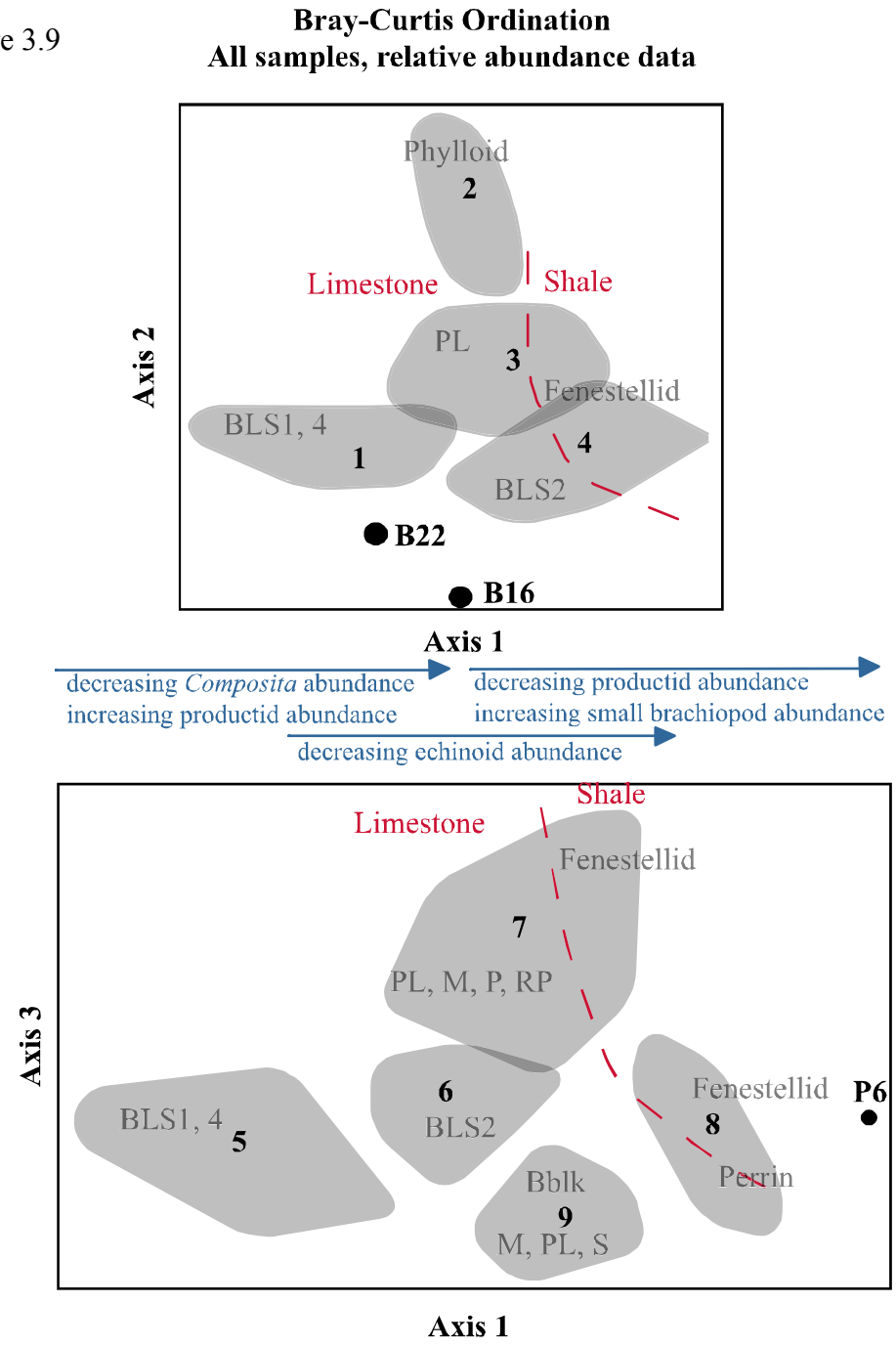

Bray-Curtis Ordination
All samples, relative abundance data
Phylloid
2
Limestone
Shale
PL
3
Fenestellid
BLS1, 4
1
4
BLS2
B22
B16
Axis 2
Axis 1
decreasing Composita abundance
increasing productid abundance
decreasing productid abundance
increasing small brachiopod abundance
decreasing echinoid abundance
Shale
Limestone
Fenestellid
7
PL, M, P, RP
6
BLS2
BLS1, 4
5
Fenestellid
8
P6
Perrin
Bblk
9
M, PL, S
Axis 3
Axis 1

Figure 3.9. Bray-Curtis ordination of all samples, relative abundance data. Axis 1 accounts for 43.6% of the original distance matrix and ordinates on echinoid + *Composita*- or fenestellid-rich samples with endmembers B27 from Brownwood LS4 and P6 from Perrin, producing a general limestone-shale-Perrin pattern plus a non-baffler/baffler pattern. Axis 2 accounts for 27.0% of the distance matrix, with a total of 70.6 of the total distance matrix explained by axes 1 and 2. Axis 2 ordinates on *Minilya*-dominated or phylloid algal samples with endmembers B16 from Brownwood LS2 and B30, a phylloid algal sample from Brownwood LS6, producing a fenestellid-baffled – non-baffled – phylloid algae-baffled pattern along the axis. Axis 3 comprises 15.2% of the remaining distance, with a total of 85.8% of the total distance matrix explained by axes 1 through 3. Axis 3 endmembers are Bblk6 from the Brownwood black shale packstones and Bsh12B, a shale sample between Brownwood LS1 and LS2, and follows a crinoid versus small, non-strophomenid brachiopod pattern. On axes 1 and 2, groups 1, 3, and 4 are densely aggregated; group 2 is not. Group 1 contains samples from Brownwood LS 1 and 4, with LS 4 samples being more left-oriented than LS 1. Group 2 is exclusively phylloid algal samples, with percent abundance of phylloid algae, from most abundant to least, determining the placement of the sample from top to bottom. Group 3 contains most other samples, including Brownwood limestone samples, some fenestellid-rich and small-brachiopod-rich shales, a small cluster of Plattsmouth samples in the upper left corner. Group 4 contains primarily Brownwood LS 2 samples and those from the shale above limestone 2, located to the center and right of the ordination. Overlap area between groups 1 and 3 contains B23, from the top of Brownwood LS 3 and B25, from the bottom of Brownwood LS 4. Overlap between groups 3 and 4 contain P4 from Perrin. Groups are slightly less aggregated on axes 1 and 3 than on axes 1 and 2. Group 5 is similar to group 1 and contains Brownwood LS 1 and 4, with a different vertical distribution than that of group 1. Group 6 is primarily comprised of Brownwood LS 2 samples. Group 7 contains a cluster of Plattsmouth samples in the upper left corner, fenestellid-rich shale samples along the right edge, and various Brownwood, Merriam, Perrin, and RP samples throughout. Group 8 contains some Brownwood LS 2 samples, samples from the shale above LS 2, and lower Perrin samples. Group 9 is contains Brownwood black shale and some non-Winchell samples. A moderate trend of decreasing echinoid abundance plus a weak trend of decreasing *Composita* and increasing productids to a moderate trend of decreasing productids and increasing small, attaching brachiopods is interpreted for axis 1.

Figure 3.10

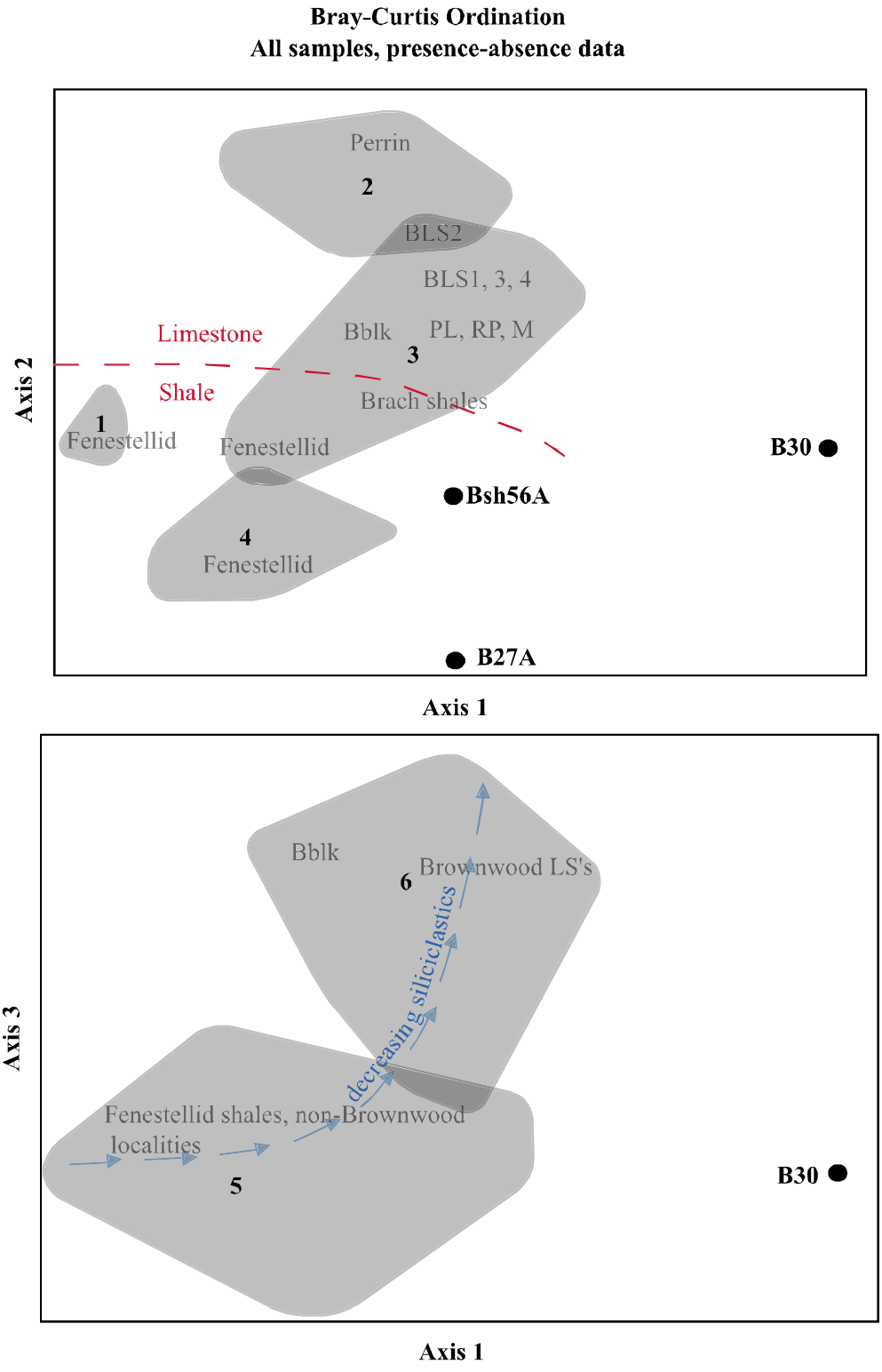

Bray-Curtis Ordination
All samples, presence-absence data
Perrin
2
BLS2
BLS1, 3, 4
Limestone
Bblk
PL, RP, M
3
Shale
Brach shales
1
Fenestellid
Fenestellid
B30
Bsh56A
4
Fenestellid
B27A
Axis 2
Axis 1
Bblk
6
Brownwood LS's
decreasing siliciclastics
Fenestellid shales, non-Brownwood localities
5
B30
Axis 3
Axis 1

Figure 3.10. Bray-Curtis ordination of all samples using presence-absence data. All axes ordinate on low diversity samples. Axis 1 endmembers are B2coq1, a *Neochonetes*- and crinoid-rich coquina in the shale above Brownwood LS2 and B30, the uppermost phylloid algal Brownwood LS6 sample and accounts for 38.2% of the distance matrix. Axis 2 endmembers are B27A from the middle of Brownwood LS 4 and P3, a lower Perrin sample, and accounts for 26.0% of the distance matrix, with axes 1 and 2 explaining 64.2% of the total distance matrix. Axis 3 endmembers are PL3, a Virgilian Plattsmouth sample, and B4 from Brownwood LS 4 and accounts for 17.2% of the distance matrix, with axes 1 through 3 explaining 81.4% of the total distance calculated. On axes 1 and 2, groups 1, 2, and 4 are loosely aggregated, whereas group 3 is fairly closely aggregated. Group 1 contains three samples from the shale above Brownwood LS 2, primarily formed by a unique combination of *Neochonetes*, crinoids, and various bryozoans. Group 2 is a very loosely aggregated group of Perrin samples. Group 3 is more tightly aggregated, and contains a tight aggregation of samples from Brownwood LS2 in the overlap between groups 2 and 3, Brownwood LS3 samples just below the overlap, various Brownwood and non-Brownwood samples scattered throughout, and small-brachiopod-rich shale samples in the lower left-bottom corner. Group 4 is a loosely aggregated group of fenestellid-rich shale samples, including the same in the overlap between groups 3 and 4. Both groups of axes 3 and 4 are very loosely aggregated with a few small, tighter aggregations of few samples throughout. Group 5 contains fenestellid-rich shale samples on the left corner, but the rest of the samples are primarily non-Brownwood samples and other Brownwood shales. Group 6 is comprised of mostly Brownwood limestone samples with a tight cluster of Brownwood black shale samples on the left bottom edge. The overlap between groups 5 and 6 contains S1, a sample from Spring Hill, PL2, a lower Plattsmouth sample, and HC, a Hickory Creek shale. Axes 1 and 3 together have a weak argillaceous/non-argillaceous trend from the lower left to top middle of the scatterplot.

Partial (Culled) Data

Relative abundance data was culled of crinoids, phylloid algae, and common or locally common organisms (crinoids, phylloid algae, echinoids, *Composita*, and *Minilya*) to compare results with those using all data. Not suprisingly, culling crinoids resulted in only minor differences in cluster analyses, mainly constrained to changes in branch lengths or re-ordering of samples within clusters (Figure 3.11). Because crinoids were not identified to individual taxa, the effects of culling this one taxon was minimal even though abundances differed between samples.

The greatest difference between crinoid-culled ordination scatterplots and those using all data is in some endmember selection (Figure 3.12). Instead of a Perrin sample as the right endmember of the all-data ordination, axis 1 of the crinoid-culled ordination contains an endmember in a coquina from the Brownwood shale between limestones 1 and 2. Likewise, in the top endmember of axis 2 of relative abundance ordination, B30 from phylloid algal limestone 6 of Brownwood is exchanged for another phylloid algal sample, F1 from the Farley Limestone, and both axis 3 endmembers are different when crinoids are culled. These differences likely result from changes in relative abundances of other taxa when crinoid abundances are subtracted from the data set. Groupings on scatterplots are also different between all-data and crinoid-culled ordinations, but general locations of sample aggregations, such as the Brownwood black shale packstones, remains very similar.

When all available data is used, phylloid algal samples are a tight cluster at the base of the tree; when phylloid algae is culled, the samples are dispersed throughout the dendrogram, but cause some re-organization within clusters (Figure 3.13). For example, Perrin samples, instead of grouping with Plattsmouth or fenestellid-rich shale samples as in all-data cluster analysis, cluster with the Brownwood black shale packstone samples and with non-Winchell samples.

In ordination, Axis 1 endmembers remain the same between all-data and phylloid algae-culled data sets, but Axis 2 not only loses the phylloid algae endmember, but also the entire group of phylloid algae samples (Figure 3.14). This results in a greater reorganization of sample groupings than when crinoids are culled, although Brownwood limestones 1 and 4 remain a distinct group. Likewise, axis 3 is also reorganized with new endmembers, resulting in an Axes 1 and 3 scatter plot different from that using all available data.

Major differences arose in cluster analyses between use of all data or culling common taxa (crinoids, echinoids, *Composita*, and *Minilya*) plus phylloid algae (Figure 3.15). Using relative abundance data, loss of common taxa and phylloid algae from the data matrix resulted in increased mixing of a few localities and units, but more often, individual units and localities were much more tightly clustered. For example, Brownwood limestone 1, which is clustered with limestone 4 samples in all-data, crinoid-culled, and phylloid algae-culled analyses, is instead clustered separately. Also, individual Brownwood shale units, such as the shale between limestones 3 and 4, cluster together more strongly, rather than the large fenestellid-rich shale cluster of previous analyses.

Not suprisingly, Bray-Curtis ordination of samples culled of common taxa plus phylloid algae differs greatly from analysis using all available data (Figure 3.16). When all data is used, or even when phylloid algae or crinoids are culled, axes almost always ordinate on samples with abundant crinoids, echinoids, *Composita*, *Minilya*, or phylloid algae. Culling these taxa from the data set results in endmember choice of samples with the next most common (i.e., *Antiquatonia*) or distinctive (i.e., *Neochonetes*, which occurs in abundance in the shale above Brownwood limestone 2) taxa.

Figure 3.11

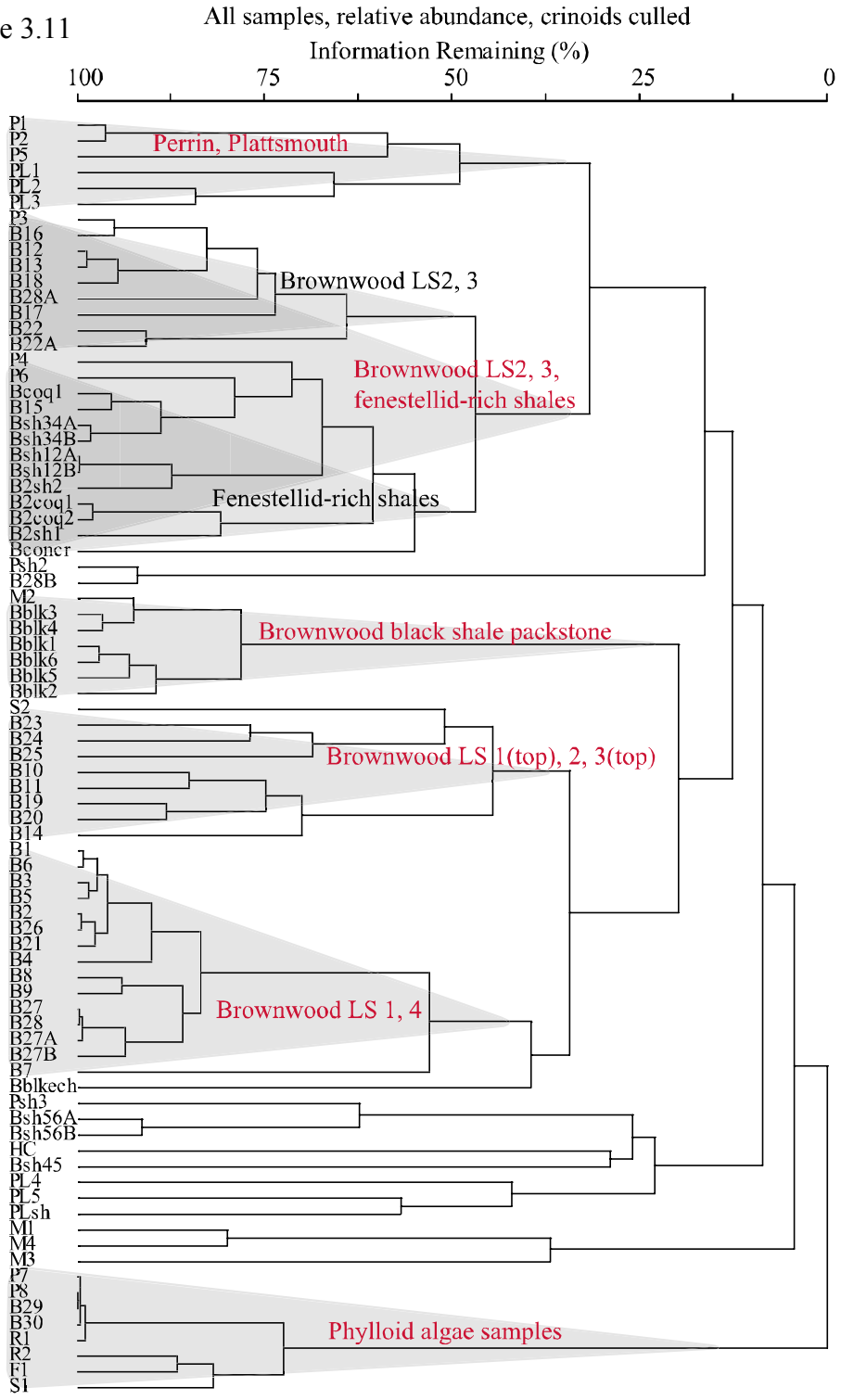

All samples, relative abundance, crinoids culled
Information Remaining (%)
100
75
50
25
0
Perrin, Plattsmouth
Brownwood LS2, 3
Brownwood LS2, 3,
fenestellid-rich shales
Fenestellid-rich shales
Brownwood black shale packstone
Brownwood LS 1(top), 2, 3(top)
Brownwood LS 1, 4
Phylloid algae samples
Pl
P2
P5
PL1
PL2
PL3
P3
B16
B12
B13
B18
B28A
B17
B22
B22A
P4
P6
Bcoq1
B15
Bsh34A
Bsh34B
Bsh12A
Bsh12B
B2sh2
B2coq1
B2coq2
B2sh1
Bconcr
Psh2
B28B
M2
Bblk3
Bblk4
Bblk1
Bblk6
Bblk5
Bblk2
S2
B23
B24
B25
B10
B11
B19
B20
B14
B1
B6
B3
B5
B2
B26
B21
B4
B8
B9
B27
B28
B27A
B27B
B7
Bblkech
Psh3
Bsh56A
Bsh56B
HC
Bsh45
PL4
PL5
PLsh
M1
M4
M3
P7
P8
B29
B30
R1
R2
F1
S1

Figure 3.11. Cluster analysis of all samples using relative abundance data, crinoids culled. Relative Sorenson distance measure and UPGMA linkage were used. Clusters were arbitrarily determined at 50% data remaining and less. Compared to cluster analysis using all data (Figure 3.7), culling crinoids resulted in some re-ordering of samples in large clusters and changes in branch length.

Figure 3.12

Bray-Curtis Ordination

All samples, relative abundance, crinoids culled

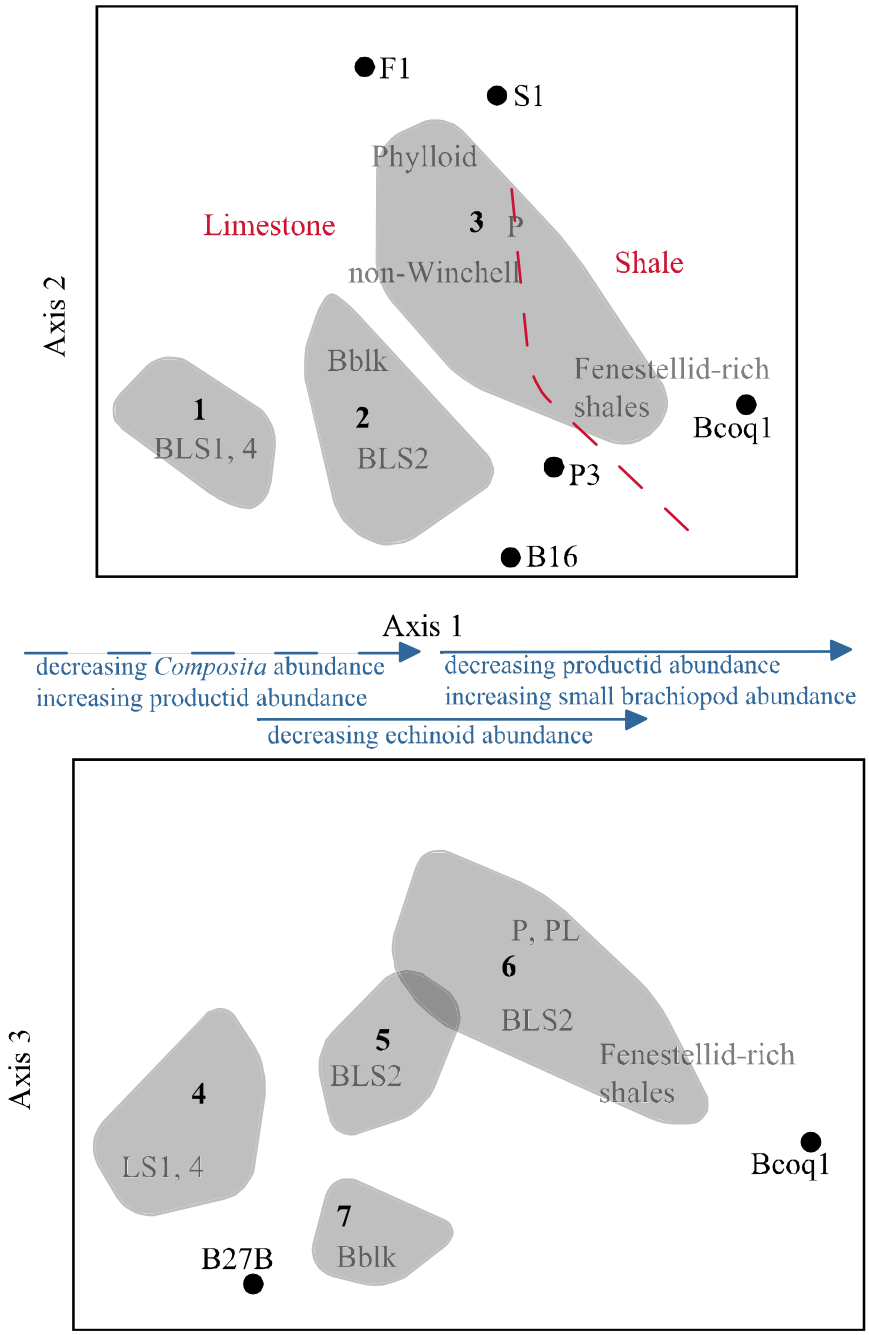


Figure 3.12. Bray-Curtis ordination of all samples using relative abundance data, crinoids culled. Axis 3 endmembers are B27B from Brownwood LS4 and R2, the upper limestone member of Winchell RP locality, and accounts for 13.0% of the distance matrix, with axes 1 through 3 explaining 85.1% of the total distance calculated. Axis 1 accounts for 45.0% of the original distance matrix and ordinates on *Composita* plus echinoid- and *Minilya*-rich samples with endmembers B27 from Brownwood LS4 and Bcoq1, a coquina in the Brownwood shale between LS 1 and 2, producing a non-baffled/baffled pattern. Axis 2 accounts for 27.1% of the distance matrix, with a total of 72.1 of the total distance matrix explained by axes 1 and 2. Axis 2 ordinates on echinoid- and phylloid algae-rich samples with endmembers B16 from Brownwood LS2 and F1, a phylloid algal sample from the Farley Limestone, producing a lesser non-baffled/baffled pattern along the axis than that of axis 1. Together, axes 1 and 2 form a limestone/shale pattern from lower left to upper right and a ternary non-baffled, fenestellid-baffled, or phylloid algae-baffled pattern from left to right to top. Axis 3 comprises 13.0% of the remaining distance, with a total of 85.1% of the total distance matrix explained by axes 1 through 3. Axis 3 ordinates on *Composita* and *Crurithyris* abundances with endmembers B27B from Brownwood LS4 and R2, the upper limestone member of Winchell RP locality, and follows a Brownwood/non-Brownwood samples pattern. On axes 1 and 2, group 1 is loosely aggregated and contains Brownwood LS 1 and 4 samples; group 2 is tightly aggregated, and contains Brownwood black shale packstone samples in a tight aggregation near the top of the group and Brownwood LS 2, 3, and 5 samples scattered in the bottom of the group; group 3 is loosely aggregated with some small, tight aggregations, including non-Winchell samples on the right side, fenestellid-rich shale samples on the bottom, and phylloid algal samples on the top, with Perrin samples scattered throughout. On axes 1 and 3, group 4 differs from group 1 only in spacing of samples; group 5 is a tight aggregation of Brownwood limestones 2 and 3; group 6 is a loose aggregation with smaller aggregations of fenestellid-rich shale samples near the bottom of the group, small-brachiopod-rich shales plus non-Winchell samples near the top of the group, and Perrin plus Plattsmouth samples in the upper right; and group 7 contains a loose aggregation of Brownwood black shale packstone samples. Although groups are located and dispersed differently ordination scatterplots using all data (Figure 3.9), locality and unit placement is generally similar to the all-data scatterplot in relation to each other. Axis 1 echinoid and brachiopod abundance gradients are similar to relative abundance ordination (Figure 3.9).

Figure 3.13

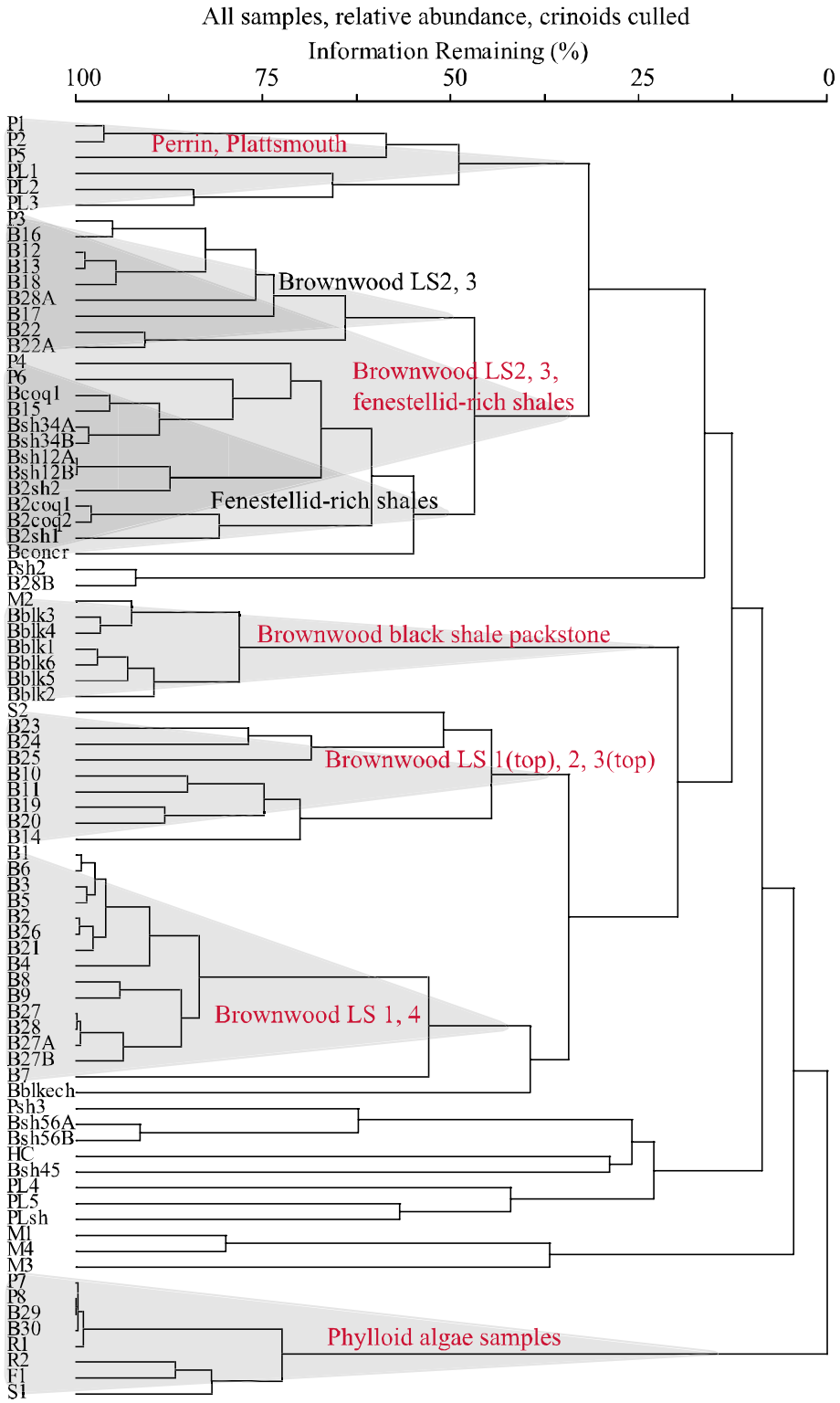

All samples, relative abundance, crinoids culled
Information Remaining (%)
100
75
50
25
0
Perrin, Plattsmouth
Brownwood LS2, 3
Brownwood LS2, 3,
fenestellid-rich shales
Fenestellid-rich shales
Brownwood black shale packstone
Brownwood LS 1(top), 2, 3(top)
Brownwood LS 1, 4
Phylloid algae samples
Pl
P2
P5
PL1
PL2
PL3
P3
B16
B12
B13
B18
B28A
B17
B22
B22A
P4
P6
Bcoq1
B15
Bsh34A
Bsh34B
Bsh12A
Bsh12B
B2sh2
B2coq1
B2coq2
B2sh1
Bconcr
Psh2
B28B
M2
Bblk3
Bblk4
Bblk1
Bblk6
Bblk5
Bblk2
S2
B23
B24
B25
B10
B11
B19
B20
B14
B1
B6
B3
B5
B2
B26
B21
B4
B8
B9
B27
B28
B27A
B27B
B7
Bblkech
Psh3
Bsh56A
Bsh56B
HC
Bsh45
PL4
PL5
PLsh
M1
M4
M3
P7
P8
B29
B30
R1
R2
F1
S1

Figure 3.13. Cluster analysis of all samples using relative abundance data, phylloid algae culled. Relative Sorenson distance measure and UPGMA linkage were used. Clusters were arbitrarily determined at 50% data remaining and less. Compared to cluster analysis using all data (Figure 3.7), culling phylloid algae scattered phylloid algal samples throughout the dendrogram and resulted in greater reorganization of samples between clusters than when crinoids are culled.

Figure 3.14 Bray-Curtis Ordination
All samples, relative abundance data, phylloid algae culled

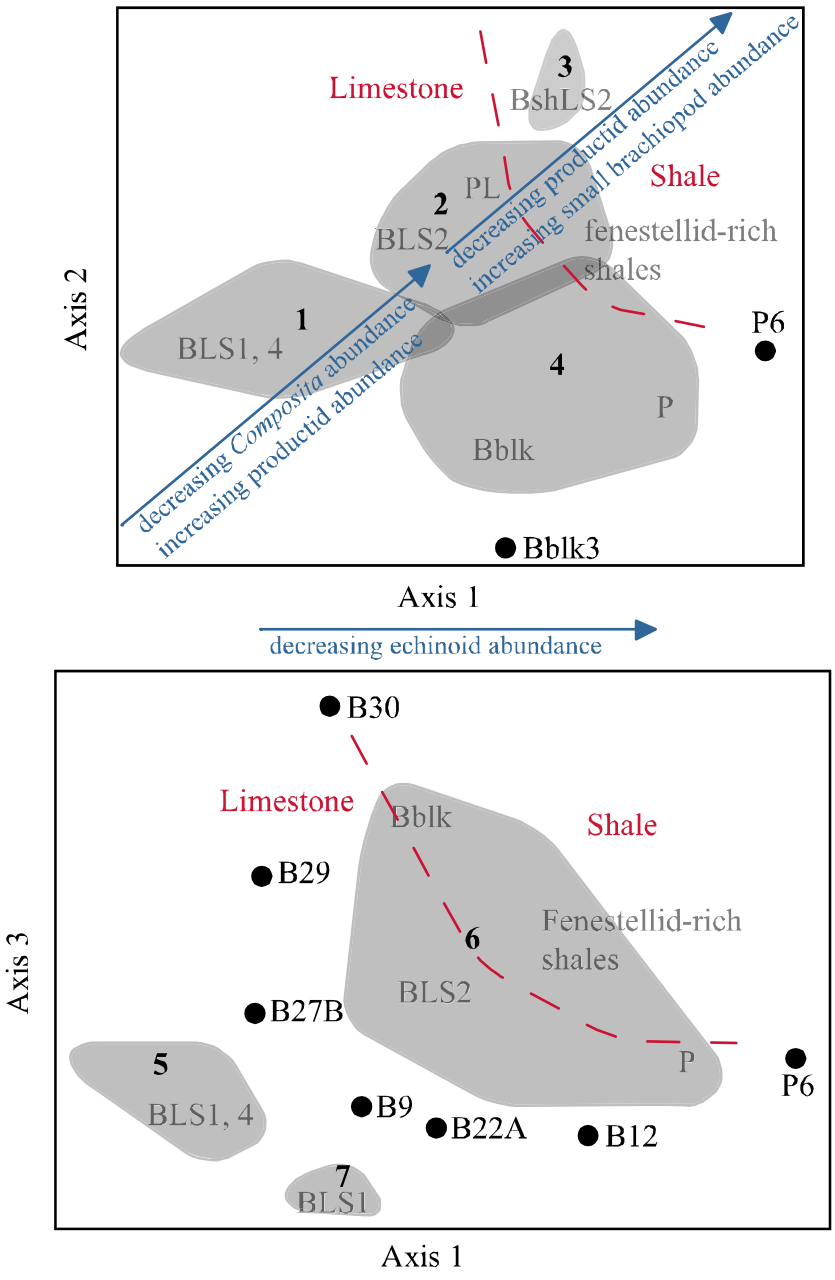


Figure 3.14. Bray-Curtis ordination of all samples using relative abundance data, phylloid algae culled. Axis 1 accounts for 46.9% of the original distance matrix and ordinates on echinoid + *Composita*- or fenestellid-rich samples with endmembers B27 from Brownwood LS4 and P6 from Perrin, producing a non-baffler/baffler pattern. Axis 2 accounts for 24.5% of the distance matrix, with a total of 71.4% of the total distance matrix explained by axes 1 and 2. Axis 2 ordinates on *Composita* and *Minilya* abundances with endmembers are Bblk3 from the Brownwood black shale packstones and Bsh12B, a shale sample between Brownwood limestones 1 and 2. Axis 3 comprises 14.2% of the remaining distance, with a total of 85.6% of the total distance matrix explained by axes 1 through 3. Axis 3 endmembers are B22 from Brownwood LS3 and B30 from Brownwood LS6, a shale sample between Brownwood LS1 and LS2, and follows an echinoid versus *Composita* pattern. Both axes 1 plus 2 and axes 1 plus 3 produce a limestone-shale pattern from the lower left to the upper right of the scatterplot, but axes 1 plus 3 include a weak increasing argillaceous trend from lower left to upper right along with the limestone-shale pattern. On axes 1 and 2, group 1 is loosely aggregated and contains *Composita, Antiquatonia,* and echinoid-rich samples from Brownwood LS1 and 4, similar to group 1 of all-data ordination (Figure 3.9); group 2 is a tight aggregation including Brownwood LS 2, shale samples, and non-Winchell samples; group 3 is a loose aggregation of *Neochonetes*- and crinoid-rich samples from Brownwood shale above LS2; and group 4 is contains overlapping aggregations of Brownwood black shale packstone samples in the lower right, non-Winchell samples in the center, and Perrin samples in the lower left of the group. On axes 1 and 3, group 5 is similar to group 1; group 6 contains overlapping aggregations of Brownwood black shale packstone samples near the top, Brownwood LS 2 and 5 near the lower left, fenestellid-rich shale samples along the right side, Perrin samples near the bottom, and non-Winchell samples scattered centrally and throughout the group; and group 7 is a loose aggregation of two Brownwood LS1 and one Brownwood LS 3 samples. Axis 1 echinoid abundance gradient is similar to relative abundance ordination (Figure 3.9), but brachiopod abundance gradient differs in that the trend is on both axes 1 and 2, with a moderate trend in decrease in *Composita* plus increase in productid abundances and decrease in productid abundances and increase in small, attaching brachiopod abundances from lower left to upper right of the scatterplot.

Figure 3.15 All samples, relative abundance, phylloid algae, crinoids, echinoids, *Composita* and *Minilya* culled

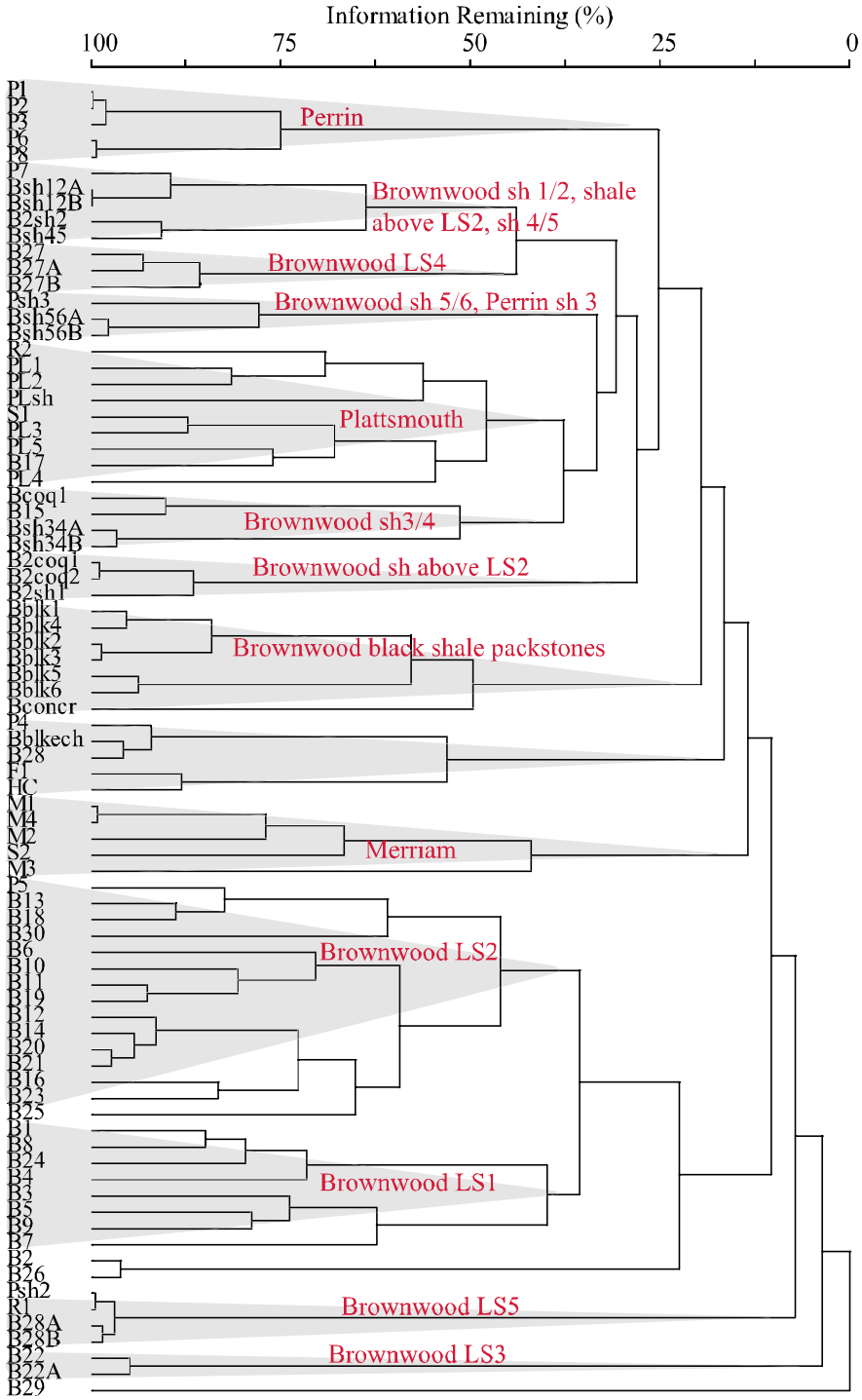
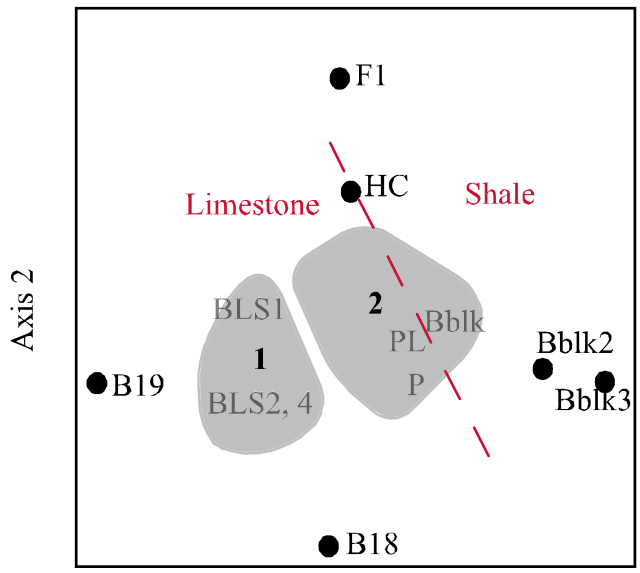


Figure 3.15. Cluster analysis of all samples using relative abundance data, common taxa (crinoids, echinoids, *Composita,* and *Minilya*) and phylloid algae culled. Relative Sorenson distance measure and UPGMA linkage were used. Clusters were arbitrarily determined at 50% data remaining and less. Compared to cluster analysis using all data (Figure 3.7), individual units and localities are more tightly clustered; for example, the large fenestellid-rich shale and Brownwood LS 1 and 4 groups of all-data cluster analysis are split into individual shale and limestone units.

Figure 3.16

Bray-Curtis Ordination

All samples, relative abundance, phylloid algae, crinoids, echinoids, *Composita,* and *Minilya* culled



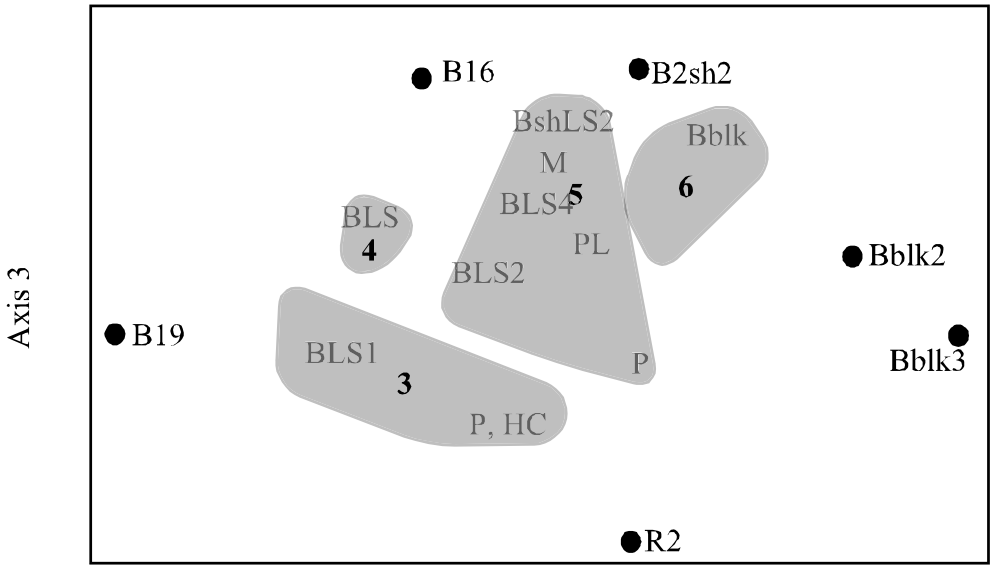


Figure 3.16. Bray-Curtis ordination of all samples, relative abundance data, common taxa (crinoids, echinoids, *Composita*, and *Minilya*) and phylloid algae culled. Axis 1 accounts for 33.1% of the original distance matrix and ordinates on *Antiquatonia*- and *Aviculopecten*-rich samples with endmembers B19 from Brownwood LS2 and Bblk3, a Brownwood black shale packstone sample. Axis 2 accounts for 19.7% of the distance matrix, with a total of 52.8% of the total distance matrix explained by axes 1 and 2. Axis 2 ordinates on *Antiquatonia*- and *Rhombopora*-rich samples with endmembers B18 from Brownwood LS2 and F1 from the Farley Limestone, resulting in a limestone-shale pattern from lower left to upper right on axes 1 and 2. Axis 3 comprises 16.3% of the remaining distance, with a total of 69.1% of the total distance matrix explained by axes 1 through 3. Axis 3 ordinates on *Crurithyris* and *Neochonetes* abundances with endmembers R2 from Winchell locality RP and B2sh2, a sample from the shale above Brownwood LS2. On axes 1 and 2, group 1 contains Brownwood LS1 at the top and Brownwood LS2 and LS4 at the bottom in a loose aggregation; and group 2 is a tight aggregation of Perrin, Plattsmouth, and Brownwood black shale packstone samples, including other Brownwood and non-Winchell samples. On axes 1 and 3, group 3 contains Brownwood LS1 in the lower portion of the loose aggregation and Perrin plus some non-Winchell samples in the bottom right portion of the group; group 4 contains various Brownwood limestone samples in a loose aggregation; group 5 is a tight aggregation of Brownwood LS2 on the left, Plattsmouth samples on the right, Perrin samples on the lower right, and Brownwood LS4, the shale above LS2, and Merriam samples in the top portion of the group; and group 6 contains Brownwood black shale packstone samples plus others.

Brachiopod or Bryozoan Data Only

Not surprisingly, *Composita* strongly affects the results of brachiopod-only cluster analysis, as it does in cluster analysis of all data. In all-data dendrograms, Brownwood limestones 1 and 4 as well as the black shale packstone samples cluster strongly in part because of the abundance of *Composita* brachiopods. However, when brachiopods only are considered, other taxa that strongly influence clustering in all-data dendrograms, such as abundant *Aviculopecten* in the Brownwood black shale packstones or echinoids in Brownwood limestones 1 and 4, are lost (Figure 3.17). Because *Composita* is very abundant in several units, a large cluster is formed primarily because of the dominance or high abundance of this brachiopod. Productids such as *Linoproductus*, *Echinaria*, *Antiquatonia*, and *Reticulatia* also influence one cluster primarily consisting of Brownwood limestone 2. *Crurithyris*, along with several other small brachiopods such as *Punctospirifer*, influence another large cluster made up of many non-Brownwood and non-fenestellid-rich Brownwood shale samples.

Major differences between the brachiopod-only cluster analysis and the all-data results occur in the grouping of localities and units. Unlike all-data cluster analysis, brachiopod-only analysis contains no fenestellid-rich shale group; instead, individual shale units are scattered throughout the dendrogram, either grouped within small brachiopod-driven clusters or as separate clusters, such as the shale above Brownwood limestone 2, which contains highly abundant *Neochonetes*. In all-data dendrograms, Brownwood limestones 1 and 4 cluster because of abundant echinoids as well as *Composita* and *Antiquatonia*, but when using brachiopod-only

data, the limestones are separated within the large *Composita*-driven cluster because of more similar *Composita* abundances between the Brownwood black shale packstones, limestone 4, and limestone 6. The tightly clustered Brownwood black shale packstone samples in all-data cluster analyses are isolated from other localities and units, unlike the brachiopod-only results. Brownwood limestone 2 samples in all-data analysis are associated either with fenestellid-rich shales or with samples from limestones 3 and 5; in brachiopod-only analyses, limestone 2 samples occur in a series of sister-clusters and contain only a few outside samples from Brownwood limestone 1 and Perrin.

Unlike all-data Bray-Curtis ordination, brachiopod-only samples are much more diffuse throughout the scatterplots, with no distinct aggregations of individual units and localities in the larger aggregation groups except for the Brownwood black shale packstones on both plots and the shale above Brownwood limestone 2 on the axis 1 and 2 plot (Figure 3.18). *Composita*, similar to the all-data plots, is a strong factor in ordination, and greatly influences axis 1, and to a lesser extent, axis 2. *Neospirifer* appears to influence all of the first three axes, particularly axis 1. A limestone-shale pattern is present, but is only manifested on axis 2 instead of a combination of axes 1 and 2, as in ordination using all available data.

In bryozoan-only cluster analysis, fenestellid-rich shale samples are a strong cluster similar to that of all-data analysis, but include several other fenestellid-rich samples of Brownwood limestones 3 and 5 and Perrin (Figure 3.19). Although *Minilya* and *Rhombopora* abundances among these samples are very similar, lithologies are dissimilar. Brownwood limestones 3 and 5 samples are grainstones, whereas bryozoan-rich Perrin samples are highly argillaceous. A series of sister

clusters to this fenestellid-rich cluster are also based on *Minilya* abundances with individual clusters controlled by abundances of other bryozoans. Other samples at the base of the tree, one of which is a cluster of several Brownwood, Perrin, and RP samples, are poor or lacking in *Minilya*, and cluster mainly on *Rhombopora* and tubuliporate abundances.

In Bray-Curtis ordination of bryozoan-only data, the limestone/shale pattern seen in many other ordinations is lacking (Figure 3.20). When bryozoans only are considered, *Minilya*, and to a lesser extent, *Rhombopora* and tubuliporate bryozoans, are greatest influences on the axes. Without other data, only relative abundances of the bryozoans are considered, which increases mixing between units and localities. For example, Brownwood limestone 1 sample B2, which only has 7.3% *Minilya* when all data are considered, contains 100% *Minilya* in bryozoan-only data sets. Because of this, sample B2 ordinates with other *Minilya*-rich samples rather than Brownwood limestone 1 and limestone 4 samples of all-data ordination.

Figure 3.17

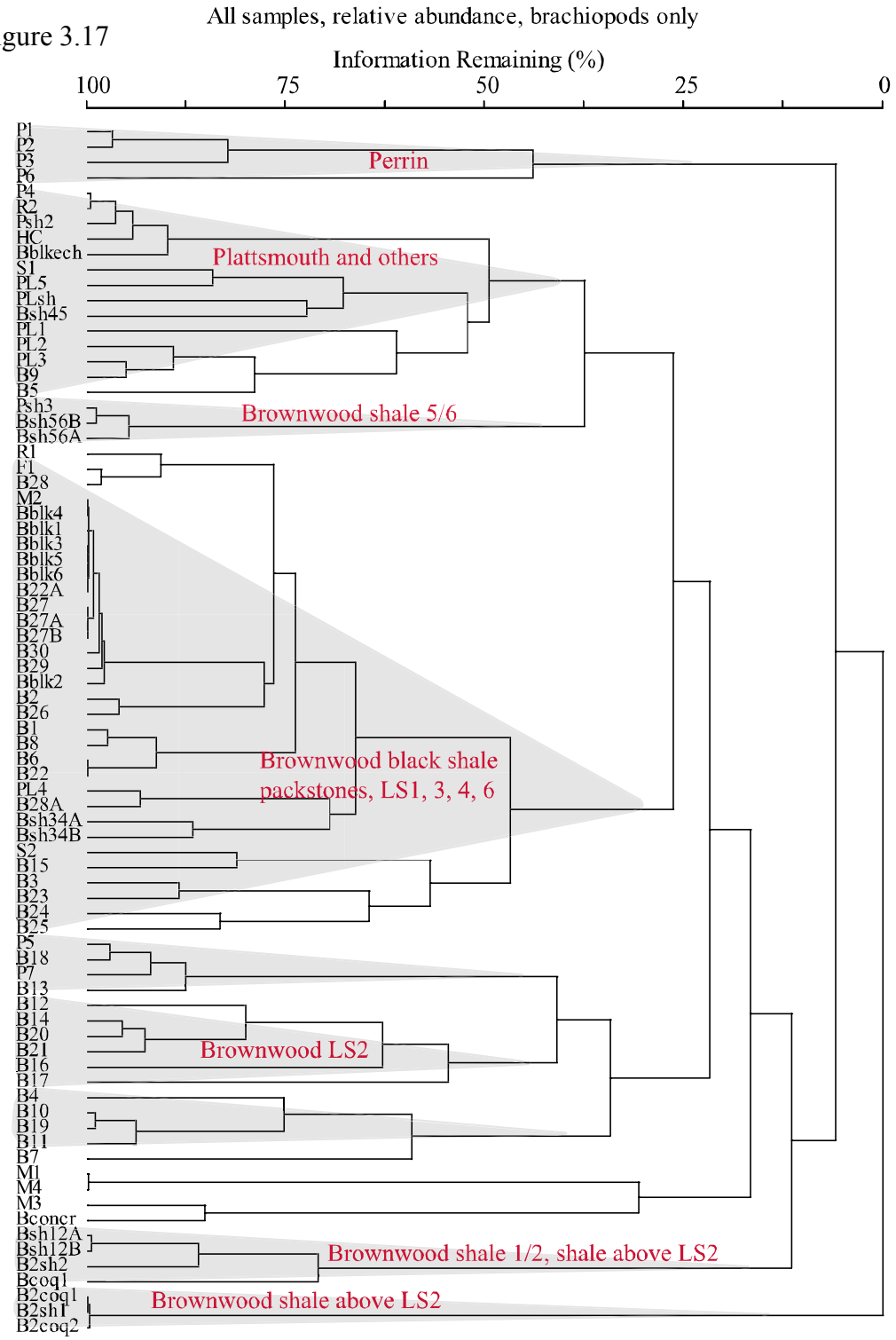

All samples, relative abundance, brachiopods only
Information Remaining (%)
100
75
50
25
0
P1
P2
P3
P6
P4
R2
Psh2
HC
Bblkech
S1
PL5
PLsh
Bsh45
PL1
PL2
PL3
B9
B5
Psh3
Bsh56B
Bsh56A
R1
P1
B28
M2
Bblk4
Bblk1
Bblk3
Bblk5
Bblk6
B22A
B27
B27A
B27B
B30
B29
Bblk2
B2
B26
B1
B8
B6
B22
PL4
B28A
Bsh34A
Bsh34B
S2
B15
B3
B23
B24
B25
P5
B18
P7
B13
B12
B14
B20
B21
B16
B17
B4
B10
B19
B11
B7
M1
M4
M3
Bconcr
Bsh12A
Bsh12B
B2sh2
Bcoq1
B2coq1
B2sh1
B2coq2
Perrin
Plattsmouth and others
Brownwood shale 5/6
Brownwood black shale packstones, LS1, 3, 4, 6
Brownwood LS2
Brownwood shale 1/2, shale above LS2
Brownwood shale above LS2

Figure 3.17. Cluster analysis of all samples using relative abundance data, brachiopods only. Relative Sorenson distance measure and UPGMA linkage were used. Clusters were arbitrarily determined at 50% data remaining and less.

Figure 3.18

Bray-Curtis Ordination
All samples, relative abundance, brachiopods only

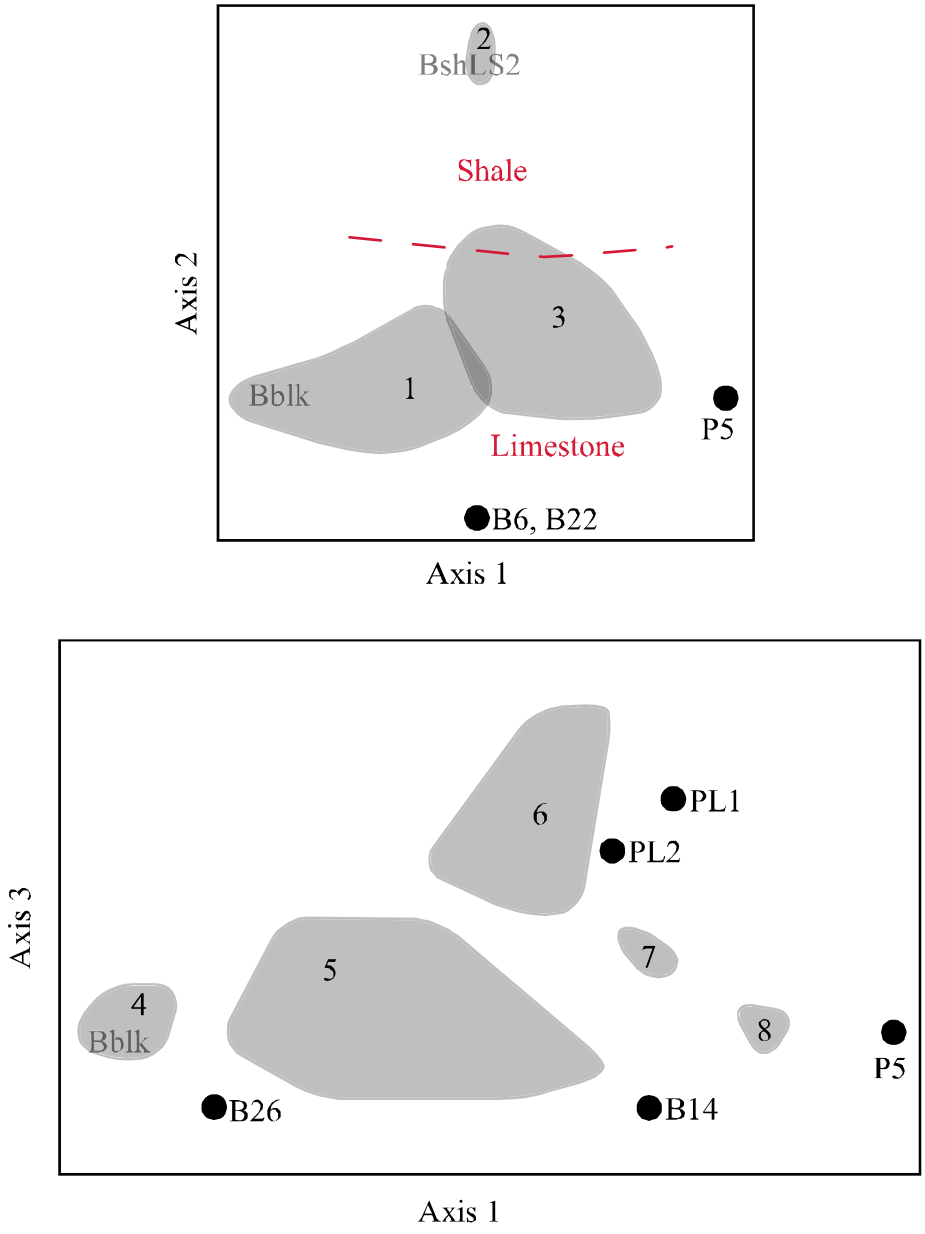


Figure 3.18. Bray-Curtis ordination of all samples, relative abundance data, brachiopods only. Axis 1 accounts for 46.6% of the original distance matrix and ordinates on *Composita* and *Neospirifer* abundances with endmembers Bblk1 from the Brownwood black shale packstones and P5 from Perrin. Axis 2 accounts for 24.7% of the distance matrix, with a total of 71.3% of the total distance matrix explained by axes 1 and 2. Axis 2 ordinates on *Composita* + *Neospirifer* and *Neochonetes* abundances with endmembers B22 from Brownwood LS3 and B2coq2, a coquina in the shale above Brownwood LS2, producing a limestone/shale pattern along the axis. Axis 3 comprises 12.7% of the remaining distance, with a total of 84.0% of the total distance matrix explained by axes 1 through 3. Axis 3 ordinates on various large productid- and *Crurithyris*-rich samples with endmembers B12 from Brownwood LS2 and Psh2, a Perrin shale horizon. On axes 1 and 2, group 1 contains a tight aggregation of Brownwood black shale packstone samples in a looser aggregation of Brownwood and non-Winchell samples; group 2 is a tight aggregation of samples from the shale above Brownwood LS2; and group 3 is a tight aggregation of samples from various units and localties. On axes 1 and 3, group 4 contains a tight aggregation of Brownwood black shale packstones with other *Composita*-rich samples; group 5 is a loose aggregation with increasing *Composita* left to right, mostly of Brownwood samples; group 6 contains a tight Brownwood and other samples aggregation plus a small clump of Brownwood LS 1 and 2 in the lower part of the group; group 7 contains a tight, small aggregation of Brownwood LS 1 and 2 samples; and group 8 contains a small aggregation with Brownwood LS2 and Perrin samples.

Figure 3.19 All samples, relative abundance, bryozoans only

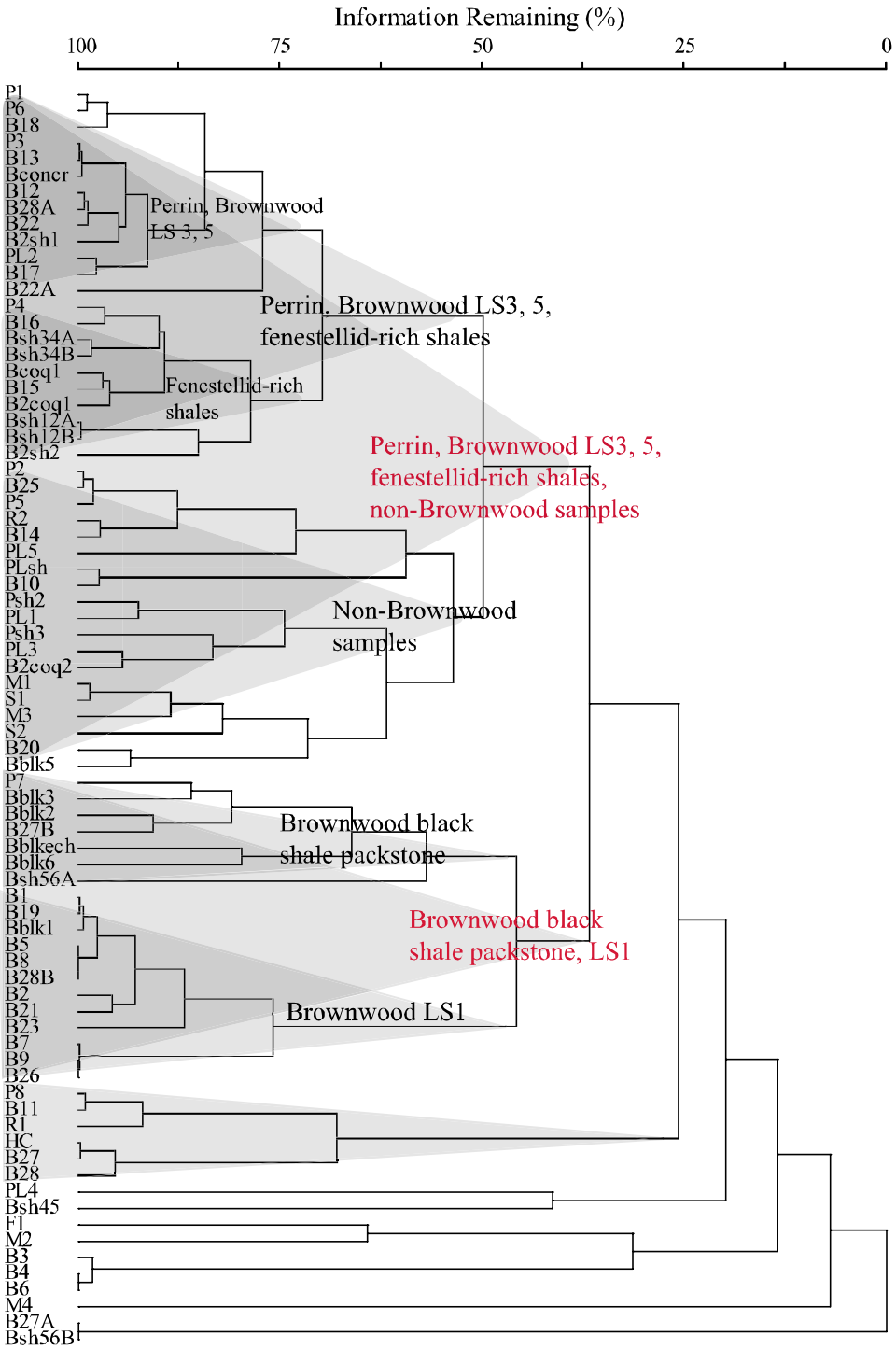
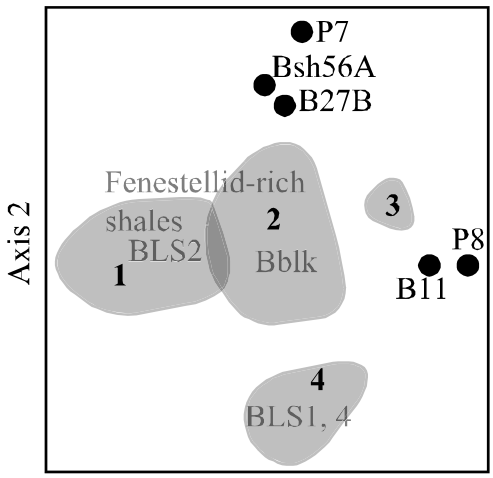


Figure 3.19. Cluster analysis of all samples using relative abundance data, bryozoans only. Relative Sorenson distance measure and UPGMA linkage were used. Clusters were arbitrarily determined at 50% data remaining and less.

Figure 3.20

Bray-Curtis Ordination

All samples, relative abundance, bryozoans only



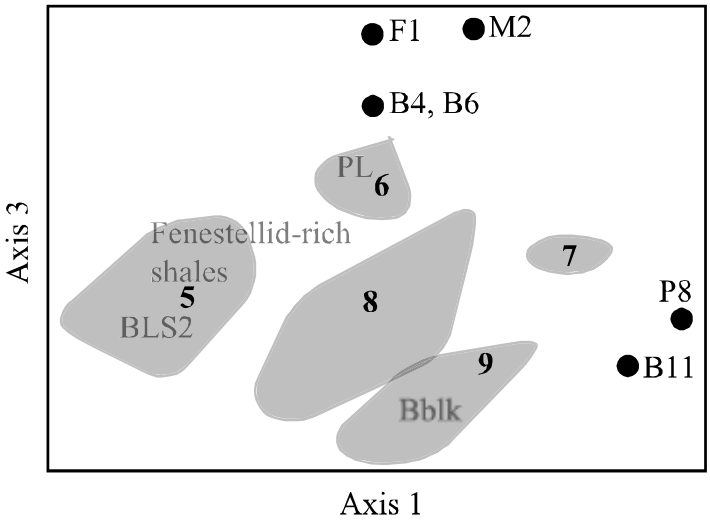


Figure 3.20. Bray-Curtis ordination of all samples, relative abundance data, bryozoans only. Axis 1 accounts for 62.0% of the original distance matrix and ordinates on *Minilya* and *Rhombopora* abundances with endmembers P4 from Perrin and PLsh, a shale from the Plattsmouth Limestone. Axis 2 accounts for 25.9% of the distance matrix, with a total of 87.9% of the total distance matrix explained by axes 1 and 2. Axis 2 ordinates on *Minilya* and tubuliporate abundances with endmembers B11 from Brownwood LS1 and Bsh56B, a shale sample between Brownwood LS5 and 6. Axis 3 comprises 8.5% of the remaining distance, with a total of 96.4% of the total distance matrix explained by axes 1 through 3. Axis 3 ordinates on *Minilya* and *Rhombopora* versus *Polypora* abundances with endmembers Bblk3, a Brownwood black shale packstone sample, and M1 from the Merriam Limestone. On axes 1 and 2, group 1 is a tight aggregation of fenestellid-rich Brownwood limestone and shale samples plus some non-Winchell samples; group 2 is a tight aggregation with smaller aggregations of Brownwood black shale packstone samples among Brownwood limestone samples; group 3 contains Brownwood, Hickory Creek, and RP samples; and group 4 contains some Brownwood limestone 1 and 4 samples in a loose aggregation. On axes 1 and 3, group 5 is a tight aggregation of Brownwood LS2 and shale samples; group 6 is a loose aggregation of Plattsmouth and shale samples; group 7 is a loose aggregation similar to group 3; group 8 is a loose aggregation of a few Brownwood limestone samples; and group 9 contains Brownwood black shale packstone samples.

Brownwood Samples

Results from cluster analysis of Brownwood samples are similar to those of all samples (Figure 3.21). Groups of Brownwood samples that cluster in analysis of all samples continue to cluster in Brownwood-only analysis. The only major difference between the two dendrograms is that non-Brownwood clusters and individual non-Brownwood samples are missing from the Brownwood-only dendrogram. Because 65 of the 81 total samples are from Brownwood, Brownwood samples exert great influence on the all-samples analyses.

Bray-Curtis ordination results for Brownwood samples differ from that of all samples more so than cluster analyses (Figure 3.22). *Composita*, *Minilya*, and phylloid algae continue to influence ordination axes and aggregations of samples on scatterplots, but crinoids have a more significant influence (axes 2 and 3) and gastropods influence the ordination of axis 2. This also affects aggregations of samples in the scatterplot as far as grouping is concerned, but aggregations of Brownwood samples in all-sample analysis, such as those of limestones 1 plus 4 and the black shale packestones, continue to occur on Brownwood-only ordination results. One major difference is that phylloidal samples occur on axis 3 instead of axis 2, causing the axis1/axis 3 scatterplot to have a ternary arrangement of non-baffled samples on the left, phylloid algae-baffled samples at the top, and bryozoan-baffled samples on the right, rather than the axis 1/axis 2 occurrence in all-sample analysis.

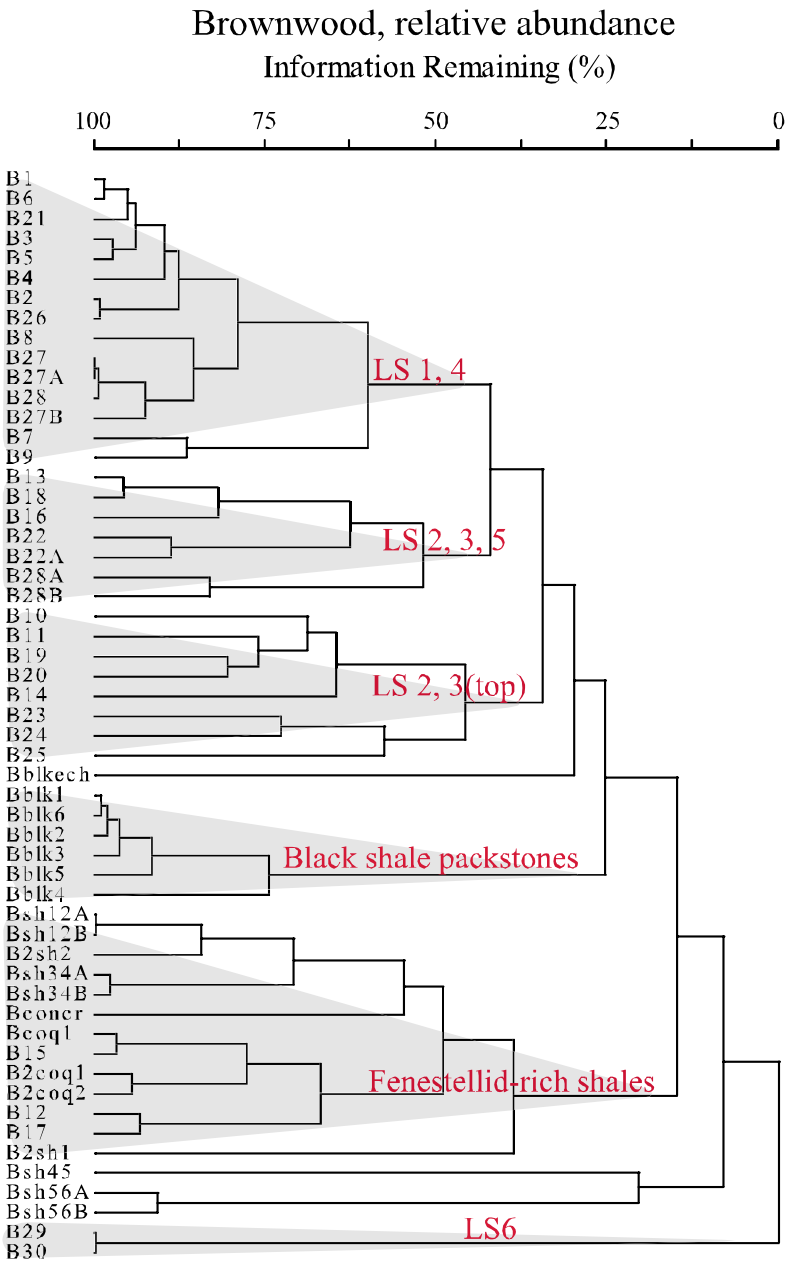


Figure 3.21. Cluster analysis of Brownwood samples using relative abundance data. Relative Sorenson distance measure and UPGMA linkage were used. Clusters were arbitrarily determined at 50% data remaining and less. Clusters are similar to those of all-data analysis (Figure 3.7), lacking non-Brownwood samples.

Bray-Curtis Ordination

Brownwood, relative abundance data

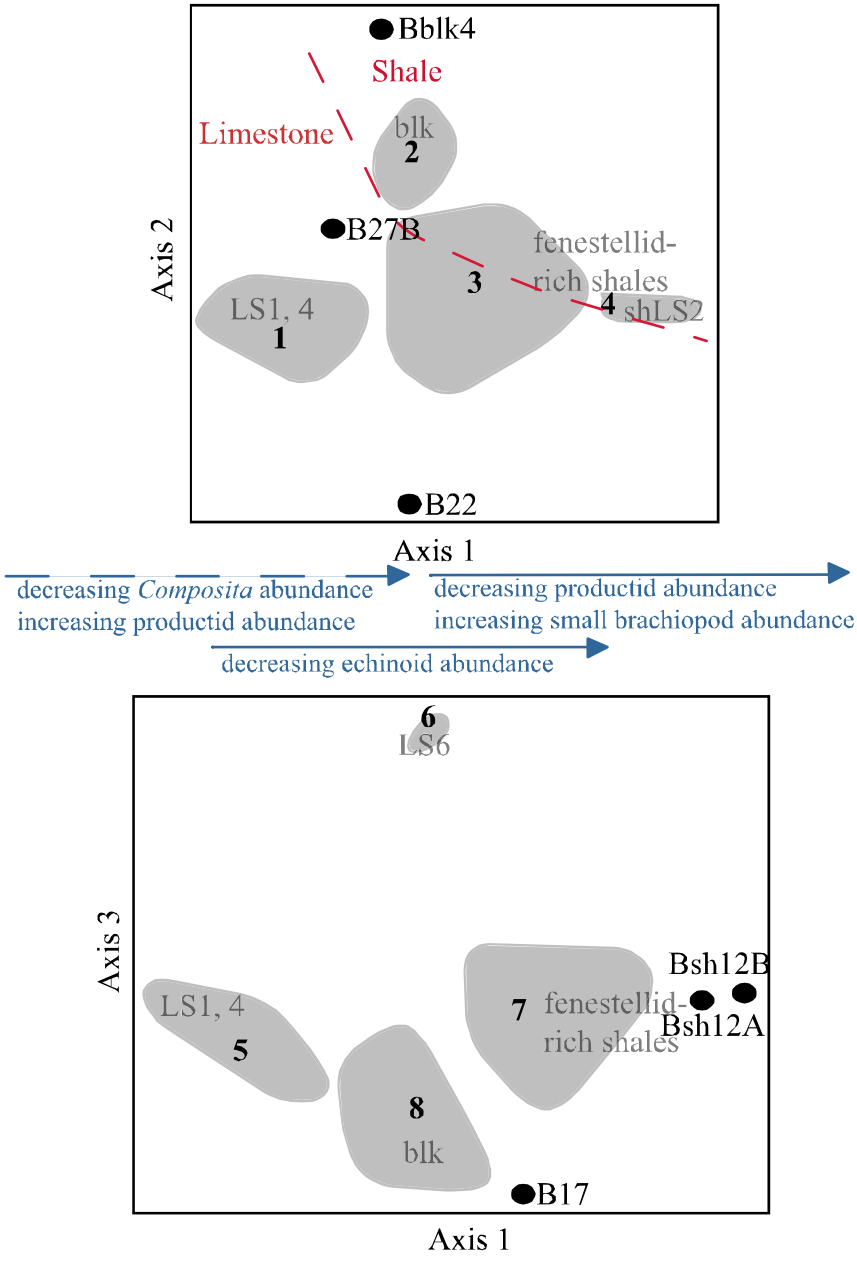


Figure 3.22. Bray-Curtis ordination of Brownwood samples, relative abundance data. Axis 1 accounts for 50.6% of the original distance matrix and ordinates on *Composita* and *Minilya* abundances with endmembers B27 from LS 4 and Bsh12B, a sample from the shale between LS 1 and 2. Axis 2 accounts for 22.6% of the distance matrix, with a total of 73.2% of the total distance matrix explained by axes 1 and 2. Axis 2 ordinates on a gastropod-rich and on *Composita* plus crinoid-rich samples with endmembers B22 from LS 3 and Bblk4, a black shale packstone sample, producing a limestone-shale pattern along axes 1 and 2 from lower left to upper right. Axis 3 comprises 14.0% of the remaining distance, with a total of 87.2% of the total distance matrix explained by axes 1 through 3. Axis 3 ordinates on *Minilya* plus crinoid- and phylloid algae-rich samples with endmembers B17 from LS 2 and B30 from LS 6, and together with axis 1 contains a ternary pattern of non-baffled samples (lower left), phylloid algae-baffled samples (top), and fenestellid-baffled samples (lower right). On axes 1 and 2, group 1 contains samples from LS1 and 4; group 2 is a loose aggregation of black shale packstone samples; group 3 is a loose aggregation of samples, including a smaller aggregation of fenestellid-rich shale samples on the upper left; and group 4 contains three samples from the shale above LS 2. On axes 1 and 3, group 5 is similar to group 1; group 6 contains the two LS 6 samples; group 7 contains a loose aggregation of fenestellid-rich shales to the right and LS 2 samples on the right; and group 8 contains black shale packstone samples and LS 3 and 5. Echinoid and brachiopod abundance trends are similar to those of relative abundance ordination of all samples (Figure 3.9).

Units and Localities

Cluster analysis of units and localities results in three main clusters (Figure 3.23). One cluster contains mostly units and localities containing phylloid algae, resulting mainly in a non-Brownwood cluster. Brownwood limestones 1 through 5 cluster together, as do fenestellid-rich shales; other shales do not closely cluster. Brownwood units tend to separate from other localities, similar to that of all-sample analysis.

In ordination, phylloid algae are a major influence of both axes 1 and 2; *Composita* has only minor influence on axis 2. Together, the two axes create a shale/limestone pattern from upper left to lower right, opposite from most other ordinations, and also includes a phylloid algal lower right corner. Limestone samples do not appear to be arranged in any sort of lithologic gradient, so none is interpreted for the scatterplot.

No ternary baffler/non-baffler arrangement occurs on either scatterplot; instead, axis 1 alone contains the pattern. Axis 1 is arranged with fenestellid-baffled units and localities on the left side of the axis; centrally located are non-baffled units and localities, and to the right are units and localities containing phylloid algae. Overall, fenestellid abundance, and particularly *Minilya*, decreases leftward. Perrin, which contains both phylloidal and *Minilya*-rich samples, is located more centrally than other phylloidal units and localities.

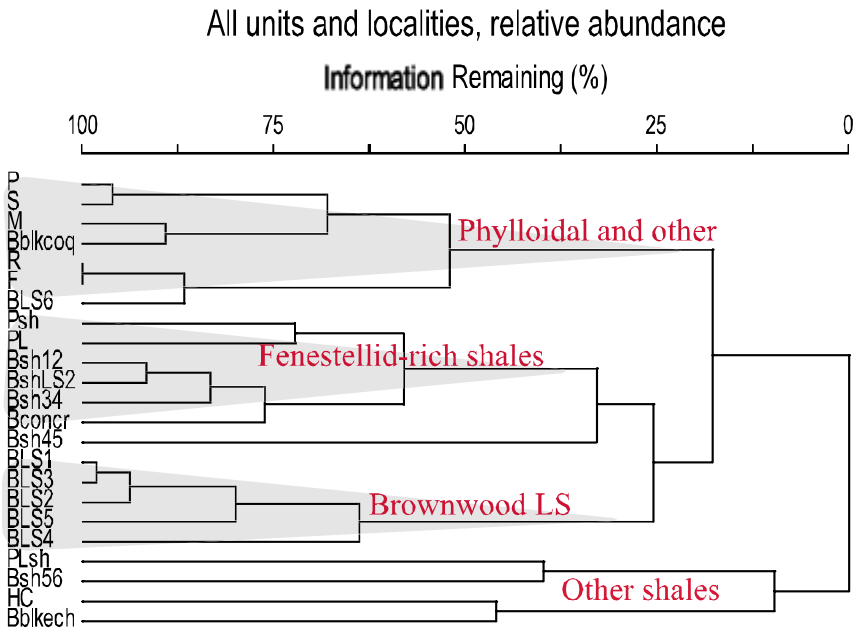


Figure 3.23. Cluster analysis of units and localities using relative abundance data. Relative Sorenson distance measure and UPGMA linkage were used. Clusters were arbitrarily determined at 50% data remaining and less.

Figure 3.24

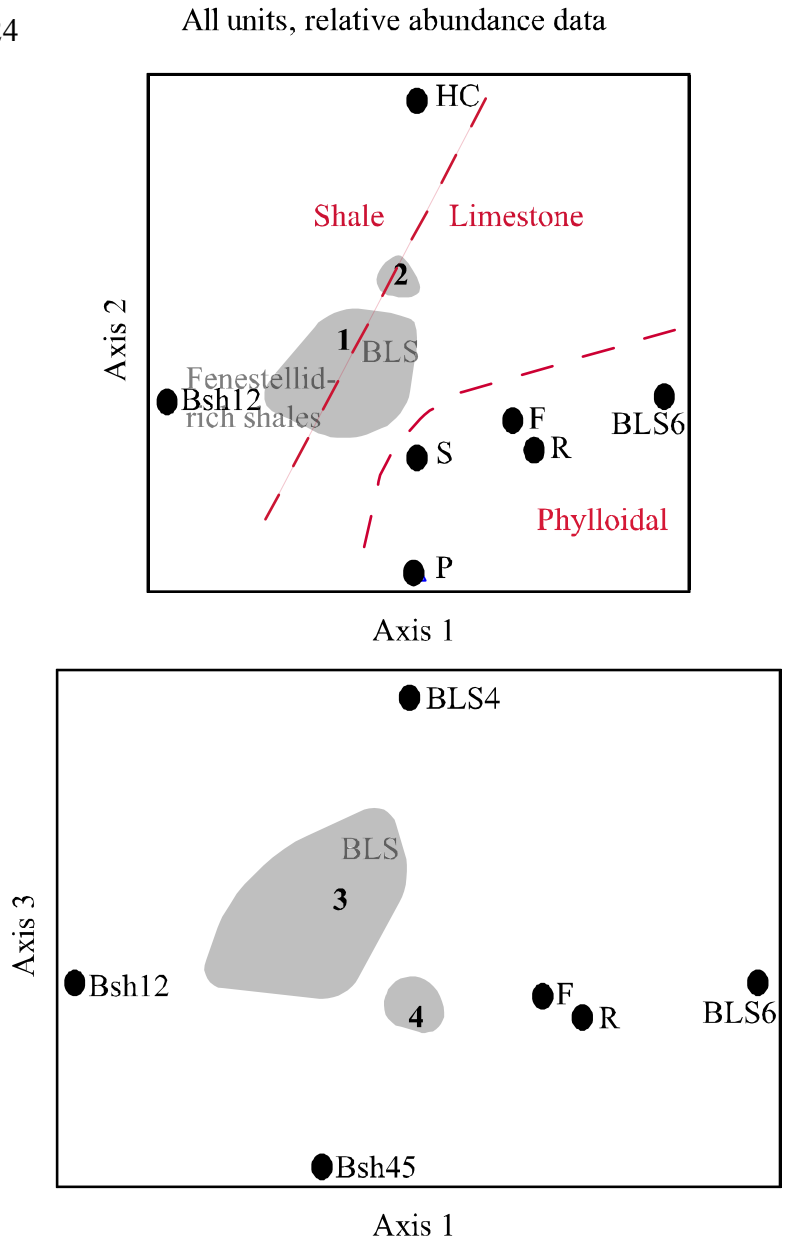

All units, relative abundance data
HC
Shale
Limestone
2
1
BLS
Fenestellid-
rich shales
Bsh12
F
R
BLS6
S
Phylloidal
P
Axis 2
Axis 1
BLS4
BLS
3
Bsh12
4
F
R
BLS6
Bsh45
Axis 3
Axis 1

Figure 3.24. Bray-Curtis ordination of Brownwood samples, relative abundance data. Axis 1 accounts for 43.0% of the original distance matrix and ordinates on *Minilya*- and phylloid algae-rich units with endmembers Bsh12, the shale between Brownwood LS 1 and 2, and BLS6, producing a fenestellid-baffled/non-baffled/phylloid algae-baffled pattern. Axis 2 accounts for 27.4% of the distance matrix, with a total of 70.4% of the total distance matrix explained by axes 1 and 2. Axis 2 ordinates on phylloidal and *Trepospira* plus *Crurithyris*-rich localities with endmembers P (Perrin) and HC (Hickory Creek). Axis 3 comprises 15.0% of the remaining distance, with a total of 85.4% of the total distance matrix explained by axes 1 through 3. Axis 3 ordinates on *Leioclema* and tubuliporate bryozoan and echinoid abundances with endmembers Bsh45, the shale between Brownwood LS 4 and 5, and BLS4. On axes 1 and 2, group 1 contains a loose aggregation of fenestellid-rich shales on the lower right and Brownwood LS on the upper left; group 2 contains a tight aggregation of Bsh56, Bblkech, and PLsh. On axes 1 and 3, group 4 contains Brownwood LS on the top with other localities dispersed throughout; group 4 contains small brachiopod-rich shales.

Ecological Patterns

Cluster analyses of taxa, whether based on samples or units, tend to follow patterns of sample and unit clusters (Figure 3.25). For example, bryozoans, which influence many ordination axes and sample clusters, form a tight cluster in R-mode cluster analysis, and include other common taxa in fenestellid-rich communities, such as crinoids*, Punctospirifer,* and *Desmoinsia.* Similarly, the large brachiopods and other taxa, such as sharks, that characterize the lower two Brownwood limestones, also tend to cluster. When all taxa are included, or when taxa occurring in 6 or less units are culled, *Composita, Antiquatonia*, and echinoids form a tight cluster, although ordering and branch length are somewhat variable.

Baffling fenestellids, which are a major component in cluster and ordination analyses of samples and units, cluster strongly, and include crinoids and those brachiopods commonly found in shales and argillaceous limestones. The other major baffler, phylloid algae, not suprisingly groups at a distance from other taxa. This agrees with the culling of phylloid algae from prior analyses; individual samples as well as units no longer retain a tight association without phylloid algae in the dataset. Although phylloid algae force samples or units to cluster, no trends are evident in the faunal community connecting phylloidal samples from different localities.

In the case of brachiopod-only R-mode cluster analysis, unlike that of sample or unit analysis, brachiopod patterns tend to reflect those of Q-mode (sample) analysis in a very general sense (Figure 3.26). Large brachiopods continue to cluster, as do small attaching brachiopods, but taxon clustering and branch lengths are different from all-taxa analysis in some of the stronger clusters when all taxa are used. For example, in brachiopod-only analyses, *Antiquatonia* and *Composita* are separated, and *Parajuresania* occurs with other productids when all

localities are used, and with the small attaching brachiopods (rather than with bivalves) when Brownwood is analyzed alone.

Generally, *Minilya* and other fenestellids occur more abundantly in shales or argillaceous limestones. *Minilya* (although not other fenestellids) is also fairly abundant in the two high-energy, grainy packstones, Brownwood LS3 and LS5. *Rhombopora* and *Leioclema*, the two ramose bryozoans, also apparently prefer shales and argillaceous limestones, but are more poorly represented in Brownwood LS3 and LS5.

Patterns of baffler dominance are recognizable when graphed against abundances (Figure 3.27). Usually, either *Minilya* or phylloid algae is abundant; where neither taxon is abundant, unbaffled communities occur. *Minilya* is a much more common component of communities than phylloid algae, but neither taxon is completely exclusive. *Minilya* is most abundant in shales and limestones of differing lithologies, whereas phylloid algae occurs in fine-grained limestones only. Like *Minilya*-rich communities, unbaffled communities occur in shales or limestones, except that some *Minilya* is usually present in limestones whereas only *Rhombopora* or tubuliporate bryozoans occur in unbaffled communities in shales.

The high correlation of sharks with *Echinaria* is not graphically apparent, but is the result of two relatively abundant shark-bearing samples from Brownwood LS2 and the hematite crust of LS3. In all other shark-bearing samples, sharks are uncommon and do not occur with *Echinaria*.

In most cases, *Composita* and echinoids co-occur, as is supported both by cluster and correlation analyses. This is not suprising, since both taxa are often abundant in both samples and units, particularly in the Brownwood locality. *Antiquatonia*, when present in samples, often occurs when both taxa are present. This close association between *Antiquatonia, Composita*, and echinoids is likely caused by the high abundances of all three taxa in Brownwood LS1 and LS4, which is also reflected in the repeated grouping of those units and samples in cluster and ordination analyses.

Echinoids strongly influence cluster and ordination analyses. Many limestone/shale patterns on ordination scatterplots also follow a decreasing echinoid trend, indicating that echinoids prefer carbonate environments. The only exception is the echinoid Lagerstätte in the Brownwood black shale. The apparent preference of echinoids for limestones adds support to the hypothesis in chapter 2 that echinoids in the black shale were only transitory or discrete migration events.

All large productids (*Antiquatonia, Reticulatia, Echinaria,* and *Linoproductus*) apparently prefer argillaceous limestones and shales, and although they correlate, have no strong co-occurring abundance patterns. *Linoproductus* occurs in shales more often than the other large productids. *Echinaria* and *Reticulatia* occur only in the argillaceous limestones, but a few *Antiquatonia* also are found in shales.

The large productid – small attaching brachiopod pattern occurring in many ordination and cluster analyses is apparent in the data (Figure 3.28). Generally, when large productids (*Antiquatonia, Reticulatia, Echinaria,* and *Linoproductus*) are abundant, small attaching brachiopods, such as *Crurithyris*, *Hustedia*, and *Punctospirifer,* are less common; the reverse is also true. Small attaching brachiopods are common in shales and in many phylloid algal samples, although there are a few exceptions, such as a few samples in argillaceous Brownwood limestones, most Perrin (highly argillaceous and some phylloid-rich), and all Plattsmouth (dense, non-argillaceous, Virgilian-age) samples. Large productids, as a whole, are more common than small attaching brachiopods in argillaceous limestones; those productids that do occur in shales are less common than the small brachiopods.

Bivalves occur predominantly in shales, although *Myalina* and, particularly, *Aviculopinna* are common in the argillaceous limestones of Brownwood. Because of one bivalve-rich, concretion-bearing sample in Brownwood, all bivalves except *Aviculopinna* cluster strongly together. Although *Aviculopinna* is represented by a few samples in the bivalve dominant community, it is much more abundant in

Brownwood LS1, LS2, and LS4 where it can attain abundances comparable to and occasionally higher than large productid brachiopods. However, *Aviculopinna* and the large productids do not correlate; instead, *Aviculopinna* correlates well with *Neospirifer*, another common, large brachiopod in Brownwood LS1 and LS2.

Encrusters, of course, occur in samples that contain biotic or abiotic host substrates. The majority of epibionts in this study are bryozoans and brachiopods, although a few solitary corals are found in some samples. Fenestellid-rich communities in shales are highly epibiotic, most commonly encrusting other fenestellids, particularly *Minilya* because of its abundance. An unexpected pattern in all fenestellid-rich communities is the pattern of encrustation with regard to interference between taxa. In almost all cases, *Minilya* growth occurred on previously broken conspecific colonies, encrusting or regrowing from the broken ends of the colony at an angle in the same plane or at some other angle to the previous plane of growth. Other fenestellids, particularly *Polypora*, encrusted *Minilya* colonies in such a way that the holdfast overgrew *Minilya* zooecia over an area encompassing multiple fenestrae; interpreting whether *Polypora* encrusters overgrew live *Minilya* requires more sampling and analysis.

Tubuliporate bryozoans are also common epibionts overgrowing *Minilya* in fenestellid communities, as well as occasional brachiopods and *Myalina* from Brownwood shale 4/5. Additionally, these encrusters often occur without attached substrate material, and in some cases, contain recurring xenomorph shapes indicating unpreserved substrate.

Trepospira and *Bellerophon* are the two most common gastropods in this study, but they rarely co-occur and are rarely abundant. *Trepospira* occurs mainly in brachiopod-rich shales, and when all samples are used, has significant correlations with the bivalve *Astartella*, also occurring in brachiopod-rich shales, as well as with the brachiopods *Crurithyris* and *Derbyia*, which are more abundant in shales than in limestones. *Trepospira* also occurs in one carbonate sample of Brownwood LS3, which contains several gastropod taxa. Several Kansas co-

occurrences of *Trepospira* with *Bellerophon* in low abundance, cause a very low but significant correlation. However, this correlation is lost when only Brownwood sample data are used; *Trepospira* instead correlates with *Hustedia* and *Neospirifer texana*, with which it occurs in Brownwood sh5/6. *Bellerophon*, conversely, occurs in a wider range of lithologies, from brachiopod-rich shales to the argillaceous limestones of Brownwood to the grain-rich, high-energy Brownwood LS3. This is supported by significant correlations using data from all localities with *Neospirifer, Reticulatia, Echinaria,* and *Aviculopinna*, with whom *Bellerophon* often occurs in Brownwood LS1 and LS2. However, only *Aviculopinna* significantly correlates with *Bellerophon* when only Brownwood data is used.

Figure 3.25 All samples, all taxa, relative-abundance data

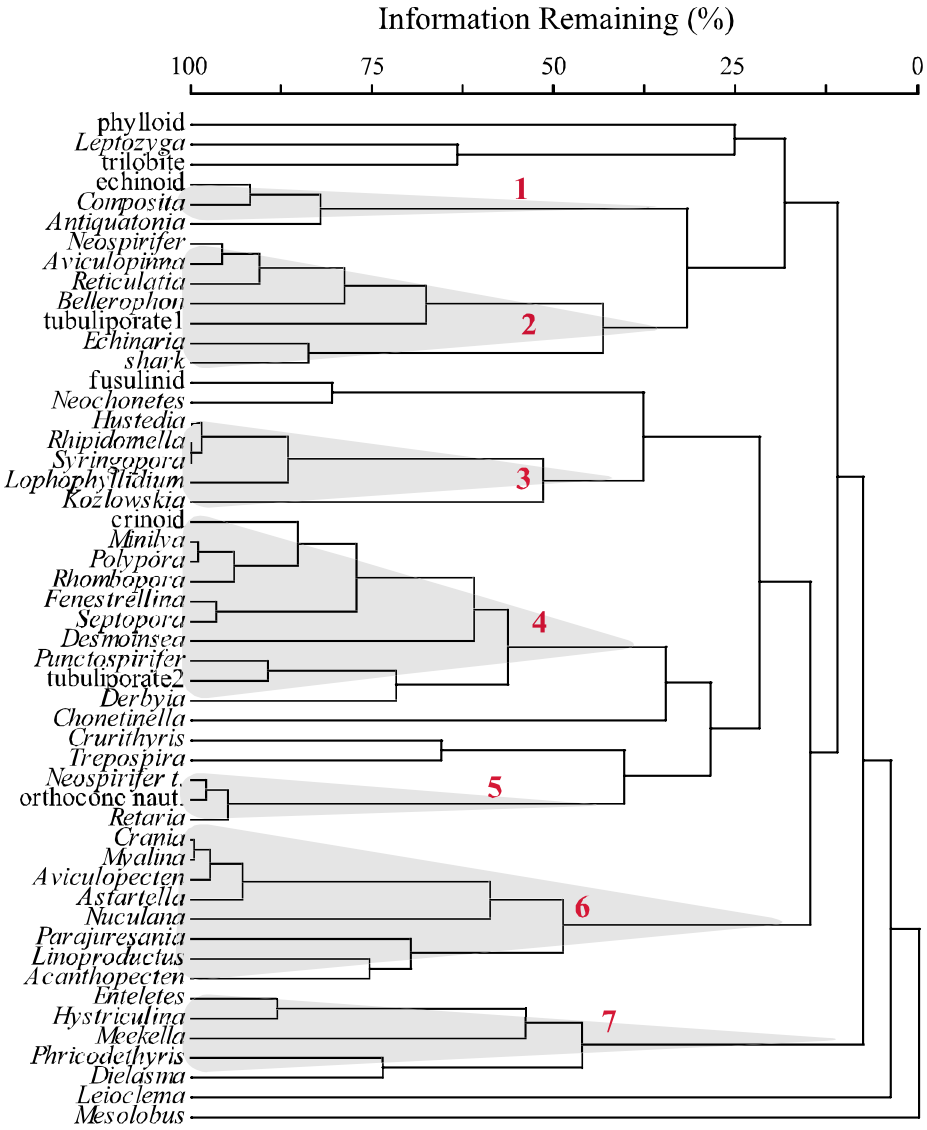


Figure 3.25. Cluster analysis of taxa in all samples using relative abundance data. Relative Sorenson distance measure and UPGMA linkage were used. Clusters were arbitrarily determined at 50% data remaining and less. Cluster 1 contains taxa from Brownwood LS 1 and 4; cluster 2 contains taxa from Brownwood LS 1 and 2 plus some Kansas and Perrin samples; cluster 3 contains taxa more common in Kansas samples; cluster 4 contains taxa common to fenestellid-rich shales, particularly in Brownwood and Perrin; cluster 5 contains taxa common in Brownwood shale 5/6; cluster 6 contains taxa common to the bivalve-rich concretions in Brownwood shale 3/4; and cluster 7 contains rare taxa.

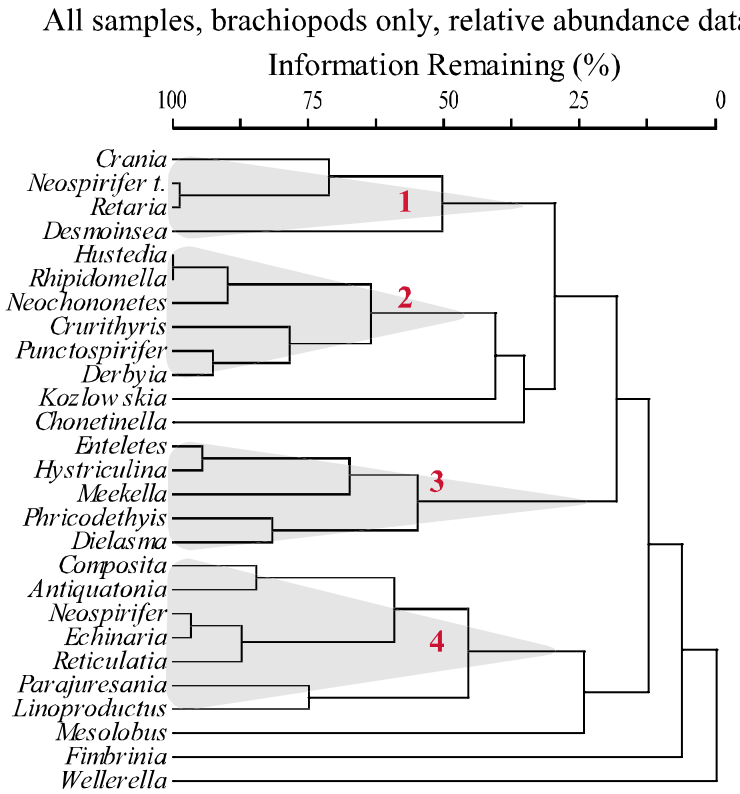


Figure 3.26. Cluster analysis of brachiopods from all samples using relative abundance data. Relative Sorenson distance measure and UPGMA linkage were used. Clusters were arbitrarily determined at 50% data remaining and less. Cluster 1 contains brachiopods from Brownwood shale 5/6; cluster 2 contains brachiopods common in shales; cluster 3 contains rare brachiopods; and cluster 4 contains brachiopods common in limestones.

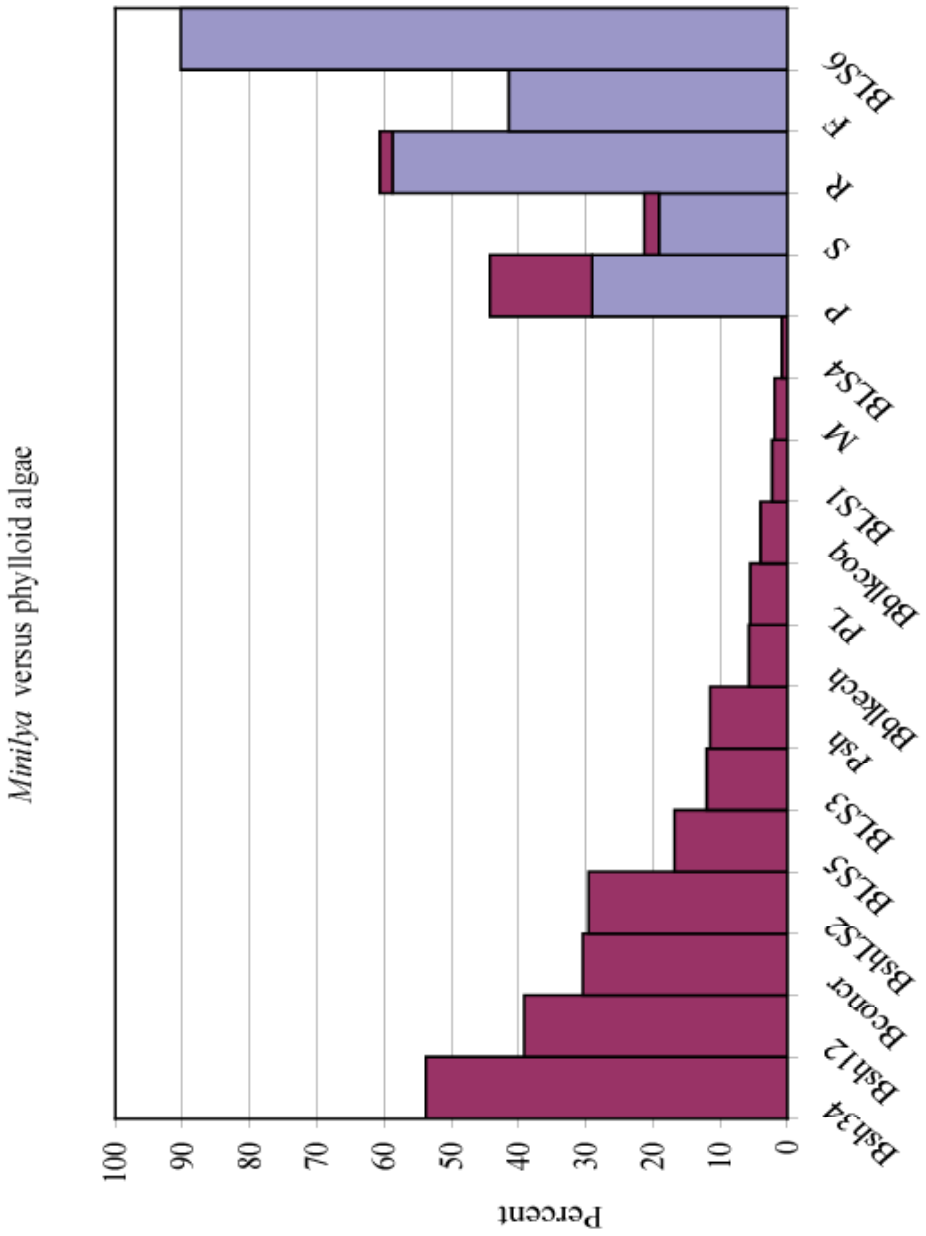


Figure 3.27. Percent of *Minilya* bryozoans and phylloid algae per unit or locality. *Minilya* in maroon; phylloid algae in blue. Most baffled units and localities contain either *Minilya* or phylloid algae.

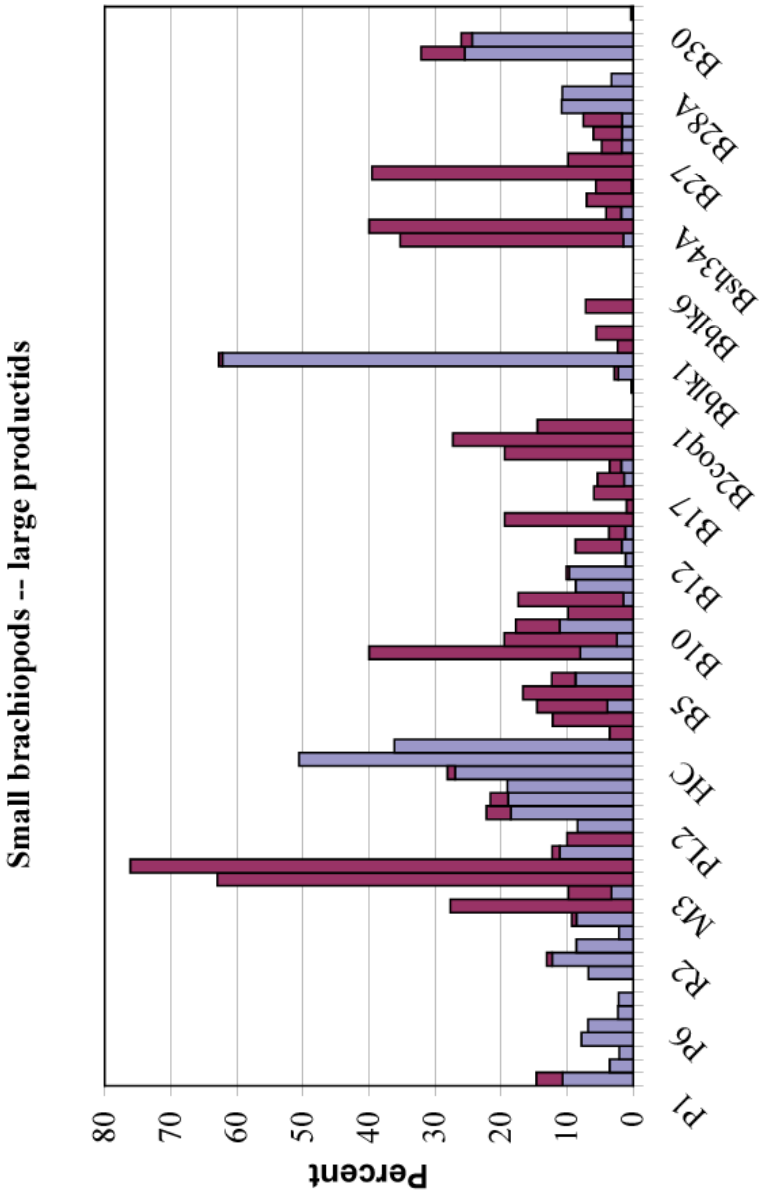


Figure 3.28. Percent of small, attaching brachiopods (*Crurithyris, Punctospirifer,* and *Hustedia*, in blue) and large productids (*Reticulatia, Antiquatonia, Echinaria,* and *Linoproductus*, in maroon) per sample. When productids are present, abundances of small brachiopods are often depressed, and when small brachiopods are present (most often in shales), large productids are rare.

DISCUSSION

Patterns in the Data

This study recognizes four distinct recurring paleocommunity types, characterized by certain taxa and usually occurring in specific lithologies. Large productids (primarily *Antiquatonia* and *Echinaria*), echinoids, *Neospirifer*, *Aviculopinna,* and *Bellerophon* are common fossils in argillaceous limestone, and are named the large productid community, because productids are the most common and easily recognized component of the fossil assemblage. Abundant echinoids and *Composita* recur in fine-grained Brownwood limestone 4, the *Composita*-echinoid community, along with *Antiquatonia*, *Crurithyris, Punctospirifer*, *Rhombopora*, and *Minilya.* The fenestellid-rich community, usually occurring in shales, contains highly abundant *Minilya* and other bryozoans plus crinoids, rugose corals, small attaching brachiopods, and occasional marginiferiformes. In non-fenestellid-rich shales, small attaching brachiopods and encrusting tubuliporate bryozoans, plus various sessile benthos, such as *Neospirifer,* occasional productids, ramose bryozoans, and *Myalina* comprise the small brachiopod-rich community. Other distinct paleocommunities, such as the bivalve-rich community in the concretions from Brownwood shale 3/4, the *Composita-Aviculopecten*-crinoid-dominated community in the black shale packstones, and the echinoid Lagerstätte at Brownwood are not preserved as recurring communities outside of their immediate units in this study. Phylloid algae-rich communities are not considered discrete community types because of differing faunal compositions between localities and the clustering of phylloidal samples within their respective localities when phylloid algae is culled from the data set.

General patterns revealed by ordination and cluster analyses support a limestone-shale differentiation of a baffled/non-baffled gradient that is often driven

by abundant fenestellid bryozoans or phylloid algae. Lithology and energy gradients rarely appear in the ordination data; this may result partly from the lithologically uncoupled nature of fenestellid bryozoan abundances from these localities. Because of high fenestellid abundance, limestones with large grain sizes often cluster, ordinate, and correlate significantly with fenestellid-dominated shales or fenestellid-rich, fine-grained limestones. Phylloid algal limestones are fine-grained, and may indicate a narrower environmental tolerance range of phylloid algae than the fenestellid *Minilya*; however, it is possible that phylloid restriction to such limestones may be preservational in nature, rather than environmental or biological. As seen in thin sections, phylloid algae fragments are completely replaced by blocky spar, whereas fenestellid bryozoan microstructures remain intact. It is possible that phylloid algae may have existed in other environments, but may have been lost to dissolution early in burial or diagenesis.

Depth gradients are not apparent in communities; instead, degree and type of baffling appears to be more important. Fenestellid bryozoans occur abundantly in many different facies and in very different communities, from some samples characterized by large productids in Brownwood LS1 and LS2, to the bivalve-dominated concretions at Brownwood. These paleontologically distinct communities often cluster together in analyses because of fenestellid abundances. Even culling of common taxa, which includes *Minilya*, does not reveal any particular depth gradient based on fauna or lithology. Separation of shales from limestones in ordination and cluster cannot be attributed to depth alone for two main reasons. Based on other studies (i.e., Olszewski and Patzkowski, 2001), the supposed shallow-water communities of this study, such as the bivalve concretions and those in the possibly estuarine black shale, are not ordinated in any logical manner on possible shallow- and deep-water endmembers (Figure 3.29). Also, the

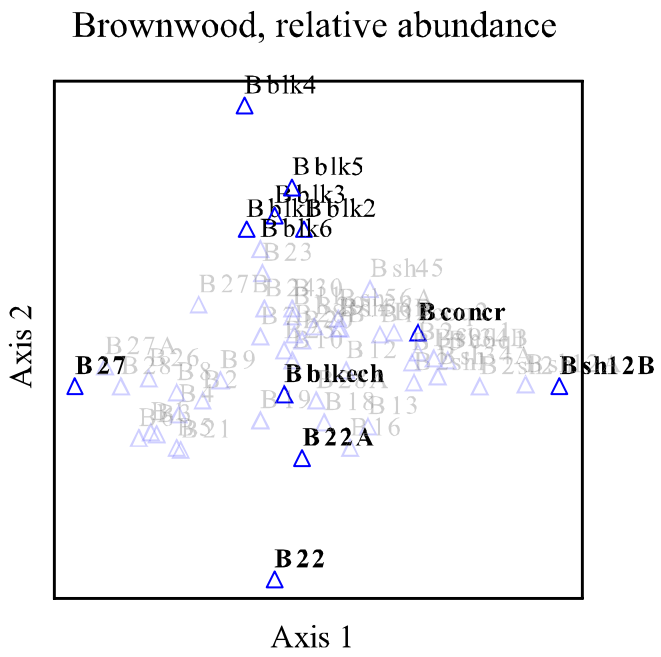


Figure 3.29. Example of lack of depth gradient. Ordination scatterplot (Figure 3.24 minus shaded groups; actual samples pictured) of axes 1 and 2 using relative abundance of Brownwood samples, emphasizing the non-ordered arrangement of shallow-water faunas even though axis 1 contains a general limestone-shale pattern. Bblk samples occur in the nearshore black shale and contain abundant *Composita* and *Aviculopecten* (coq) or the echinoid lagerstatten (ech); Bconcr contains abundant bivalves, *Myalina,* and *Parajuresania* in iron-stained concretions from a gray shale; B22 and B22a are samples are from a grainstone, interpreted to be from a high-energy environment and contain many small gastropods, *Minilya*, and echinoids; Bsh12B is a fenestellid-rich shale sample; and B27 is a *Composita*- and echinoid-dominated sample from limestone 4.

influence of siliciclastic input in Pennsylvanian rocks of north-central Texas was highly variable through time, meaning that shales may not always be the shallowest part of the section and instead may exist as a result of high terrigenous input.

A brachiopod-only depth gradient could be interpreted based on lithology if other fossil data was ignored. Small brachiopods are very common in shales, whereas productids are common in limestones. In non-brachiopod taxa, communities in shales are highly variable, and fenestellid-rich or small-brachiopod-rich communities are difficult to place in a faunal-based depth gradient. Lithologic differences in depth are difficult to ascertain in Winchell Formation rocks because of varying amounts and aerial extent of siliciclastic input through time. Therefore, when all fossil data are used, it is apparent that communities in this study are affected by multiple environmental and biotic controls rather than depth-associated factors alone.

A biological-mediation gradient can be proposed for the communities studied. In some ordinations, the scatterplots result in a ternary arrangement of fenestellid-, phylloid algae- and non-baffler-samples (all-data ordination, figure 3.9; Brownwood ordination, figure 3.24; pattern, figure 3.30). Communities that are extremely baffled, such as those with highly abundant phylloid algae or fenestellids, and non-baffled communities containing echinoids and various large brachiopods are deficient in taxa that characterize other endpoints in the ternary arrangement. Overall, the ternary pattern of bafflers and non-baffled communities represents a continuum. For example, on the entirely baffled axis of the ternary diagram, as *Minilya* decreases in phylloidal samples, phylloid algae abundances increase. Additionally, on the fenestellid-baffled/non-baffled axis, *Minilya* is present and at times abundant in the large brachiopod- and echinoid-rich limestones at Brownwood.

Fenestellid-rich communities and communities that are unbaffled were generally recurrent in taxon lists and abundances, with some significant differences such as the high abundance of *Chonetinella* in the fenestellid-rich Brownwood

LSsh2. Extremes in abundances may reflect recruitment/species pool variability through geologic time encompassing the sampled rocks, or may be the response of taxa to preferred habitats. Allowing for a few exceptions of unusual, single-taxon abundances (such as *Neochonetes* in the fenestellid-rich shale above Brownwood limestone 2) within communities, diversity and abundance patterns of non-phylloidal communities recur.

Primary and secondary tiering is readily apparent in all communities. In productid-rich communities of argillaceous limestones, primary tiers include brachiopods on the lowest tier and fenstellid and crinoids on upper tiers. Secondary tierers include few brachiopods and encrusting bryozoans. Fenestellid-rich communities in shales are very complexly tiered, with many of the bryozoan taxa being both the primary and secondary tierers. Small-brachiopod-rich communities in shales contain brachiopods in the lowest tier and ramose bryozoans and crinoids in the upper tiers, but likely include an unknown possible organism in the upper tier to support the abundant epibionts. In *Composita* and echinoid-rich communities of Brownwood limestone 4, brachiopods comprise the lower primary tier with some bryozoans and echinoids in the upper tiers; this creates additional complexity because of the abundance of highly mobile echinoids.

Brachiopods tended to form two distinct clusters. Large brachiopods, including large productids plus *Neospirifer* usually occurred in limestones; small, non-strophomenid brachiopods, comprised mostly of pedunculate attachers, are characteristic of shales (i.e., Figure 3.28). Small attachers essentially occur in any community where attachment sites are available, but small brachiopods are more abundant in shales containing both obvious attachment sites as well as in shales lacking sufficient preserved substrates. In non-fenestellid shales, attaching

Figure 3.30

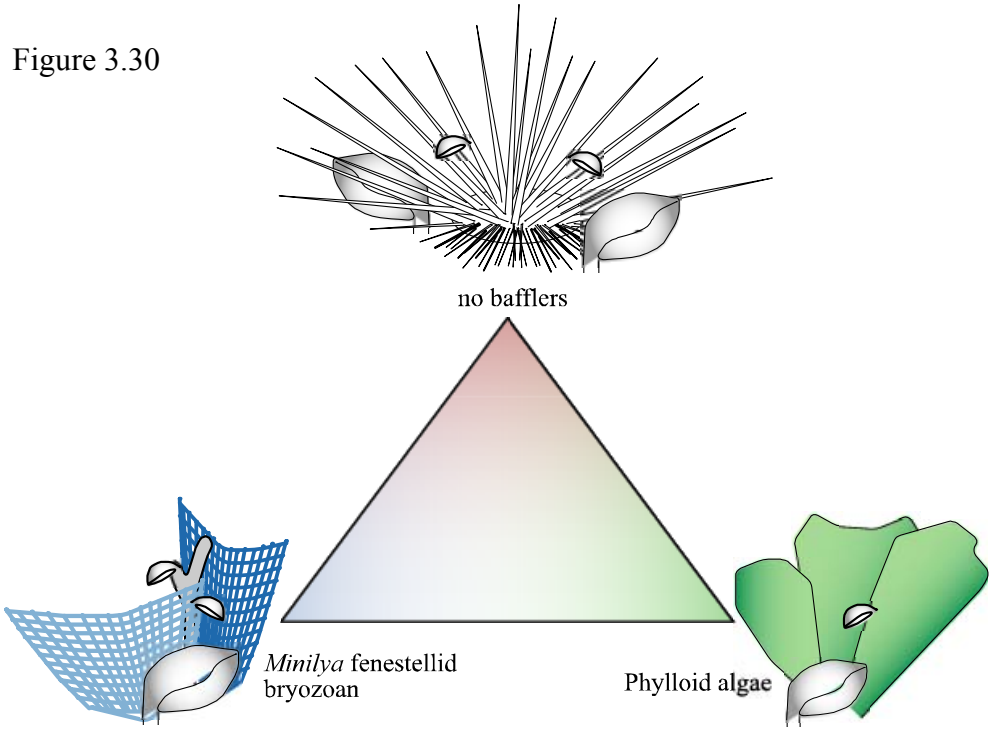


Figure 3.30. Ternary arrangement of baffled communities seen on ordinatio scatter plots. Fenestellid-baffled, unbaffled, and phylloid-algal-baffled communities form end members of the three gradients that often are in a ternary arrangement in ordination scatter plots. Each side of the diagram represents a gradient between endpoints. Fenestellid-baffled communities include abundant *Minilya*, *Polypora, Septopora, Fenestrellina, Rhombopora*, and small brachiopods. Non-baffled communities are mostly characterized by large brachiopods, echinoids, and *Aviculopinna*. Communities dominated phylloid algae often contain different faunas.

brachiopods often far outnumber potential attachment sites on other brachiopods, such as *Derbyia, Parajuresania, Linoproductus,* and *Composita*. In these small-brachiopod-rich communities, encrusting tubuliporate bryozoans are common, but are often unattached to a substrate or retain a xenomorph of the host surface. This would suggest the prior presence of unpreserved, soft-tissue or readily-dissolved attachment sites in these shales, such as algae or aragonitic skeletal material.

Small attaching brachiopods also occur more commonly in fenestellid-rich shales than limestones, but are preserved as loose specimens free of any attachment site. Other common epibionts in these shales include encrusting tubuliporate bryozoans, other fenestellids, *Rhombopora*, and *Lophophyllidium,* all of which were found attached to fenestellid bryozoans, mainly *Minilya*. When encrusted by any taxon, *Minilya* growth was disrupted by interference overgrowths of other taxa, and calcification of epibiont sites in distinct patterns. *Lophophyllidium* encrusted only an area equal to its body size but affected *Minilya* zooecia by covering them. All epibiont sites found on *Minilya* in these shales were characteristic of bryozoan and rugose coral attachers; in no case could an attachment site be attributed to a brachiopod. However, pedicle traces are small and easily can be overlooked (Bromley and Surlyk, 1973), so brachiopod attachment to fenestellid bryozoans remains a possibility. As in small brachiopod-rich shales, encrusting bryozoans often contained no host surface or a faint xenomorph of the host surface, which, as often as not, had a non-fenestrate pattern.

Brachiopods such as *Rhipidomella, Derbyia,* and *Parajuresania* occurred frequently in shales and less frequently in limestones, providing further evidence of environmental preferences of these taxa. *Composita* and *Neospirifer* were largely cosmopolitan, occurring in most communities. Large productids other than *Parajuresania* tended to prefer lime-mud substrates, primarily occurring in argillaceous and fine-grained limestones with low abundances of baffling organisms.

The large brachiopod (productids plus *Neospirifer*) – small attaching brachiopod pattern that recurs in several ordination scatterplots (i.e., figure 3.9) essentially reflects the preferred substrates and lithologic occurrence of the taxa. Small attaching brachiopods require a surface on which to attach; in muddy sediments, these roles are often filled by organisms elevated off the substrate, such as crinoids (Sandy, 1996) and echinoids (chapter 2; Schneider, in press). In this study, shales generally contain many small attaching brachiopods and few co-occurring large productids. In argillaceous limestones, however, large productids are much more common, either artificially depressing relative abundance of small brachiopods, or in most cases, reflecting an actual decreased abundance of small attaching brachiopods. Large brachiopods, most of which were sediment floaters, apparently did not provide suitable substrate to support abundant attaching brachiopods, particularly when other substrates such as crinoids were rare. Conversely, small brachiopods may have been intolerant of paleoenvironments of argillaceous limestones, although this is unlikely because small brachiopods readily occur in other limestones and shales.

The productid brachiopod *Echinaria* grouped strongly with sharks in cluster analyses; this is a highly significant association in Pearson's correlation, but other large productids and *Neospirifer* also correlated significantly with sharks. This is likely caused by the overall abundance of shark material in Brownwood LS1 and LS2, and in particular, several beds that contained a high abundance of shark debris. Shark material is mostly lost upsection with the disappearance of large productids; this could weakly suggest possible predator-prey relationships between sharks and large productids, but is unlikely because of lack of predation traces.

The bivalves *Aviculopinna, Acanthopecten*, and *Myalina* were not restricted to the few bivalve-rich communities. *Aviculopinna* and *Myalina* were abundant in argillaceous shales with large productid brachiopods, with *Aviculopinna* occasionally meeting or surpassing abundances typical of the co-occurring large brachiopods. Although lack of preservation of other bivalves cannot be discounted

for paleoenvironments of argillaceous limestones, gastropods such as *Bellerophon* and *Trepospira* were also present, although not abundant, indicating that less-preservable, aragonitic taxa had the potential of being represented. *Acanthopecten* occurred in the Brownwood black shale packstones and bivalve concretions usually indicative of nearshore environments, particularly in association with *Composita* brachiopods or other bivalves.

The paleosol above limestone 4 at the Lake Brownwood Spillway forms a boundary for community types at this Winchell Formation locality. Below the boundary, limestones are characterized by large productids, abundant echinoids, crinoids, *Neospirifer, Composita*, fenestellid bryozoans, *Aviculopinna*, *Myalina,* and sharks. Above this boundary, the two limestones are either commmunities containing fusulinids, crinoids, echinoids, and *Minilya* (LS5), or phylloid algae with abundant *Composita* (LS6). Shales below the boundary are almost exclusively fenestellid-rich, with the exception of communities in the bivalve-rich concretions and the black shale. Above the paleosol boundary, shales are brachiopod-dominated and contain molluscs, such as *Myalina*, *Trepospira*, and orthocone nautiloids, and, when present, a distinctly different crinoid assemblage. This suggests a major shift in community composition, either from a major change in environmental conditions or changes in recruitment/species pool availability, from lower to upper Winchell Formation at this locality.

Holterhoff (1996) restated an important point when considering community data at different scales: even if a community is controlled, on a regional scale, by variations in environment and recruitment resulting in independently reacting taxa, communities that are local and contemporaneous are indeed influenced by organism interactions, such as predator-prey interactions and resource competition. Even in cases where taxa do not directly compete for food resources, substrate resources may be important, as evidenced in the fenestellid-rich communities. Although the recurring patterns of fenestellid-rich communities appear synchronized with lithology, the physical and dominance structures of these communities may instead

reflect spatial competition between fenestellid, ramose, and tubuliporate bryozoans. This is seen most strongly in non-interference growth of *Minilya* on conspecifics, and interference growth of *Polypora, Rhombopora*, and encrusting tubuliporate bryozoans on *Minilya* and on each other.

Outside of rare epibiont competitors, it is difficult to observe direct competition in the fossil record. Even in communities where competition is not evident, spatial resources are still important considerations for the settling larva, which must a have suitable attachment site and room to grow. Additionally, attaining sufficient food while limiting competition from neighboring organisms is also important, but equally as difficult to discern in the fossil record. One study by Hermoyian et al. (2002) used a limiting similarity model to reconstruct the potential for competition between brachiopods; each brachiopod species within communities was morphologically distinct from all other brachiopods. Although not stated, their work also supports the idea that morphologically similar brachiopods tended not to co-occur in assemblages, which also limits interspecific competition.

In Brownwood communities, competitive interaction appears to have been infrequent. Using the idea of limiting similarity, large productids in general often co-occur, and may not have experienced high levels of competition between morphologically similar taxa. This apparent, general lack of competition can be explained four ways: spatial and food resources were not limiting and therefore sufficient for multiple, contemporaneous, morphologically-similar taxa to coexist; taxa were time averaged and therefore, not contemporaneous; taxa simply did not compete, indicating different methods of resource acquisition; or morphology of potential competitors must be more precise than a general category of large productids. As Hermoyian et al. (2002) pointed out, the morphological feature under scrutiny must be relevant to the investigation of competition for a particular resource; therefore, general size and bauplan may be too vague to indicate competition.

Certainly resources appeared to be sufficient for many large productids to coexist, and if time-averaging was minimal and at least some portion of individuals on bedding planes were contemporaneous, competition between large productids in general appeared to be nonexistent. Both *Echinaria* and *Linoproductus*, the largest of the productids, correlate in Brownwood samples, but only co-occur in 7 out of 28 total samples containing either taxon. The two taxa do not correlate when all samples are considered, and co-occurrence is 8 out of 35 samples containing either taxon. Additionally, in those few samples of co-occurrence, when one taxon occurs, the other is often conspicuously less abundant. These data and analyses, combined with the fact that *Linoproductus* also is tolerant of substrates composed entirely of siliciclastic muds (indicating environmental differentiation from *Echinaria*) suggests possible competitive interactions. The same is true for the smaller taxa of the large productid category, *Reticulatia* and *Antiquatonia*. Neither correlate in either Brownwood or all samples analysis, but when both taxa are present (5 out of 31 occurrences of either taxon), one is often much less abundant, and *Antiquatonia* has a wider range of substrate tolerances. Although these patterns may simply reflect environmental preferences, the possibility of competitive interaction exists for each pair of taxa, but not for large productids in general.

Predation interactions are more obvious when predators or predation scars are present. In lower Winchell Formation communities, predation by sharks on large productids may have occurred; shark presence correlates strongly with large productids in Brownwood-only and in all-sample analyses. Direct traces of crushing predation, however, are difficult to observe in the fossil record unless an organism was crushed, survived, and managed to repair itself. Such predation scars are rare in Pennsylvanian fossils, and may either reflect decreased crushing predation or the increased efficiency of crushing predators (Vermeij, 1987; Leighton, 2002). Boreholes in brachiopods were occasionally noted in productids from lower Winchell Formation communities in Brownwood, but did not occur in any of the samples in this study. The rarity of boreholes is not unusual for

Pennsylvanian communities because Late Paleozoic drilling predation appears to have been rare (Kowalewski et al., 1998; Hoffmeister et al., 2001).

An important, although often overlooked, area of community interactions in data sets using all fossil data is that among epibionts and between epibionts and their hosts. The most obvious interactions in this study occur in the fenestellid-rich shale communities, where overgrowths of *Minilya* by other taxa are obvious, assuming that the *Minilya* communities were alive at the time of encrustation. Less obvious are the effects of epibionts on other organisms, but with more careful analysis, possible effects can be discerned. The echinoid community at Brownwood contains abundant epibionts, particularly *Crurithyris*, *Minilya*, and encrusting tubuliporate bryozoans, on the echinoid spines. As discussed in chapter 2 and in Schneider (in press), possible effects on echinoids may be decreased spine movement and increased weight, but overall effects are minor for the echinoid and greater for the epibionts, such as suitable substrate, transport, and increased water currents. Epibionts in other communities may also have had minor effects such as shell weakening, energy resources spent on shell repair, and additional weight if these organisms were alive at the time of encrustation, such as Brownwood shale 4/5 barnacle borings and bryozoans on *Myalina* and *Derbyia*.

Adding epibionts to a community emphasizes several important facts about the community: substrates must be available, whether preserved or unpreserved, diversity is increased, and resources must be sufficient to support the increased diversity and biomass in the community. In some samples of this study, tubuliporate bryozoans clearly indicate the presence of other, unpreserved substrates. Brownwood shale 5/6, which has high abundances of *Crurithyris, Punctospirifer,* and *Hustedia* as well as encrusting bryozoans, had sufficient substrates to support the brachiopod epibiont portion of the community. Clearly, in this assemblage, preserved substrates are extremely limited; other, benthic brachiopods are small, crinoids are extremely rare, and echinoids are lacking. Therefore, to support epibionts in Brownwood shale 5/6, the volume and type of

substrate needed is simply not preserved, indicating the prior presence of some other inorganic surface or organic substrate, such as lightly calcified or aragonitic organisms or algae.

The idea that epibionts may indicate missing substrate strongly implies a higher community diversity than skeletal material could directly represent. Occasional xenomorphs on epibiont surfaces in the fossil record have indicated distinct host organisms and surfaces, such as in oyster attachment scars containing molds of other organisms (Evans and Todd, 1997), and diversity can be directly measured. Unfortunately, xenomorphs in encrusters of this study, such as angular, globe-like, and blade-like impressions in tubuliporate bryozoans, are either vague or enigmatic and cannot be securely identified even at the level of organic or inorganic composition.

Adding epibionts to a community automatically increases diversity and biomass, and with the addition of attaching organisms indicates the presence of resources to support these organisms. Spatial resources, such as appropriate substrate, are obvious necessities, but other resources such as food are also important. Lescinsky (1996) suggested that the proportion of epibionts in a community reflects primary productivity. Although this is problematic in the sense that epibionts as well as other taxa are dependent on preservational processes, and primary productivity cannot be directly measured, this idea of increased primary productivity may be valid in the sense that more resources are necessary than if epibionts were not present in the community. In other words, epibiont presence in any community indicates a higher level of resources than if epibionts did not exist.

Detection of r- and K-selected taxa in the fossil record is not always obvious as in modern communities, but can be detected by using occurrences among multiple localities and paleoenvironments. Taxa that are r-selected are tolerant of a wide range of environments and have a relative lack of specialization whereas K-selected taxa are less likely to occur in multiple and unstable environments and show a greater degree of specialization (Pianka, 1970; Levington, 1970; Valentine,

1971; Hickey and Younker, 1981). In this study, the brachiopod *Composita* is clearly r-selected because it is present to abundant in nearly every sample, regardless of lithology. Likewise, *Neospirifer, Rhombopora,* and echinoids, in particular *Archaeocidaris*, may also show a degree of r-selectivity because they are common, although not as pervasive as *Composita.* *Crurithyris* and several Pennsylvanian chonetids (although not *Chonetinella*) also were described as r-selected by other authors (Hickey and Younker, 1981). Taxa that are K-selected are more difficult to discern in this study. It is possible that the large productid brachiopods *Reticulatia* and *Echinaria* may be K-selected because they occur only in the argillaceous limestones.

This study generally agrees with the notion of regional species pools, local biotic interactions, and environmental tolerances put forth by Holterhoff (1996). It is likely that a regional species pool, or two similar regional species pools for Texas and Kansas, was the source for all communities in this study, with larva of each species responding to habitat preferences during settlement. Larger temporal scales in this study reveal several community types that tend to track lithologies; however, two community types – the fenestellid-dominated communities and the small-brachiopod communities – may have biotic constraints as well. In both cases, substrates were necessary for abundant and characteristic attaching organisms, resulting in a biologically influenced, three-dimensionally structured community. Fenestellid-dominated communities obviously fulfilled the substrate role via abundant *Minilya*; communities characterized by small, attached brachiopods were dependent on some unpreserved substrate, as documented by bryozoan xenomorphs and epibiont abundances.

Unit and locality analyses agreed with broad patterns produced by individual sample analyses. Such analyses reduced the data set to be analyzed and smoothed out variability in abundances between samples. Although large-scale patterns agreed with fine-scale sample analyses, the large-scale units and localities missed

variability within those units, such as samples that were more similar to and clustered with samples from other lithologies, localities, or units.

Community recurrence is strongest within localities or lithologic units as evidenced by repeated patterns in cluster and ordination analyses; exceptions to this include phylloid algal limestones and small brachiopod-rich communities in shales. Likewise, there was stronger cohesion between Brownwood units than with any other locality, including other Winchell Formation localities. This suggests that community recurrence in this study reflects a geographical constraint, and is strongest within a single locality or unit than across localities or between basins. A similar pattern of variance differences was seen in Devonian Hamilton Group outcrops by Lafferty et al. (1994). Within-outcrop, sample-based variance was less than the variance described between outcrops of their study; therefore, the geographic patterns of this Pennsylvanian study are not unique, although the cause these geographic constraints remains unexplained. Although between-outcrop variance may be a reflection of the limited number of localities, the number of samples and sample sizes should have captured any mixing between localities. The geographical nature of these results may also simply be emphasizing the heterogeneity of north-central Texas Winchell Formation outcrops, resulting in distinct clusters of the three Winchell Formation localities separate from the Kansas outcrops used in this study. It is also possible that species pools were spatially limited and smaller than the entire Midland Basin shelf, or that paleoenvironmental differences between outcrops were distinct enough to cause community similarity within an outcrop to override any similarities between outcrops.

Use of All Available Data

Observations of ecological interactions, community structure, and recurrence patterns are emphasized by using all fossil data. Proxy data, assemblages of one or

few taxa, and use of indicator species used to analyze whole community patterns and processes are insufficient to capture the holistic nature and details of community recurrence and paleoecological patterns. Even the omission of phylloid algae from data sets significantly weakens the pattern of biologically mediated, baffled environments. In all cases brachiopod- and bryozoan-only analyses missed the ternary baffled/non-baffled community gradient, strong clustering of units, and the strong ecological segregation of localities. Limestone/shale patterns appeared in most ordination analyses, but were entirely lacking in bryozoan-only analyis.

The use of indicator taxa, such as the non-strophomenid brachiopods used by Peters and Bork (1999) is entirely inappropriate for capturing whole-community patterns. Use of relative abundances of brachiopods- or bryozoans-only in ordination resulted in the loss of the ternary baffling gradient. Neither analysis revealed baffler patterns in the data, nor the large productid – small attaching brachiopod patterns seen in ordination scatterplots. Therefore, to maximize capture of all such patterns and to better interpret processes in community analyses, complete fossil data are necessary; indicator taxa truly may not be indicators of fossil community patterns or processes.

This does not imply that such methods of limited data are entirely insufficient; data and analyses to be used are always dependent on the questions asked or hypotheses posed as well as the scale of the question. If, for example, this study posed a broad-scale hypothesis of 'limestone communities are distinct from shale communities' based on brachiopods or bryozoans, the data might support such a position. In investigating similar large-scale patterns from the Midcontinent, Olszewski and Patzkowski (2001) revealed a striking but not suprising differentiation between bivalve-dominated and brachiopod-dominated communities. These patterns were then thought to be the result of environmental gradients such as oxygenation in the water column (brachiopods) and restricted-open habitats (bivalves); however, a similar bivalve- and brachiopod-pattern was not found in this study, either in Brownwood or inclusive of all samples. Bivalves, such as *Myalina*,

Aviculopinna, Acanthopecten, and *Astartella* were common in many communities containing abundant brachiopods. Brachiopods were present, and at times, abundant, in possible restricted and nearshore communities, such as the estuarine black shale and the brachiopod shales. Use of limited taxa may or may not reveal a real ecological pattern; without additional data using all fossils, such patterns using limited data cannot be tested for actuality. Interactions and other important biological processes such as significant mediation of environments by bafflers and presence of attachment sites are lost in considerations of few taxa.

The method of using all fossil data does pose difficulties. Collecting all fossil data is time-consuming and requires sufficient knowledge of the taxa and nature of the taphonomy and paleoenvironments. Addition of microfauna, which would provide yet another level of detail to community analysis, is also labor-intensive and not readily carried out on the outcrop surface or the surface of a screening table. The use of whole community data also produces additional noise in the data set at very fine scales; larger patterns must be discerned and generalized to help sort out actual fine-scale patterns and processes from noise.

CONCLUSIONS, CHAPTER 3

Implications for Paleoecology

As stated previously, the nature and scale of any study will determine whether all fossil data are necessary or not. Use of all fossil data becomes a powerful tool; community patterns become strongly apparent, organism covariances, interactions, and tolerances are more readily observed, and processes behind community structure can be more readily captured.

Previous work in community paleoecology recognized the possibility of capturing fine-scale ecological processes and community structure in fossil data

(i.e., Hickey and Younker, 1981). Recently, studies have emphasized fossil record inadequacies, with many paleoecologists going so far to state that only large-scale diversity patterns are recoverable in the fossil record and that fine-scale processes are completely lost to the researcher (i.e., Valentine and Jablonski, 1993). Although the current bias recognizes only the possibility of biodiversity study, many researchers have been investigating fine-scale paleoecological interactions, such as predation, competition, spatial relationships, and epibiosis. Investigating ecological phenomena in the fossil record has required a union of current ecological theory with new techniques to account for and take advantage of the temporal and preservational nature of the fossil record (i.e., predation investigations of Leighton, 2002; "Limiting Similarity" competition investigations of Hermoyian et al., 2002; Neighbor Proximity Analysis, Leighton 2001; epibiosis as a proxy for primary productivity, Lescinsky, 1997). Community paleoecology based on taxon lists emphasizes recurrence and change in biodiversity and/or environment, with little to no attempt to investigate community structure, trophic relationships, or biological interactions. This is not to say that biodiversity patterns are not important, rather that paleoecology should not be isolated from modern ecology. By pushing beyond the paradigm of an inadequate fossil record, modern ecological theories and questions can be investigated using the fossil record.

Some of the tools necessary for ecological study in the fossil record are already in place. Investigation into predation, competition, and epibiosis have been ongoing; exploration into spatial relationships and trophic levels are also being increasingly studied. With techniques created to study ecological phenomena in deep time, current hotspots in ecology, such as spatial relationships, trophic relationships, and top-down/bottom-up controls on ecosystems, are possible to study using carefully collected and analyzed paleontological data. Because of the deep-time advantage, such ecological theories can be investigated through recurrence, in different faunas and environments, throughout development of ecological phenomena through time, and as reactions to environmental or ecological crises.

Like biological interactions in the fossil record, community paleoecology will need new techniques and approaches to answer pure ecological questions. The purpose of this study was not to discover new techniques, but to investigate if ecological-scale investigations are possible in the fossil record, or if the fossil record is simply too inadequate. The discoveries of biological environmental mediation in non-reefal communities and spatial competition in fenestellid-rich communities were made possible through commonly used techniques (Bray-Curtis ordination and cluster analysis), indicating that insights into community structure and processes are indeed possible in the fossil record with careful sampling and analysis of results. Therefore, as new techniques are developed to investigate community paleoecology, researchers can push beyond biodiversity issues when necessary and explore relevant ecological phenomena.

Modern ecology can be studied on short time scales and over distance; with these variables, results can be projected into the future with limited success. The fossil record is unique from modern ecology in that it includes a time variable, and that communities have been shown to recur (or not) on various temporal, spatial, and hierarchical scales. Therefore, the fossil record can be an excellent setting to investigate modern community hypotheses because of the recurring nature of paleocommunities, given new, exclusively paleoecological techniques and an open mind. The fossil record will never contain all data necessary to reconstruct a community, but with fine-scale investigations, means for recovering missing data, such as xenomorphs in tubuliporate bryozoans and carbonate environmental preferences of echinoids, can be discovered.

Results of this Study

This study recognizes four recurring community types in the Winchell Formation and contemporaneous outcrops in Kansas: 1) large productids,

Neospirifer, echinoids, *Aviculopinna,* and *Bellerophon* in argillaceous limestones; 2) highly abundant fenestellids plus other bryozoans, small attaching brachiopods, crinoids, and occasional marginiferiformes in shale; 3) small attaching brachiopods and tubuliporate bryozoans plus various sessile benthos such as *Neospirifer,* occasional productids, and *Myalina*; and 4) abundant *Composita* and echinoids with *Antiquatonia, Crurithyris, Punctospirifer, Rhombopora,* and tubuliporate bryozoans. Other distinct communities are present, including those found in the echinoid Lagerstätte in the Brownwood black shale; *Composita-Acanthopecten* packstones in the Brownwood black shale; and diverse bivalves plus *Parajuresania* and *Minilya* in iron-stained concretions, but none of these communities recur outside their respective units.

In ordination, a strong limestone-shale pattern repeatedly occurs on major axes, but no gradient, such as depth, energy, or percent siliciclastics, is seen. Because this occurs using both relative abundance and presence-absence data, the pattern is real and not an artifact of differences between sampling limestones and shales.

A biological mediation gradient is proposed for the communities herein, in a ternary arrangement. The three endmembers – fenestellid-baffled communities (fenestellid-rich shales, and possibly the bivalve concretion community plus a few *Minilya*-rich limestones), phylloid algae-baffled communities (phylloid algal limestones), and non-baffled communities (all others) – are all gradational, with no distinct boundaries. This does not discount the presence of bafflers in the prior live communities in the non-baffled end of the gradients. Baffling organisms, such as non-calcareous algae, may have originally been present, simply unpreserved.

Above Brownwood limestone 4, there is a major shift in community types from fenestellid-rich shales and large-brachiopod-rich limestones below to small-brachiopod-rich shales and one phylloid algal limestone above. The cause of this is unknown, and may either be a major shift in environmental conditions or a change in the regional species pool.

Competition between all large productids is not evident, but possible competition may have existed between *Linoproductus* and *Echinaria* as well as between *Antiquatonia* and *Reticulatia.* Hypothesized competition is supported by morphological and size similarity in each pair of taxa and tolerance of *Linoproductus* and *Antiquatonia* for increased siliciclastics.

Epibionts, including high abundances of small attaching brachiopods and detached encrusting tubuliporate bryozoans, strongly indicate the presence of unpreserved host substrates in shales. However, the biotic/abiotic nature and calcification of the substrate is unknown.

In this study, *Composita* is determined to be an r-selected taxon. This is supported by the presence, and often high abundance of *Composita* in most communities.

Fenestellid-dominated shales contain strong evidence for interference competition via encrustation and overgrowth of less-abundant bryozoans on *Minilya*, disrupting *Minilya* colony growth. Conversely, *Minilya* conspecific encrustation occurs on the ends of broken colonies, with no disruption of previous zooecia.

Use of all fossil data at fine spatial and temporal scales reveals more details about patterns and processes in communities than do single- or few-taxon assemblages alone. Therefore, caution is suggested in the use of indicator taxa or limited taxon lists to represent whole-community patterns and processes. Because acquiring all fossil data takes use effort, the nature of the research question is important to consider in determining whether to use all fossil data or limited taxon lists.

Analysis carried out on all fossil data at fine scales can recover details about community structure and ecological interactions. Communities in this study had differing degrees of tiering and physical structure, from low-epibiont, productid-rich communities of argillaceous limestones to highly encrusted, secondarily-tiered fenestellid-rich communities in shales. Resources are interpreted to be adequate

enough for all communities, and in some cases, resources were high enough to support a diverse epibiont fauna, such as small, attaching brachiopod-rich communities in shales. Spatial competition is apparent and may even have been strong between bryozoans in fenestellid-rich communities and between productids of similar shape and size. In general, communities were either unbaffled or baffled by organisms, indicating a biotic component in community structure and control on recurrence.

Chapter 4: Human Artifacts in Paleocommunity Analysis

BAMBACH GUILDS, COMPETITORS, OR TAXA? COMMUNITY ANALYSIS USING DIFFERENT CLASSIFICATIONS.

INTRODUCTION

Guilds were first proposed by Root (1967) to discern groupings of functionally similar species in a community. Bambach (1983) extended this idea to the fossil record, using space utilization, bauplan, and food source as means of differentiating guilds. Pianka (1994) also used functional similarities between taxa and suggested that guilds are made up of organisms that have high potentials for intense interspecific competition. In Pianka's definition, interactions between organisms were strongest between guild members and weakest between those of two distinct guilds. A somewhat different definition of guilds was applied to organisms of carbonate buildups by Fagerstrom (1987, 1988), based on roles of taxa in the construction and maintenance of biologically mediated habitats.

Bambach's (1983) defining guild parameters allow the assignment of fossil taxa to guilds with little apparent discrepancy between individual studies. By assigning a category of each parameter – space utilization, bauplan, and food source – to each taxon, taxa within communities can be partitioned into larger groupings of guilds (Appendix 3). Because of preservational shortcomings of fossil community data, Bambach recognized the existence of superguilds, those which commonly contained over 10 taxa in a community that cannot be distributed into smaller guilds because of lack of data (Bambach, 1983).

Fagerstrom used guilds as a means of recognizing biotic versus hydrodynamic mediation of carbonate accumulation in fossil reefs (Fagerstrom and Bradshaw, 2002). By defining roles of taxa as framebuilders, binders, bafflers, and

such, and recognizing common spatial preservation of these guilds, Fagerstrom and Bradshaw (2002) were able to determine whether a buildup was a biotically created and maintained three-dimensional structure or was an accumulation of organism-baffled sediments. Additionally, the proportion and roles of each guild could be determined for a single buildup, allowing the reconstruction of currents and energy and their role in life history processes such as recruitment and food access.

Guilds are useful in examining change or stasis in community structure over long time periods without the complications of changing taxonomic composition (Bambach, 1983). Aberhan (1994) used guilds to quantitatively investigate increased Mesozoic infaunalization by bivalves, defining guilds for each community studied and comparing guild proportions through time. This method served as a means of investigating the nature and cause of infaunal bivalve expansion though Jurassic and early Cretaceous communities.

An important point in guild classification is its independence of lineage and taxonomic composition. Guilds can be polyphyletic groups of taxa with similar niches (Bambach, 1983; Aberhan, 1994), the use of which allows within- and between-niche diversity and richness to be investigated in community data. Use of presence-absence data in guild classification, the most common means of investigating guild relationships in paleontological studies, circumvents problems with taxonomic composition and abundance caused by taphonomy, temporal, and sampling differences (Patzkowsky and Holland, 1999) and allows total niche exploitation and richness within guilds to be evaluated (Bambach, 1983). Relative abundance data, though more rarely used in guild analyses, allows for proportion of each guild per community to be revealed (Aberhan, 1994).

Renewed interest into biotic interactions in the fossil record led to quantitative methods of recognizing potential competition among contemporaneous taxa ('limiting similarity', Hermoyian et al., 2002). Furthermore, invertebrate predation recently became a popular topic of interest among paleoecologists, and potential predators, or predator types in the absence of preserved taxa, are being

recognized. Therefore, Pianka's idea of intense competition defining guilds is possible in paleoecological investigations.

This study uses relative abundance data of 55 samples from diverse lithologies and environments from a Winchell Formation (Pennsylvanian) outcrop at the Lake Brownwood Spillway locality in north-central Texas to investigate the nature of guilds. Guild analyses were performed using both Bambach's and Pianka's definitions of guilds, with each guild list composed by different researchers to eliminate potential biases. Additionally, because of the short-time frame and taxonomic continuity throughout the Winchell Formation outcrop, both guild classifications will be compared to taxonomic analyses to investigate the similarities and differences between Q-mode (sample) cluster results.

GEOLOGY AND METHODS

The Winchell Formation, north-central Texas, exposed at the Lake Brownwood Spillway, near Brownwood in Brown County contains six distinct, informal limestone units (limestones 1 through 6), intervening shales, and several exposure surfaces including one large paleosol and two covered sandstone fluvial deposits (Figure 4.1). Limestones range from argillaceous wackestone to packstone (limestones 1 and 2), micritic wackestone to packstone (limestones 4 and 6), and packstone to grainstones with little micrite or mud infill (limestones 3 and 5), and all are characterized by differing compositions and abundances of large brachiopods and echinoderm material. Shales are mainly shallow marine, with some minor differences in depth and fauna, such as a submarine or estuarine channel with a fully marine fauna (black shale beneath limestone 3), abundant-fenestellid shales (between limestones 1 and 2, above 2, and above 3), brachiopod-dominated shales (beneath and above limestone 5), or one shale characterized by bivalves (concretion layer above limestone 3).

Samples were either point-counted on limestone surfaces in the field at 2- and 5-cm intervals; shales were bulk collected and later screened for fossil content in the lab. To account for differences in spatial variability and the limitations of point-counting, multiple surfaces from the same horizon or multiple surfaces from adjacent horizons, in the case of laterally discontinuous beds, were taken where possible. All fossil material, including identifiable fragments, were included in point-counts, and all material seen under a 10X hand lens was included in the data. Fragments were rare in limestones 1-4 and 6, but were the common component in the grainy limestones 3 and 5.

Shale fossils were counted for minimum number of individuals and colonies using a morphologic feature, such as a brachiopod cardinal process, or other proxy, such as bryozoan size and weight measurements. Square centimeters of fenestellid colonies and linear centimeters of the ramose bryozoans *Rhombopora* and *Leioclema* were determined from the total weight of a sampled taxon divided by the weight of a measured piece of the same taxon. Colony size was taken from the largest intact colonies from intact samples in coquinas associated with shale communities, and total square or linear cm of each taxon was divided by this maximum colony size to derive minimum number of colonies.

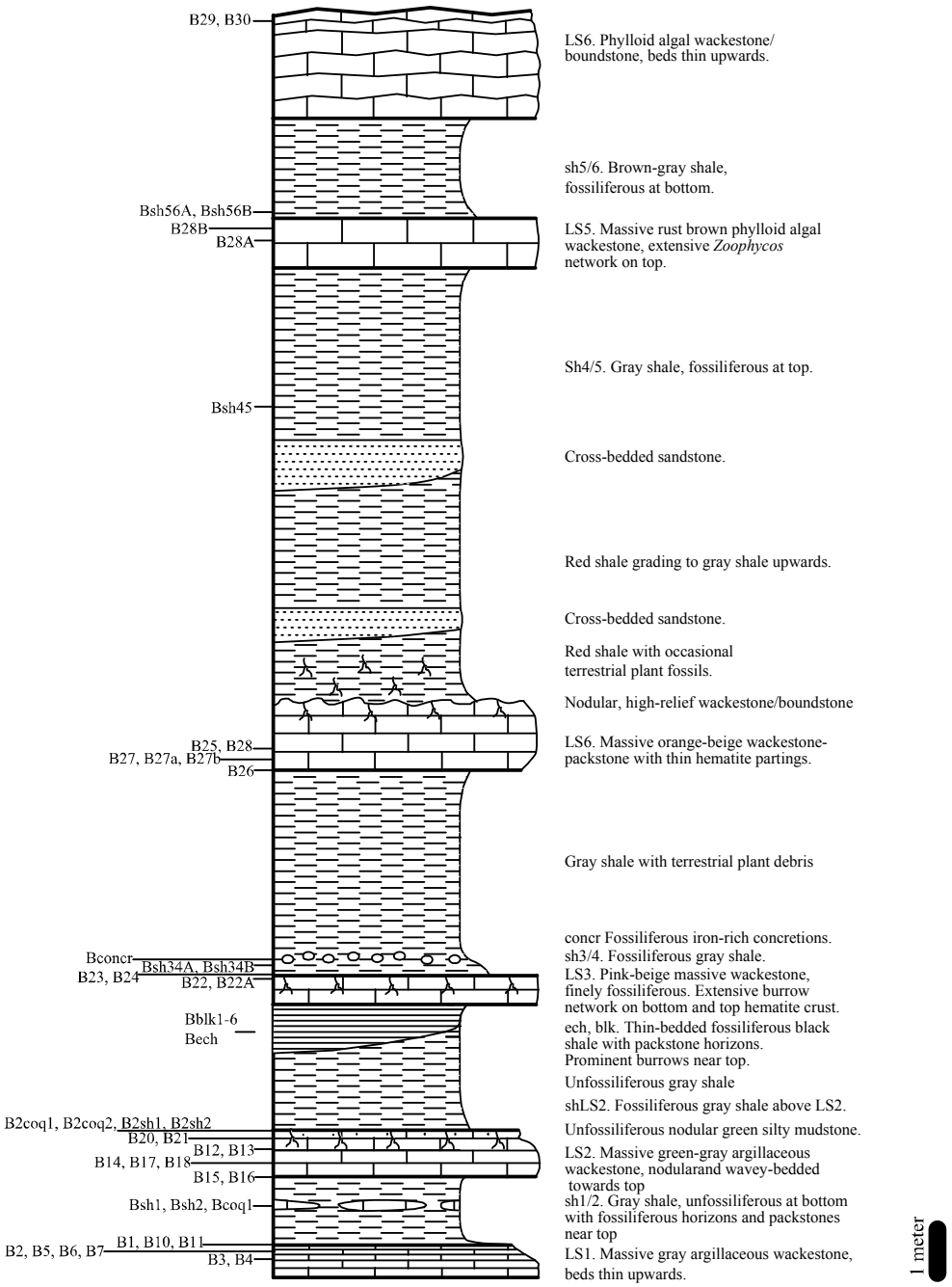


Figure 4.1. Stratigraphic section of the Pennsylvanian (Missourian) Winchell Formation at the Lake Brownwood Spillway, north of Brownwood, north-central Texas.

Crinoid material remained a problem between shale and limestone samples, because all identifiable crinoid elements were noted in point counts but minimum number of individuals was possible in shales. This problem was compounded with the fact that point-counts represent surfaces and bulk samples are volumetric, crinoids were instead lumped as one taxon. Echinoids also were treated as a single taxon, although almost all (>99%) echinoid material is represented by one species of *Archaeocidaris*. The non-*Archaeocidaris* material includes echinocystid and lepidocentrid plates and two spines of one other *Archaeocidaris* species.

Taxa were identified to genera because most genera were either monospecific, or in the case of polyspecific *Composita* and others, species often were indistinguishable in outcrop. For guild analyses, genera were separated into specific guilds by two different researchers, one using Bambach's classification and the other using Pianka's competitor definition (Appendix 3)

Both taxa and guilds were analyzed in Q-mode (sample) cluster analyses to distinguish community patterns of recurrence and community types in the Brownwood locality. Cluster analyses were run using relative Sorenson distance measure and group average (UPGMA) group linkage method in PCOrd (McCune and Mefford, 1999). Additionally, a quantitative R-mode (taxon) cluster analysis for guild differentiation was also performed using single linkage method, also in PCOrd.

RESULTS

Taxon-based clusters essentially differentiate limestones and shales, with smaller clusters split between and within limestones and between and within fenestellid and brachiopod-dominated shale samples (Figure 4.2). Limestones 1 and 4 cluster together because of abundant echinoid material plus similar high levels of *Composita* and *Antiquitonia* and low levels of *Minilya* bryozoans. Limestone 2 groups with samples from Limestone 1, 3, and 5 in two distinct clusters based on

echinoid and crinoid abundances and large productid brachiopod composition. The black shale coquinas, primarily comprised of *Composita* plus *Acanthopecten*, group distinctly as a unit, as do most of the fenestellid-dominated shales. The bivalve concretion layer is included in the fenestellid-dominated shales because of abundant *Minilya* bryozoans. Brachiopod-rich shales form a loose cluster of the three shale samples, but limestone 6, dominated by phylloid algae, forms a tight grouping.

Guilds using Bambach's classification resulted in a continued grouping of limestones 1 and 4, but some mixing and re-ordering of other samples (Figure 4.2B). A large, brachiopod-dominated group of limestone samples included shale 5/6, which contains a community dominated by small brachiopods. A second grouping, including most of the black shale coquinas, a coquina from the shale above limestone 2, and two limestone 2 samples cluster mainly because of crinoids. Fenestellid-dominated shales, the bivalve concretion layer, and limestone samples with abundant fenestellids from limestone 2 form another group, which is associated with a cluster of limestones 3 and 5, characterized by abundant foraminifera, echinoids, and crinoids. Limestone 6 samples, dominated by phylloid algae, remain a solitary group.

Competitor-defined guilds result in fewer limestone 1 and 4 samples clustering together, and include a sample from limestone 3, all of which are clustering as a result of abundant echinoids and *Composita* (Figure 4.2). Large productids appear to be the primary cause of one cluster containing various limestone samples, mainly from limestone 1 and 2; this group is associated with another series of clusters with samples containing abundant *Composita*. *Neospirifer* is an abundant brachiopod figuring into the next associated cluster of various limestones, including several limestone 1 and 2 samples. The *Crurithryis/Punctospirifer* guild is abundant in the shale above limestone 5 and in

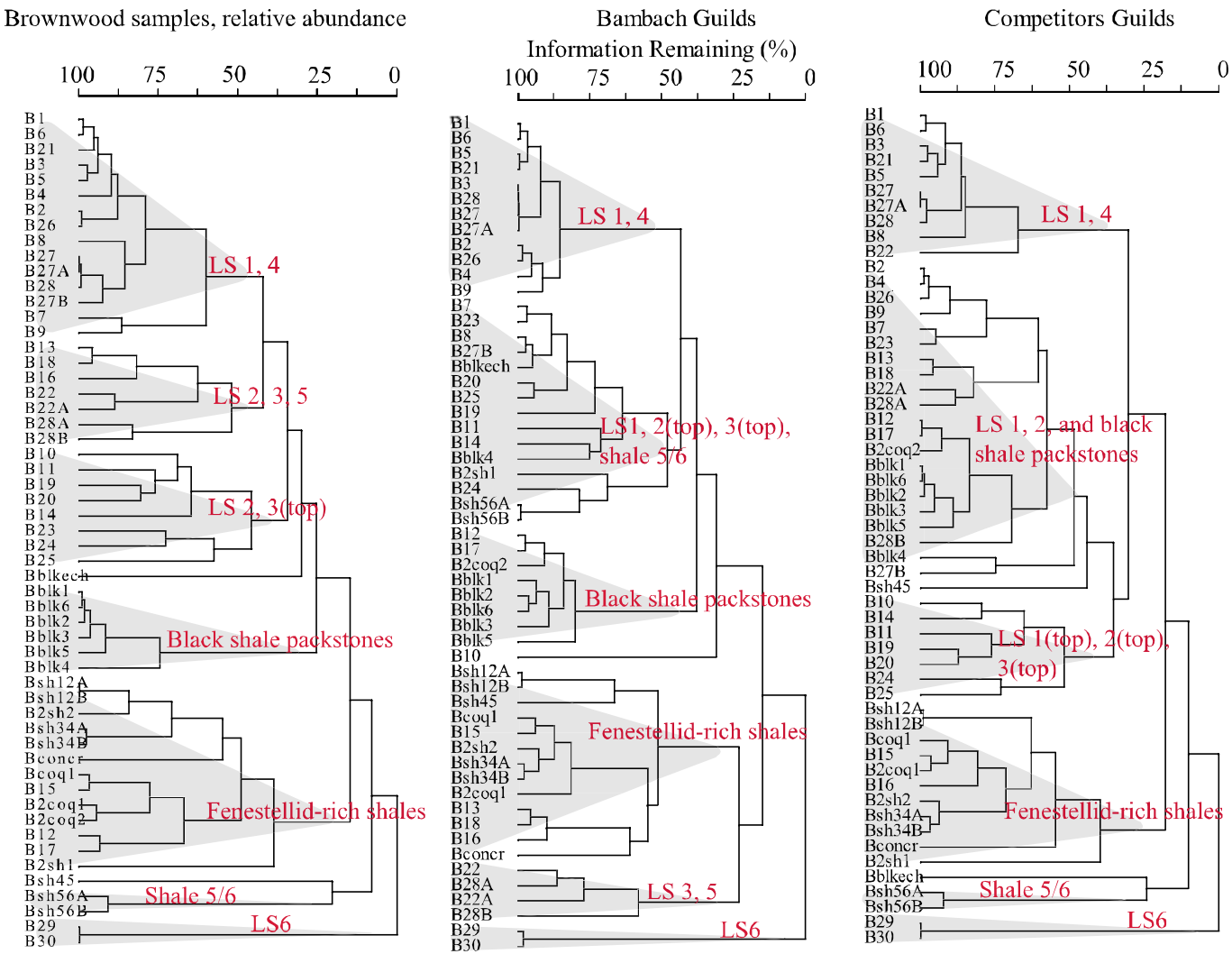

Brownwood samples, relative abundance
100 75 50 25 0
B1 B6 B21 B3 B5 B4 B2 B26 B8 B27 B27A B28 B27B B7 B9 B13 B18 B16 B22 B22A B28A B28B B10 B11 B19 B20 B14 B23 B24 B25 Bblkech Bblk1 Bblk6 Bblk2 Bblk3 Bblk5 Bblk4 Bsh12A Bsh12B B2sh2 Bsh34A Bsh34B Bconcr Bcoq1 B15 B2coq1 B2coq2 B12 B17 B2sh1 Bsh45 Bsh56A Bsh56B B29 B30
LS 1, 4
LS 2, 3, 5
LS 2, 3(top)
Black shale packstones
Fenestellid-rich shales
Shale 5/6
LS6
Bambach Guilds
Information Remaining (%)
100 75 50 25 0
B1 B6 B5 B21 B3 B28 B27 B27A B2 B26 B4 B9 B7 B23 B8 B27B Bblkech B20 B25 B19 B11 B14 Bblk4 B2sh1 B24 Bsh56A Bsh56B B12 B17 B2coq2 Bblk1 Bblk2 Bblk6 Bblk3 Bblk5 B10 Bsh12A Bsh12B Bsh45 Bcoq1 B15 B2sh2 Bsh34A Bsh34B B2coq1 B13 B18 B16 Bconcr B22 B28A B22A B28B B29 B30
LS 1, 4
LS1, 2(top), 3(top), shale 5/6
Black shale packstones
Fenestellid-rich shales
LS 3, 5
LS6
Competitors Guilds
100 75 50 25 0
B1 B6 B3 B21 B5 B27 B27A B28 B8 B22 B2 B4 B26 B9 B7 B23 B13 B18 B22A B28A B12 B17 B2coq2 Bblk1 Bblk6 Bblk2 Bblk3 Bblk5 B28B Bblk4 B27B Bsh45 B10 B14 B11 B19 B20 B24 B25 Bsh12A Bsh12B Bcoq1 B15 B2coq1 B16 B2sh2 Bsh34A Bsh34B Bconcr B2sh1 Bblkech Bsh56A Bsh56B B29 B30
LS 1, 4
LS 1, 2, and black shale packstones
LS 1(top), 2(top), 3(top)
Fenestellid-rich shales
Shale 5/6
LS6

Figure 4.2. Cluster analysis of taxa and guilds in all samples using relative abundance data. Relative Sorenson distance measure and UPGMA linkage were used. Winchell Formation, Lake Brownwood Spillway samples based on relative abundance data of all samples using all taxa, Bambach (1983) classification of guilds, and guilds of potentially intense interspecific competitors. Limestone 6, which is phylloidal, persistently clusters in all analyses; limestones 1 and 4 also cluster in all analyses, but some samples in the limestone 1 and 4 cluster of all-taxa analysis occur in other clusters in guild analyses. The shale between limestones 5 and 6 clusters in all-samples and competitor guild analyses, but is included with limestone samples in Bambach guild analysis. Fenestellid-rich shales cluster in all analyses, but each cluster is different in grouping and sample content. Black shale packstones are a single cluster in all-taxa and Bambach guild analyses, but are included with limestones in competitor guild analysis. Limestones 3 and 5, which are grainstone samples, occur in different clusters in each analysis. All-taxa analysis appears to be based on abundances of *Composita*, different productids, echinoids, *Minilya*, and phylloid algae. Guilds based on Bambach's definition appear to cluster based on brachiopod and bryozoan sessile, epifaunal, suspension feeder guilds. Competitor-based guild analysis appears to cluster based on echinoids, *Composita*-like, fenestellid, and phylloid algae guilds.

the black echinoid community, forming a loose cluster between those two units. Finally, as in the above two analyses, abundant phylloid algae drives the grouping of the two limestone 6 samples.

DISCUSSION

Although details differ among the three cluster analyses, all three patterns contain a differentiation between limestones and fenestellid-dominated shale communities. Not suprisingly, these samples, characterized by large brachiopods for the limestones and abundant *Minilya* for the fenestellid shales, continue to group fairly strongly with some mixing depending on the analysis. Also not suprising is the repeated cluster of the phylloid algal limestone 6; in these samples, phylloid algae are extremely abundant in point counts, and remain a separate taxonomic and guild group in each analysis. Greatest differences appear in the placement of samples from the grainy limestones 3 and 5, and the shale samples below and above limestone 5. Although taxonomically the limestones group with samples of limestone 2 and the shales remain a separate, though loose, association, guild classifications force these samples into grouping with other samples. The Bambach classification scheme, however, makes the greatest intuitive sense for the limestones 3 and 5 cluster, because of similarity in grain size, high-energy interpretation, and abundant foraminifera and fusulinids.

On a large scale, these differentiations between limestones and fenestellid-rich shales are coherent patterns between analyses and therefore indicate the strength of these two, large, separate groupings through repeated results. Both taxonomically and in guild classification, these two groups indicate two very distinct, large-scale community structures. Shales with abundant fenestellids are dominated by baffling organisms, mainly bryozoans, and abundant attaching organisms, such as bryozoans, small brachiopods, and occasional rugose corals. In the sense of Ausich and Bottjer (1982), these communities are highly tiered, and

because of frequent epibiosis, may have a high level of direct, preserved organism interaction. This is reflected both taxonomically by the recurring genera, but also the high abundances of epifaunal, attached, suspension feeder (bryozoans) guild under the Bambach classification and fenestellid, ramose bryozoan, encrusting bryozoan, *Crurithyris/Punctospirifer*, crinoid, and margininferiform competitor guilds.

Limestones other than 6, and in a limited way, 3 and 5, are characterized by abundant echinoids and large brachiopods including productids, *Composita*, and *Neospirifer*, with locally abundant organisms such as fenestellids, fusulinids, *Aviculopinna*, and *Bellerophon.* Black shale coquinas are included in this general grouping of limestones in all cases because of abundant *Composita*. High echinoid and overall brachiopod abundances create two strong groups using Bambach's classifications.

Therefore, on the broadest scale, all methods recognize either large brachiopod/echinoid or bryozoan/small, attaching brachiopod community types. Additionally, phylloid-algae baffled communities remain distinct from all other samples, indicating yet another very different, broad-scale community type for the Brownwood locality. Guild analysis, based on the qualitative assessments of two different researchers using Bambach and competitor definitions, only define minor differences in community structure in these three community types.

Pianka (1994) suggested a quantitative method for guild definition using single-linkage cluster analyses, in which a guild was defined by the distance between the two most disparate members in a cluster. This method was used to attempt a guild classification for Brownwood taxa; however, results were far from satisfying. For instance, sharks are included in a cluster of large productids and *Neospirifer*; therefore, this guild would be comprised of sharks and brachiopods, organisms which disagree strongly with all other definitions of taxa to be included in a guild. Instead, these organisms may cluster strongly because of relatively high abundance of all of these taxa in limestones 1 and 2. Although the idea behind

single-linkage cluster, which is based on the similarities and small distances between taxa in R-mode (taxa) cluster analysis, is relevant to guild definition, the reality of incorporating it into whole-community paleontological data is impractical.

RESEARCHER SPECIALTY BIAS ON DATA COLLECTION

INTRODUCTION

Sampling method for optimal community representation is an important aspect in both ecology and paleoecology. Most previous work has concerned the efficiency of sampling methods or the effects of sampling on analyses (Bennington and Rutherford, 1999; Kidwell et al., 2002). However, a human factor is equally important, and can include bias against certain fossils (the "ugly fossil syndrome" of Tang, 2000), discordant methods (McCune and Mefford, 1999), flawed assumptions (Leighton, 2002), inappropriate combintations of techniques (Bookstein, 1996) and differences in interpretation (Kaplan and Baumiller, 2001; Wilson and Palmer, 2001). This preliminary study investigates human effects on fossil community sampling in lower limestones of the Winchell Formation at the Lake Brownwood Spillway near Brownwood, Texas.

GEOLOGY AND METHODS

Three fossiliferous limestones from the Pennsylvanian (Missourian) Winchell Formation at the Lake Brownwood Spillway, limestones 1, 2, and 4, were point counted on 13 outcrop surfaces by three researchers with different experience and specialties. Both limestones 1 and 2 were argillaceous wacke- to packstones and characterized by faunas containing abundant echinoids, fairly common crinoids, several large productid brachiopods, *Minilya* bryozoans, and *Aviculopinna* bivalves. Limestone 4, a micritic wackestone to packstone, contained abundant echinoids and crinoids with locally abundant *Antiquatonia* brachiopods and *Rhombopora* bryozoans. Researchers included: A, an echinoderm and general paleocommunity worker; B, a brachiopod specialist experienced in Pennsylvanian faunas; and C, a cephalopod and trilobite specialist with limited experience in Pennsylvanian communities. Researchers A and B repeatedly sampled at this locality; C was present for one visit including two days of field work.

All samples were point-counted on bedding planes using 2- or 5-cm grids, with minimum counts of 200 or, where spatially limited, over the full extent of the exposed surface. All material seen in a 10X hand lens at each point was recorded.

Crinoid identification and brachiopod fragment abundances were plotted to investigate the differences between specialties of the different researchers. Number of identified crinoid pieces was plotted against total points per grid, whereas number of brachiopod fragments was plotted against total identified brachiopods in the assemblage.

RESULTS

Both brachiopod and crinoid data indicate higher levels of identification of taxa within each group by specialists than by the other two researchers. Researcher B recorded fewer unidentified brachiopod fragments than either A or C (Figure 4.3). Early point counts by C, the researcher least experienced in Pennsylvanian faunas, were high in percentage of unidentified brachiopod fragments, but later samples contained fewer unidentified fragments. Sample data collected by A were highly variable in brachiopod identification, with both high and low abundances of unidentified brachiopod fragments.

Identification of crinoid plates was most often highest in samples recorded by A; both B and C contained variable amounts of crinoid information, from few to many crinoid elements recognized in outcrop (Figure 4.4). Unlike brachiopod recognition by researcher C, levels of crinoid identification did not appear to change with time.

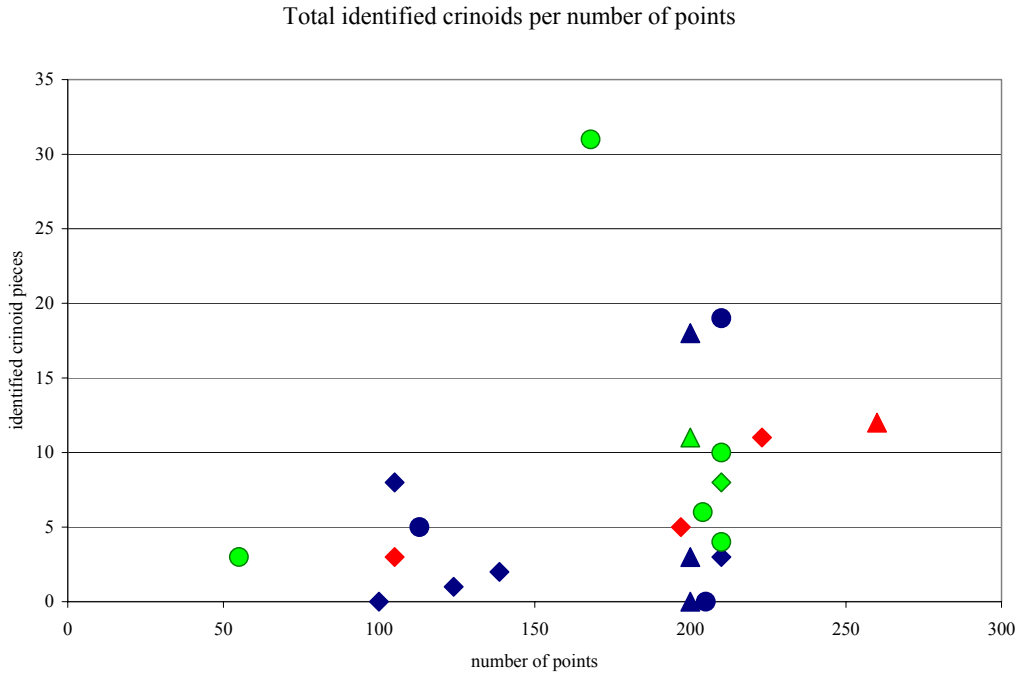


Figure 4.3. Crinoid identification per total number of points in point-counts on limestone surfaces. Diamond shapes are limestone 1, circles are limestone 2, and triangles are limestone 3. Light green is researcher A, dark blue is researcher B, and medium red is researcher C.

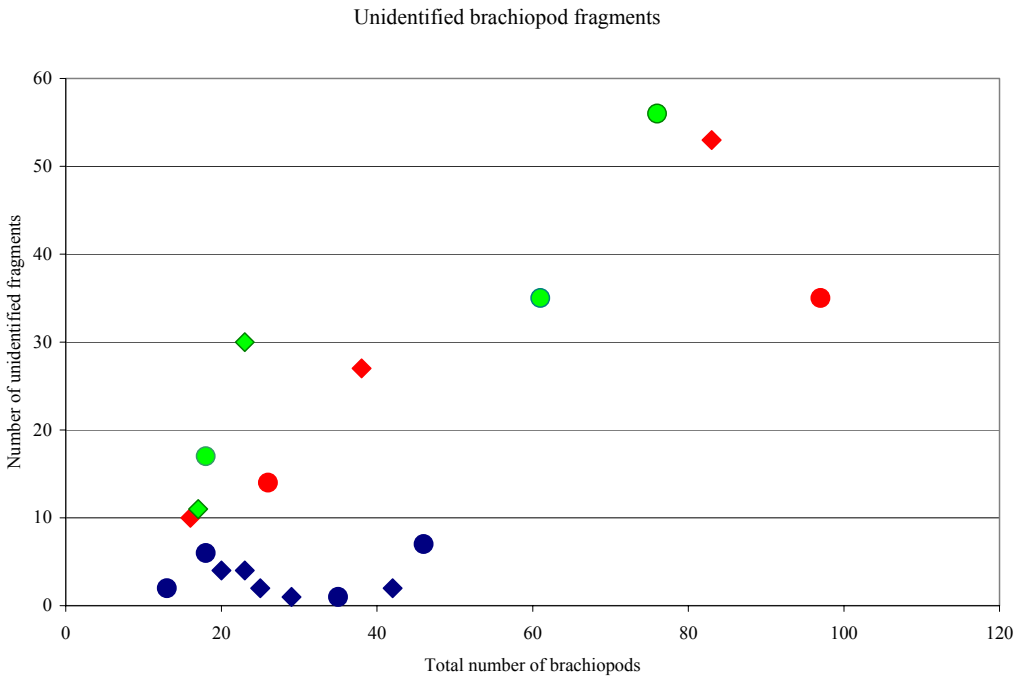


Figure 4.4. Number of unidentified brachiopod fragments per brachiopods in point counts on limestone surfaces. Diamond shapes are limestone 1, circles are limestone 2, and triangles are limestone 3. Light green is researcher A, dark blue is researcher B, and medium red is researcher C.

DISCUSSION

Brachiopod and crinoid data indicate slight biases toward better identification by specialists and against accurate data by inexperienced researchers. Although graphs show such patterns, these phenomena were qualitatively noted in the field during discussions of taxa and community patterns. As a result, each specialist shared their knowledge with the other two researchers, increasing the likelihood of fossil identification. This is evidenced by C's decrease in unidentified brachiopod fragments with continued experience, and may be suggested by the high amounts of crinoid elements identified by B and C and by variable unidentified brachiopod fragment abundances of A.

Although all three researchers were focused on collecting whole community data, discussions about the nature of the data were frequent and provided some insight into personal biases. Researcher A, familiar with echinoderms, often identified smaller crinoid fragments than the two other researchers; as a result, later data collection by B and C emphasized greater amounts of small crinoid elements. Brachiopod fragments were more recognizable by researcher B because of experience with Pennsylvanian brachiopods, and qualitative observations on spatial patterns, morphological differences, and population data were of great interest to B. Researchers A and C, though involved in the speculations proposed by B, may have

spent less effort on each brachiopod fragment because of lack of specialization in these animals and more interest in community collection.

Because trilobites and cephalopods are rare at the Lake Brownwood Spillway locality, and because of decreased experience in Missourian Texas rocks, researcher C was more prone to examine multiple surfaces over large distances, whereas A and B were likely to count fossiliferous surfaces as they occurred in order of appearance. Researchers A and B likely restricted exploration because of prior investigations and more familiarity with the outcrop.

Cluster analysis was not used to investigate researcher bias because of circularity of any argument. Although these analyses are based on similarities between samples, such similarities may arise from either real correspondence between samples or may instead be the result of biases induced by fossil identification. Therefore, such analyses are good only when samples collected by individual researchers cluster together; this is likely an unusual case for paleontologists familiar with the fossil data.

CONCLUSIONS, CHAPTER 4

Taxon- and guild-based cluster analyses agree on large-scale community types: those dominated by brachiopods and echinoids, those that are fenestellid-baffled with frequent occurrences of encrustation, and those that are baffled by phylloid algae are three, recurrent fossil assemblages. Both Bambach (1983) classification for guilds and guilds based on the potential for intense competition (Pianka, 1994) provide similar large-scale patterns, but detailed associations

between samples are distinctly different between analyses as well as from the taxon-based analysis. Therefore, different interpretations of guilds and the use of taxa to analyze large-scale patterns are valid, but for more detailed questions about biodiversity, composition, niche differentiation, and community structure, an appropriate classification scheme must be utilized.

Researcher bias in point-counts on limestone surfaces mainly occurs in areas of specialization. Increased levels of correct identification occurred with both researcher specialization or with time spent at the outcrop and in discussion with the other two researchers. Further research is needed to understand the full impact of researcher bias on fossil collections.

Chapter 5: The Echinoid Ball

At the end of one such lengthy day
When papers and rocks had turned to naught,
The janitor's broom chased dust away,
I found myself in frustrated thought.

My fossils all about me strewn,
But each their answers blurring.
My eyes were heavy, and sleep was soon
While about me things were stirring.

I watched in awe as one by one
With spines upright, the echinoids danced
In circles and swirls, a patterned run;
My eyes enrapt, entranced.

And then as soon, began to move
Brachiopods large and others small
Lined with militaristic groove
And marched, en valve, held tall.

The snails by then had found their feet
And wrote in patterns of fossil dust,
Their tapestry notes in spirals neat
In gray shale and hematite rust.

The bivalves, too, came out to play
And froliked ‘round the border
Betwixt and between the echinoid fray
Upsetting the brachiopod order.

The brachs were quite consterned at this
With bivalves dancing all around,
But just regrouped at each remiss.
The snails to their spirals bound.

When slowly, stately, from the right,
A ballet of crinoids swaying;
Each one in time, their cirrals tight,
Between the pelecypods playing.

And then the band began their song
With conulariid and rugosan horns,
An entire drumming tabulate throng
And a bryozoan-harp adorned.

The music sank behind my eyes
And deep in my ears, the echinoids danced.
The maddening crescendo began to rise,
Each to its purpose entranced.

The echinoids twirled, the crinoids lept!
While bivalves crazed, the brachs marched fast!
And all in pattern, the gastropods swept
When the band gave their finale blast.

And slowly then the music faded;
The fossils, spent, from their gala ball,
Crept back to their places, sated,
To drawers and cabinets, one and all.

But one last conulariid pipe
Stayed behind, not ready for its bed,
Gave one last song in revelry-type;
‘Twas when I woke, and lifted my head.

And where I left them, my fossils around.
I laughed, for it was but a jest,
Or a simple dream! But then I found
A conulariid on my desk.

Appendix 1: Community Definitions and Comments about Communities

Allaby, 1998, p. 93

"**community** A general term applied to any grouping of populations of different organismms found living together in a particular environment; essentially the biotic component of an ecosystem. The organisms interact (by competition, predation, mutualism, etc.) and give the community a structure. Globally, climax communities characteristic of particular regional climates are called biomes."

"**community ecology** An approach to ecological study which emphasizes the living components of an ecosystem (the community). Typically it involves description and analysis of patterns within the community, employing methods of classification and ordination, and examines the interactions of the community members, e.g. in the partitioning of resources and in succession."

Bambach, 2001, p. 437

A community contains "populations of a variety of species that live together in local geographic areas" with no requisite bounding conditions for an interactive network of individuals.

Bennington and Bambach, 1996

"Entities identified as paleocommunities are normally recognized by the recurrence of species, usually with a characteristic pattern of relative abundances" (p. 107).

A neoecological community is "an aggregation of local species populations (avatars) among which interactions can, and, even in chance aggregations, will occur" (p. 109).

"Because of information losses, knowledge of the actual range of interactions and the documentation of their quantitative distributions for any organism, even if well preserved, is not possible in paleoecology" (p. 109)

To recur, samples representing the same community must be statistically and significantly indistinct.

Boucot 1999a, p. 3

A community is a "recurring association of taxa" with "relative abundances more or less fixed."

Boucot, 1999b, p. 13

A community is a "recurring association of fossils in which relative abundances of the constituant taxa remain similar."

Boucot, 1999c, p. 549

"The holistic concept of a community has never actually been employed outside of elementary textbooks."

Bretsky, 1969, p. 46

A community is an "association of recurring species that are numerically dominant and may show some linkage to a physical environmental parameter."

Brewer, 1979

In a community, "certain species live together in a certain habitat and this combination of species tends to recur, more or less exactly, as the habitat recurs, with habitat and organisms bound together by interactions" (p. 120)

"Community: a group of organisms occupying a particular area; the connotation is of a coacting system" (p. 284)

Cody and Diamond, 1975, p. 7

Community structure is the "pattern of resource allocation among the species in a community and the patterns of their spatial and temporal abundances."

DiMichele and Philips, 1995

A community exists during "a period of persistent species associations and ecomorphic patterns", but species turnover may occur without changes in community structure and dynamics. Community change occurs when there is a change in structure and dynamics.

Frest et al., 1999, p. 640

A paleocommunity is made up of "entire, regularly recurring suites of preserved organisms in a particular biofacies."

" It is clear that there is no truly ideal definition in practice of the term community."

Gleason, 1929

"A community is frequently so heterogeneous as to lead observers to conflicting ideas as to its associational identity, its boundaries may be so poorly marked that they can not be located with any degree of accuracy, its origin and disappearance may be so gradual that its time-boundaries can not be located; small fragments of associations with only a small proportion of their normal components of species are often observed…" (p. 13).

"Under the individualistic concept…it is rather the visible expression, through the juxtaposition of individuals, of the same or different species and either with or without mutual influence, of the result of causes in continuous operation. These primary causes, migration and environmental selection, operate independently on each area, no matter how small, and have no relation to the process on any other area" (p. 25).

Gopal and Bhardwaj, 1979, p. 55

"The community is defined as an assemblage of a number of organisms usually of different species, which occupy the same habitat" and implies interaction.

Hickey and Younker, 1981

Fossil communities are “recurring associations of organisms”, in which “preservational processes modified the original community composition” and “certain structural aspects cannot be detected” (p. 1-2).

Statistical definitions of communities can be artificial because communities can actually be gradational in space and time.

Holt, 1993, p. 39

“A local community – to a first approximation and viewed over a significantly long time span – is an ephemeral ensemble of species that originated somewhere else.”

Kauffman and Scott, 1976

“The *holistic concept of ecological units* (communities) consists of four elements: (1) total biotic composition (as complete an inventory as possible), (2) structure defined by species interaction and energy flow, (3) the nature of constraining and interacting environmental parameters, and (4) the character of unit boundaries” (p. 5).

“Anything less sacrifices the “ecology” of the unit for the ease and efficiency of defining consistently statistically recurring groups of organisms in the living and fossil record” (p. 5).

“The community, the basic unit of ecology and paleoecology, is a unique congregation of diverse organisms having a unique structure based on organism interactions, and in some cases interdependent, as well as on energy flow; the community is adapted to and restricted by a particular suite of environmental

parameters (physical, chemical, and biological). Communities can be any size and are recurrent in space and time…" (p. 18).

Krebs, 1972, p. 379

"Neither organisms nor species populations exist by themselves in nature but are always part of an assemblage of species populations living together in the same area." A community is " any assemblage of populations of living organisms in a prescribed area or habitat" and may be of any size.

Kríž, 1999, p. 229

A community is a "sample of fossils limited by a certain area (large or small) obtained from a certain type and thickness of sediment and corresponding to a certain environment."

Laporte, 1968

"Assemblages of organisms are either statistical associations or integrated communities. Whatever the degree of species interactions, the assemblage composition is environmentally controlled."

Laporte, 1979

An integrated community contains a "high degree of interaction in component species", especially in food and space resources, and is a closed system.

Lawson, 1999, p. 7

"Most so-called communities are arbitrary and convenient segments of a continuum of species with overlapping ecological requirements, not involving a high level of interdependence. Since the levels of interdependence in modern communities have not really been measured, observed, or experimented to any extent, one cannot obviously, expect that data from the fossil record will be very helpful in this regard. However, one cannot assume that some level of interdependence is totally absent."

Maurer, 1999, p. 48

"Community ecologists have been very sloppy about what they have called communities in the past."

Meusel, 1939 in Gopal and Bhardwaj, 1979

A community is "a tapestry woven of threads of many colours which in orderly distribution through space form the variegated patterns that meet our eyes."

Miller, 1990, p. 32

"Using the terms "community" and "paleocommunity" for any recurrent aggregation of fossils makes some otherwise useful contributions difficult to compare with other studies…"

Miller, 1993, p. 182

Community recurrence is the "appearance of the same characters (taxonomic composition, relative or rank abundance, and skeletal morphology) at different stratigraphic levels and geographic localities."

Mobius, 1877 in Gopal and Bhardwaj, 1979

A community, based on observations of an oyster bed, is "where the sum of species and individuals mutually limited and selected have continued in possession of a certain definite territory."

Newell et al., 1959 in Charles, 1974

A habitat-defined community is "a natural association of organisms set apart according to certain defined features of the environment."

An organism-defined community is "a regularly recurring part combination of certain types of organisms … delineated without regard to habitat characteristics."

Odum, 1971, p. 140

A biotic community is "all organisms in an environment."

A community is "any assemblage of populations living in a prescribed area or habitat; it is an organized unit to the extent that it has characteristics additional to its individual and population components and functions as a unit through coupled metabolic transformations." "It is the living part of the ecosystem."

A community has a “definite functional unity with characteristic trophic structures and patterns of energy flow” and has “compositional unity and the probability that certain species will occur together.”

“‘Community’ emphasizes that diverse organisms usually live together in an orderly manner, but are constantly changing appearance while having describable structures and functions.”

Odum, 1975, p. 4

A community “in the ecological sense (sometimes designated as the biotic community) includes all of the populations of a given area.”

Owen, 1974

A community is an “assemblage of plants and animals found in an area” consisting of a variety of species, many of which are not seen, with intricate inter- and intra-species interactions.

Pianka, 1994, p. 7

“All of the biotic components of an ecosystem, or all of the living organisms in it, comprise the ecological community.”

Putnam and Wratten, 1984

“A community may be very simply defined as an assemblage of animal and plant species occurring together in a particular area” (p. 43).

The "community is a functional unit, described in terms of operation, never frozen" (p. 44).

Rahel, 1990, p. 328

"Community persistence is such a hierarchical concept wherein scales involving the spatial, temporal, and taxonomic resolution of species' abundance data can influence the perception of assemblages as being constant or fluctuating."

Ricklefs, 1973

The community is made vital by a complex spectrum of interactions, directly or indirectly tying all its members together into a vast web."

"The term 'community' has been given such a variety of meanings by ecologists that it is in danger of becoming useless."

Ricklefs, 1990a

A community is "tied together via feeding relationships and other interactions;" it is a "complex whole" (p. 654).

Interrelationships include energy flow, element cycling, and feedback and control of populations.

"The community is an association of interacting populations" (p. 654)

Ricklefs, 1990b

A biological community is "the species comprising a temporally and spatially localized assemblage" (p. 1).

Ricklefs and Miller, 2000

A community is an "association of coexisting populations of species" usually defined by the nature of organism interactions or by the place where it occurs.

"The historical record preserved in fossils, fragmentary as it is concerning the organization of communities, especially supports the opposing perspectives of change and stable association" (p. 531)

Robertson, 1999, p. 418

"The ecological structure, based on functional interactions between the organisms in the community, is particularly important in this definition (Kauffman and Scott, 1976). Hence, in paleoecology a fossil community should also be defined by its structure. Owing to the inadequacies in the fossil record this is usually not possible."

"The only way to distinguish ecological structure in these fossil associations is by analogy with modern biocoenoses. These associations do not compare well with biocoenoses described from recent environments (Robertson, unpub. PhD. thesis, 1985); differences being attributed, in part at least, to preservation failure."

Ross, 1981, p. 2

A community is "a collection of organisms of all trophic positions that interact directly and indirectly and that occur in a particular habitat."

Smith, 1986

A community is "the assemblage of plants and animals in any given physical environment." It is the "biotic portion of the ecosystem" (p. 437)

"Community: group of interacting plants and animals inhabiting a given area" (p. 612).

Staff et al., 1986, p. 428

"Biological communities are made up of contemporaneous individuals that live within habitats having measurable physical limits." These "measurable physical limits" include taxonomic composition, diversity, and trophic structure.

Underwood and Petraitis, 1993, p. 39

Assemblages are "cooccurring species in a given habitat in a specific time and place." 'Community' use is not advocated because of "Clemmentsian super-organism connotations." "Community has too many meanings to different researchers."

Valentine, 1973

"The fossil record deserves to be taken seriously" (p. 9).

"…We may accept the concept of a community as a "recurrent association" with the proviso that the association is flexibly defined and need only include a certain percentage of the species in some definitive set of species in order to qualify" (p. 270)

Valentine and Jablonski, 1993, p. 341

"Removal, addition, and substitution of species in marine communities is common in nature and is the rule over time."

"The fossil record cannot be used routinely to study the details of population and community interactions and dynamics, it can reveal patterns of association and change in community composition over time scales that are beyond the reach of neontology, and to which modern patterns cannot necessarily be extrapolated."

Warming, 1909 in McNaughton and Wolfe, 1979

"Certain species group themselves into natural associations, that is to say, into communities which we meet with more or less frequently and which exhibit the same combination of growth forms."

Whittaker, 1970, in Gopal and Bhardwaj, 1979 and others

A community is a "functional system of interacting niche differentiated by species populations that tend to complement one-another, rather than directly competing, in their utilization of the community's space, time resources, and possible kinds of interactions."

Whittaker, 1975, p. 60

"A community consists of species – many species with different kinds of population fluctuation and interaction with one another."

Appendix 2: Localities and Data

LOCALITIES:

Brownwood: Winchell Formation, Canyon Group, Missourian
Lake Brownwood Spillway, Brownwood, Texas

Perrin: Winchell Formation, Canyon Group, Missourian
West of Perrin, Texas on FM Road 2210.

RP1: Winchell Formation, Canyon Group, Missourian
East of Placid, Texas on FM Road 1028.

Farley Limestone Member, Wyandotte Formation, Kansas City Group, Missourian
Merriam Limestone Member, Spring Hill Limestone Member, Hickory Creek Shale Member,
I-435 and I-70 cloverleaf, Kansas City, Kansas

Plattsmouth Limestone Member, Oread Formation, Shawnee Group, Virgilian
NE of I-35 and County 31, 5 miles east of Beto Junction

Phylloid algae, foraminifera, echinoderms, brachiopods, and bryozoans: pp. 181-192

Molluscs, corals, trilobites, and sharks: pp. 193-204.

65taxa	Perrin									
81samples	Winchell Formation									
	P1	P2	P3	P4	P5	P6	P7	P8	Psh2	Psh3
phylloid					9		39	84		
fusulinid									105	
foraminifera										
crinoid	14	31	24	26	12	18	1	4	14	18
echinoid		3	4		1				2	
Crania										1
Enteletes	3	1	1							
Wellerella						1				
Composita	2									6
Phricodothyris	2	2								
Hustedia				1					4	6
Dielasma										
Crurithyris	5	1		3	2				8	14
Neospirifer					8		2			1
Neospirifer t.										43
Punctospirifer					1		1		1	11
Rhipidomella										1
Derbyia						1				1
Meekella										
Chonetinella										12
Mesolobus										
Neochonetes									1	
Fimbrinia										
Desmoinsea										12
Hystriculina	13	4	2		2	1				
Kozlowskia										
Retaria										
Antiquatonia										
Reticulatia										
Echinaria										
Parajuresania										1
Linoproductus	3									1
Minilya	14	4	13	20	4	13		1	14	37
Fenestrellina									22	48
Septopora									1	1
Polypora									2	4
Rhombopora	18	7	4		5	10	1	1	8	24
Leioclema										
Sheet tub.	1	2		1						
Tubuliporate							2		9	1
Treptostome										

RP		
Winchell Formation		
	R2	R1
phylloid	33	91
fusulinid		14
foraminifera		
crinoid	6	23
echinoid	9	2
Crania		
Enteletes		
Wellerella		
Composita	1	3
Phricodothyris		
Hustedia	1	1
Dielasma		
Crurithyris	5	2
Neospirifer		1
Neospirifer t.		
Punctospirifer		
Rhipidomella		
Derbyia		
Meekella		
Chonetinella		
Mesolobus		
Neochonetes		
Fimbrinia		
Desmoinsea		
Hystriculina		
Kozlowskia		
Retaria		
Antiquatonia		
Reticulatia		
Echinaria		
Parajuresania		
Linoproductus		
Minilya	3	1
Fenestrellina		
Septopora		
Polypora		
Rhombopora	4	2
Leioclema		
Sheet tub.	1	
Tubuliporate		
Treptostome	1	1

	Brownwood										
	Winchell Formation										
	LS 1										
	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11
phylloid											
fusulinid					1						4
foraminifera											
crinoid	2	9	3	8	5		8	1	11	2	16
echinoid	20	18	58	21	33	23	9	15	15	10	9
Crania											
Enteletes			1								
Wellerella											
Composita	3	5	13		3	4	4	10	4		
Phricodothyris			1								
Hustedia							1				
Dielasma											
Crurithyris			3		5		3	1	4		1
Neospirifer	1	1	3		2	4	1	4	2	5	8
Neospirifer t.											
Punctospirifer									1		
Rhipidomella											
Derbyia											
Meekella							3		2		
Chonetinella											
Mesolobus											
Neochonetes											
Fimbrinia											
Desmoinsea							1		1		
Hystriculina											
Kozlowskia											
Retaria			4		1						
Antiquatonia			6	3	1		13	4	3	5	11
Reticulatia		4	2				2				
Echinaria	1		3	3	1			3		2	
Parajuresania							1				
Linoproductus		1									
Minilya	1	3	1		3		1	2	1		1
Fenestrellina											
Septopora											
Polypora			3	1		1					
Rhombopora										3	1
Leioclema											
Sheet tub.											
Tubuliporate											
Treptostome											

Brownwood			
Winchell Formation			
	Sh1/2		
	Bsh12 A	Bsh12 B	Bcoq1
phylloid			
fusulinid			
foraminifera			
crinoid	8	13	83
echinoid	2	2	5
Crania			
Enteletes			
Wellerella			
Composita		2	
Phricodothyris			
Hustedia			
Dielasma			
Crurithyris			
Neospirifer	1		
Neospirifer t.			
Punctospirifer	10	43	7
Rhipidomella			
Derbyia	1	5	
Meekella			
Chonetinella		5	
Mesolobus			
Neochonetes			
Fimbrinia			
Desmoinsea			6
Hystriculina			
Kozlowskia			
Retaria			
Antiquatonia		2	
Reticulatia			
Echinaria			
Parajuresania			
Linoproductus			
Minilya	38	161	259
Fenestrellina		2	127
Septopora	1	1	41
Polypora	2	27	42
Rhombopora	4	26	26
Leioclema			
Sheet tub.			
Tubuliporate	46	156	13
Treptostome			

Brownwood										
Winchell Formation										
	LS2									
	B12	B13	B14	B15	B16	B17	B18	B19	B20	B21
phylloid										
fusulinid		3			1	3	1			
foraminifera										
crinoid	42	8	10	19	5	31	6	3	4	2
echinoid	18	18	4	7	27	3	15	20	6	41
Crania										
Enteletes										
Wellerella										
Composita			4	1		1		1	1	3
Phricodothyris				1						
Hustedia										
Dielasma										
Crurithyris						1	1			
Neospirifer	4	9	47	1	1	2	4	10	4	5
Neospirifer t.										
Punctospirifer	2	1								
Rhipidomella										
Derbyia				1		4		1		1
Meekella										
Chonetinella	5	3			1					
Mesolobus					1					
Neochonetes										
Fimbrinia										
Desmoinsea										
Hystriculina										
Kozlowskia										
Retaria										
Antiquatonia					3			7	2	
Reticulatia	6		27		2	2			5	5
Echinaria		1	12					7	1	1
Parajuresania		1				1				
Linoproductus	2		6	1	1		1		1	4
Minilya	24	27	12	46	52	13	12	3	1	4
Fenestrellina				14	2	1				
Septopora										
Polypora					2	2			2	
Rhombopora	4	6	11	6	1	3	8		2	1
Leioclema										
Sheet tub.	1		6			1	2			
Tubuliporate						1				
Treptostome										

Brownwood				
Winchell Formation				
	shLS2			
	B2coq 1	B2coq 2	B2sh1	B2sh2
phylloid				
fusulinid				
foraminifera				
crinoid	44	74	10	5
echinoid	7	2	1	1
Crania				
Enteletes				
Wellerella				
Composita			1	1
Phricodothyris				
Hustedia				
Dielasma				
Crurithyris				
Neospirifer				
Neospirifer t.				
Punctospirifer			1	4
Rhipidomella				
Derbyia	1	7	1	1
Meekella				
Chonetinella	37	44	222	1
Mesolobus				
Neochonetes				
Fimbrinia				
Desmoinsea				
Hystriculina				
Kozlowskia				
Retaria				
Antiquatonia				
Reticulatia				
Echinaria				
Parajuresania				1
Linoproductus				
Minilya	65	39	88	87
Fenestrellina	27	14	1	5
Septopora	5	1	1	1
Polypora	6	10	2	10
Rhombopora	5	3	8	
Leioclema			1	28
Sheet tub.				
Tubuliporate	2		33	32
Treptostome				

Brownwood							
Winchell Formation							
	Black sh						
	Bblkech	Bblk1	Bblk2	Bblk3	Bblk4	Bblk5	Bblk6
phylloid							
fusulinid							
foraminifera							
crinoid	2	45	20	20	8	8	24
echinoid	45	10	4	1			4
Crania							
Enteletes							
Wellerella							
Composita	4	36	10	9	22	11	16
Phricodothyris							
Hustedia							
Dielasma							
Crurithyris	120						
Neospirifer							
Neospirifer t.							
Punctospirifer							
Rhipidomella							
Derbyia							
Meekella							
Chonetinella							
Mesolobus							
Neochonetes							
Fimbrinia							
Desmoinsea							
Hystriculina							
Kozlowskia							
Retaria							
Antiquatonia							
Reticulatia							
Echinaria							
Parajuresania		1	1				
Linoproductus	1	2	2		3		
Minilya	11	5	4	1		1	3
Fenestrellina						1	
Septopora						1	2
Polypora			1			2	
Rhombopora			3	1		2	1
Leioclema							
Sheet tub.							
Tubuliporate	10	1	2	1		1	1
Treptostome							

Brownwood							
Winchell Formation							
	LS3				Sh3/4		
	B22	B22A	B23	B24	Bsh34 A	Bsh34 B	Bconc r
phylloid							
fusulinid		2	2				
foraminifera	30	44					
crinoid		14	12	4	2	1	46
echinoid	48	29	7	8	1		
Crania							4
Enteletes							
Wellerella							
Composita	1	4	12	12	13	11	11
Phricodothyris							
Hustedia							
Dielasma							
Crurithyris			1		4		
Neospirifer	1		4	14	1		
Neospirifer t.							
Punctospirifer							1
Rhipidomella					1		
Derbyia					4	1	
Meekella							
Chonetinella			1			1	
Mesolobus			1				
Neochonetes							
Fimbrinia							
Desmoinsea					2	3	
Hystriculina							
Kozlowskia							
Retaria							
Antiquatonia			5	4			3
Reticulatia			6			1	
Echinaria			5	21		3	
Parajuresania					2		21
Linoproductus			7	11	3	4	3
Minilya	29	17	3		128	51	151
Fenestrellina			1		1	1	2
Septopora					1	1	7
Polypora		1			31	11	11
Rhombopora		3			18	13	32
Leioclema						1	
Sheet tub.			1				
Tubuliporate		1			8	7	
Treptostome							

Brownwood						
Winchell Formation						
	LS4					
	B25	B26	B27	B27A	B27B	B28
phylloid						
fusulinid						
foraminifera						
crinoid		18			11	3
echinoid	6	61	143	120	34	45
Crania						
Enteletes						
Wellerella						
Composita	5	27	72	90	50	23
Phricodothyris						
Hustedia						
Dielasma			1			
Crurithyris						8
Neospirifer	1					
Neospirifer t.						
Punctospirifer			4	4	2	1
Rhipidomella						
Derbyia			1	2	1	1
Meekella						
Chonetinella			1			
Mesolobus		1				
Neochonetes						
Fimbrinia						
Desmoinsea						1
Hystriculina						
Kozlowskia				3		
Retaria						
Antiquatonia			6	10	7	
Reticulatia	2	12				
Echinaria	14					
Parajuresania						
Linoproductus	1		1			
Minilya	3	3			1	
Fenestrellina						
Septopora						
Polypora					3	
Rhombopora	4		2		5	1
Leioclema						
Sheet tub.	1					
Tubuliporate				2	5	
Treptostome						

Brownwood							
Winchell Formation							
	Sh4/5	LS5		Sh5/6		LS6	
	Bsh45	B28A	B28B	Bsh56 A	Bsh56 B	B29	B30
phylloid						221	281
fusulinid		21	19				1
foraminifera							
crinoid	11	16	12		1		
echinoid	1	24	7			1	
Crania					1		
Enteletes		1					
Wellerella							
Composita	4	3		6		4	33
Phricodothyris							
Hustedia	1			4	6		
Dielasma							
Crurithyris	5			11	14		1
Neospirifer					1		6
Neospirifer t.				32	46		
Punctospirifer	3	2		12	9		
Rhipidomella	3			7			
Derbyia	4	1		6	1		1
Meekella							
Chonetinella	1			8	12		
Mesolobus							
Neochonetes							
Fimbrinia							
Desmoinsea						1	
Hystriculina							
Kozlowskia							
Retaria				4	12		
Antiquatonia				5			
Reticulatia							
Echinaria							
Parajuresania				2	1		
Linoproductus					1		
Minilya		20	2				
Fenestrellina							
Septopora							
Polypora		2					
Rhombopora	1	1					
Leioclema	20						
Sheet tub.							
Tubuliporate	16			7	1		
Treptostome							

	Farley	Merriam				Spring Hill		Hickory
	Wyandotte Formation							Creek
	F1	M1	M2	M3	M4	S1	S2	HC
phylloid	58					31	13	
fusulinid						2	1	
foraminifera								
crinoid	26	60	33	25	10	19	69	1
echinoid	1	9	3	3		1	8	
Crania								
Enteletes						2		
Wellerella								
Composita	26	1	93	1		3	9	8
Phricodothyris	3					1	5	
Hustedia	3					5		7
Dielasma							3	
Crurithyris	8		5			2		40
Neospirifer								
Neospirifer t.								
Punctospirifer	1					1		4
Rhipidomella								
Derbyia	1						1	2
Meekella						1		
Chonetinella								4
Mesolobus								
Neochonetes						1		
Fimbrinia	1							
Desmoinsea	1							4
Hystriculina	1							
Kozlowskia								
Retaria								
Antiquatonia		2					3	
Reticulatia								
Echinaria				3				
Parajuresania	1	3		55	10	1	3	
Linoproductus		31	10	10	57		8	
Minilya		6	1	2		3	2	
Fenestrellina	1	7	1	2	10	8	5	
Septopora								
Polypora		7	1	6		5	2	
Rhombopora		2				2	3	1
Leioclema								
Sheet tub.		1		1		1	1	
Tubuliporate								
Treptostome								

	Plattsmouth					
	Oread Formation					
	PL1	PL2	PL3	PL4	PL5	PLsh
phylloid						
fusulinid					18	3
foraminifera						
crinoid	32	3				1
echinoid	8				2	1
Crania						
Enteletes	1		1		3	1
Wellerella				1		
Composita		2	5	10	5	17
Phricodothyris						
Hustedia	1	1	1	2	10	85
Dielasma					2	
Crurithyris	5	3	4		7	21
Neospirifer	2	1	2	2	1	3
Neospirifer t.						
Punctospirifer	1	1	1	5	4	29
Rhipidomella						49
Derbyia	1		2	1	13	4
Meekella		1	2		3	
Chonetinella						
Mesolobus						
Neochonetes						1
Fimbrinia						
Desmoinsea						
Hystriculina	4	2	1			
Kozlowskia	4					1
Retaria						
Antiquatonia			1			
Reticulatia		1				
Echinaria						
Parajuresania					1	
Linoproductus						
Minilya	5	5	6			
Fenestrellina	8		3		1	1
Septopora						
Polypora	1	1	4	4	1	1
Rhombopora	5	2	2	5	12	14
Leioclema	4			4		
Sheet tub.			2	8	2	
Tubuliporate	1					
Treptostome						

	Perrin									
	Winchell Formation									
	P1	P2	P3	P4	P5	P6	P7	P8	Psh2	Psh3
Nucula										
Nuculana		1								
Myalina										
Aviculopinna										
Aviculopecten										
Acanthopecten										
Astartella										
Allorisma										
Bellerophon										
Pharkodonotus										
Trepospira										8
Lg high spire										
Leptozyga										
Goniasma										
Straparollus										
Anchura										
nautiloid										2
Lophophyllidium										
Caninia										
unk. coral										
Syringopora										
sponge										
trilobite										
shark										

RP		
Winchell Formation		
	R2	R1
Nucula		
Nuculana		
Myalina		
Aviculopinna		
Aviculopecten		
Acanthopecten		
Astartella		
Allorisma		
Bellerophon		
Pharkodonotus		
Trepospira	1	
Lg high spire		
Leptozyga		
Goniasma		
Straparollus		
Anchura		
nautiloid		
Lophophyllidium	3	
Caninia		
unk. coral	1	
Syringopora	1	
sponge		
trilobite		
shark		

	Brownwood			LS1								
	Winchell Formation											
	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	
Nucula												
Nuculana												
Myalina							2			3	4	
Aviculopinna			1			2			1	40	14	
Aviculopecten								1				
Acanthopecten												
Astartella												
Allorisma												
Bellerophon					1		1					
Pharkodonotus												
Trepospira										1		
Lg high spire												
Leptozyga			1		1							
Goniasma												
Straparollus												
Anchura												
nautiloid												
Lophophyllidium												
Caninia												
unk. coral												
Syringopora												
sponge												
trilobite												
shark												

Brownwood	Sh1/2			
Winchell Formation				
	Bsh12 A	Bsh12 B	Bcoq1	
Nucula				
Nuculana				
Myalina				
Aviculopinna				
Aviculopecten				
Acanthopecten				
Astartella				
Allorisma				
Bellerophon	1			
Pharkodonotus				
Trepospira				
Lg high spire				
Leptozyga				
Goniasma				
Straparollus				
Anchura				
nautiloid				
Lophophyllidium				
Caninia				
unk. coral				
Syringopora				
sponge				
trilobite	1			
shark				

Brownwood	LS2									
Winchell Formation										
	B12	B13	B14	B15	B16	B17	B18	B19	B20	B21
Nucula										
Nuculana		1								
Myalina			20							
Aviculopinna	6	4	64		2	5	4	12	4	2
Aviculopecten										
Acanthopecten										
Astartella				1						
Allorisma										
Bellerophon			7				1			
Pharkodonotus										
Trepospira										
Lg high spire										
Leptozyga								1		
Goniasma										
Straparollus										
Anchura							1			
nautiloid										
Lophophyllidium										
Caninia										
unk. coral										
Syringopora										
sponge										
trilobite										
shark			1	1				7		

Brownwood				
Winchell Formation	shLS2			
	B2coq1	B2coq2	B2sh1	B2sh2
Nucula				
Nuculana				
Myalina				
Aviculopinna				
Aviculopecten				
Acanthopecten				
Astartella				
Allorisma				
Bellerophon				
Pharkodonotus				
Trepospira				
Lg high spire				
Leptozyga				
Goniasma				
Straparollus				
Anchura				
nautiloid				
Lophophyllidium				
Caninia				
unk. coral				
Syringopora				
sponge				
trilobite		2	1	
shark				

Brownwood	Black sh							
Winchell Formation								
	Bblkech	Bblk1	Bblk2	Bblk3	Bblk4	Bblk5	Bblk6	
Nucula								
Nuculana		2						
Myalina								
Aviculopinna								
Aviculopecten		20	7	2	8	2	3	
Acanthopecten								
Astartella		1						
Allorisma								
Bellerophon								
Pharkodonotus								
Trepospira						1	1	
Lg high spire								
Leptozyga		4				1	2	
Goniasma					1			
Straparollus								
Anchura								
nautiloid								
Lophophyllidium								
Caninia								
unk. coral								
Syringopora								
sponge								
trilobite		1					2	
shark		1						

Brownwood	LS3				Sh3/4			
Winchell Formation								
	B22	B22A	B23	B24	Bsh34 A	Bsh34 B	Bconc r	
Nucula							4	
Nuculana							1	
Myalina							105	
Aviculopinna							8	
Aviculopecten							58	
Acanthopecten							1	
Astartella							24	
Allorisma							2	
Bellerophon		3						
Pharkodonotus								
Trepospira	1	2		1				
Lg high spire								
Leptozyga	1	5						
Goniasma								
Straparollus		11						
Anchura								
nautiloid							1	
Lophophyllidium						3		
Caninia								
unk. coral								
Syringopora								
sponge								
trilobite	1							
shark	2			15				

Brownwood	LS4					
Winchell Formation						
	B25	B26	B27	B27A	B27B	B28
Nucula						
Nuculana						
Myalina						
Aviculopinna	6					
Aviculopecten						
Acanthopecten						
Astartella						
Allorisma						
Bellerophon						
Pharkodonotus						
Trepospira						
Lg high spire						
Leptozyga						
Goniasma						
Straparollus						
Anchura						
nautiloid						
Lophophyllidium				2		
Caninia						
unk. coral						
Syringopora						
sponge						
trilobite						
shark						

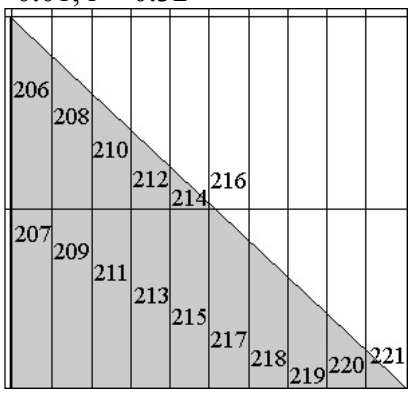
Brownwood	Sh4/5	LS5		Sh5/6		LS6		
Winchell Formation								
	Bsh45	B28A	B28B	Bsh56 A	Bsh56 B	B29	B30	
Nucula								
Nuculana								
Myalina	6							
Aviculopinna								
Aviculopecten								
Acanthopecten								
Astartella	1							
Allorisma								
Bellerophon	2						3	
Pharkodonotus								
Trepospira	4				8			
Lg high spire	1							
Leptozyga							2	
Goniasma								
Straparollus								
Anchura								
nautiloid				1	5			
Lophophyllidium							1	
Caninia								
unk. coral								
Syringopora								
sponge								
trilobite								
shark				1				

	Farley	Merriam				Spring Hill			Hickory
	Wyandotte Formation								Creek
	F1	M1	M2	M3	M4	S1	S2	HC	
Nucula									
Nuculana									
Myalina									
Aviculopinna		1							
Aviculopecten									
Acanthopecten					1				
Astartella	6						1	16	
Allorisma									
Bellerophon								2	
Pharkodonotus								1	
Trepospira	1							43	
Lg high spire									
Leptozyga	1					1	1		
Goniasma									
Straparollus									
Anchura									
nautiloid									
Lophophyllidium			6					8	
Caninia							2		
unk. coral									
Syringopora									
sponge									
trilobite									
shark									

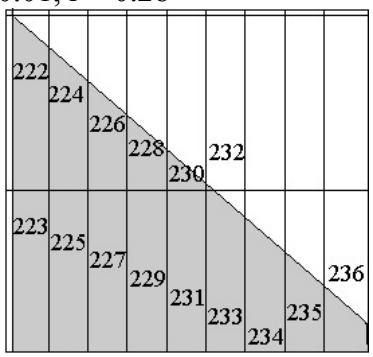
	Plattsmouth					
	Oread Formation					
	PL1	PL2	PL3	PL4	PL5	PLsh
Nucula						
Nuculana						
Myalina						
Aviculopinna						
Aviculopecten						
Acanthopecten					1	
Astartella					1	
Allorisma						
Bellerophon						1
Pharkodonotus						
Trepospira						1
Lg high spire						
Leptozyga					1	
Goniasma						
Straparollus						
Anchura						
nautiloid						3
Lophophyllidium	6	1			1	15
Caninia		1				
unk. coral						
Syringopora	4	2				17
sponge	2					
trilobite						
shark						

Appendix 3: Correlation

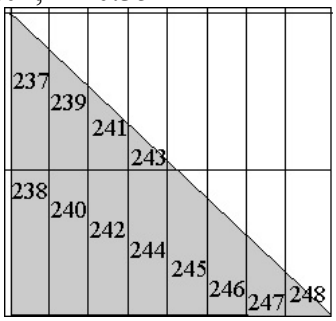
Sample correlation: pp. 206-221
63 degrees of freedom, p = 0.01, r = 0.32



Taxa correlation using all samples: pp. 222-236
79 degrees of freedom, p = 0.01, r = 0.28



Taxa correlation using Brownwood samples: pp. 237-248
52 degrees of freedom, p = 0.01, r = 0.35



	P1	*P2*	*P3*	*P4*	*P5*	*P6*	*P7*	*P8*
P1	1.00							63 d.f.
P2	**0.66**	1.00						r=0.32
P3	**0.71**	**0.92**	1.00					p=0.01
P4	**0.64**	**0.82**	**0.96**	1.00				
P5	**0.58**	**0.71**	**0.70**	**0.64**	1.00			
P6	**0.83**	**0.85**	**0.94**	**0.90**	**0.69**	1.00		
P7	-0.02	0.00	-0.01	-0.01	**0.52**	0.00	1.00	
P8	-0.01	0.02	0.02	0.02	**0.51**	0.02	1.00	1.00
Psh2	0.11	0.12	0.14	0.15	0.08	0.15	-0.02	-0.02
Psh3	**0.43**	0.27	**0.38**	**0.41**	0.26	**0.47**	-0.04	-0.03
R2	0.14	0.18	0.19	0.16	**0.61**	0.17	**0.93**	**0.94**
R1	0.08	0.21	0.19	0.17	**0.62**	0.16	**0.96**	**0.97**
F1	0.16	**0.33**	0.29	0.27	**0.64**	0.23	**0.84**	**0.85**
M1	**0.46**	**0.85**	**0.80**	**0.72**	**0.57**	**0.68**	-0.01	0.01
M2	0.19	0.29	0.26	0.24	0.18	0.22	-0.02	-0.01
M3	0.16	**0.37**	**0.34**	0.31	0.22	0.28	-0.02	-0.01
M4	0.12	0.13	0.11	0.10	0.06	0.09	-0.02	-0.02
S1	0.25	**0.47**	**0.44**	**0.42**	**0.73**	**0.39**	**0.82**	**0.83**
S2	**0.46**	**0.93**	**0.84**	**0.76**	**0.71**	**0.72**	0.18	0.20
PL1	**0.57**	**0.92**	**0.87**	**0.78**	**0.67**	**0.77**	-0.02	0.00
PL2	**0.74**	**0.48**	**0.63**	**0.69**	**0.51**	**0.69**	-0.04	-0.03
PL3	**0.42**	0.06	0.22	**0.32**	0.20	0.31	-0.05	-0.05
PL4	0.16	0.03	-0.03	-0.05	0.07	0.07	-0.03	-0.04
PL5	0.21	0.03	-0.01	-0.04	0.06	0.11	-0.04	-0.05
PLsh	0.03	-0.02	-0.04	-0.01	0.00	-0.01	-0.03	-0.04
HC	0.05	-0.02	-0.05	0.02	0.01	-0.05	-0.04	-0.04
B1	0.03	0.16	0.22	0.08	0.10	0.06	-0.02	-0.02
B2	0.22	**0.47**	**0.52**	**0.39**	**0.32**	**0.35**	-0.02	-0.01
B3	-0.01	0.10	0.15	0.01	0.06	0.00	-0.03	-0.03
B4	0.11	**0.39**	**0.41**	0.25	0.23	0.22	-0.02	-0.01
B5	0.08	0.21	0.27	0.15	0.16	0.11	-0.02	-0.02
B6	-0.05	0.05	0.10	-0.04	0.08	-0.04	-0.02	-0.02
B7	0.17	**0.42**	**0.42**	**0.34**	0.28	0.29	-0.04	-0.02
B8	0.04	0.08	0.16	0.06	0.13	0.04	-0.03	-0.03
B9	0.26	**0.58**	**0.58**	**0.46**	**0.43**	**0.40**	-0.02	-0.01
B10	0.00	0.04	0.04	0.00	0.06	0.02	-0.02	-0.03
B11	0.24	**0.57**	**0.54**	**0.46**	**0.50**	**0.43**	-0.02	-0.01
Bsh12A	**0.34**	0.18	**0.38**	**0.46**	0.20	**0.42**	0.02	-0.02
Bsh12B	**0.36**	0.12	**0.36**	**0.44**	0.17	**0.43**	0.01	-0.02
Bcoq1	**0.52**	**0.35**	**0.62**	**0.71**	**0.34**	**0.66**	-0.03	-0.01
B12	**0.59**	**0.85**	**0.95**	**0.90**	**0.66**	**0.85**	-0.01	0.01

B13	**0.50**	**0.35**	**0.62**	**0.62**	**0.45**	**0.61**	-0.02	-0.02
	P1	*P2*	*P3*	*P4*	*P5*	*P6*	*P7*	*P8*
B14	0.11	0.10	0.12	0.12	0.30	0.14	-0.01	-0.04
B15	**0.61**	**0.46**	**0.74**	**0.81**	**0.43**	**0.77**	-0.02	0.00
B16	**0.42**	0.20	**0.53**	**0.58**	0.24	**0.52**	-0.03	-0.01
B17	**0.60**	**0.92**	**0.96**	**0.93**	**0.69**	**0.89**	-0.01	0.01
B18	**0.54**	**0.43**	**0.60**	**0.51**	**0.45**	**0.60**	-0.02	-0.02
B19	0.00	0.12	0.19	0.09	0.21	0.07	-0.03	-0.04
B20	0.24	**0.40**	**0.41**	0.29	**0.42**	**0.33**	-0.02	-0.03
B21	0.03	0.11	0.19	0.06	0.11	0.05	-0.02	-0.02
B2coq1	**0.54**	**0.54**	**0.75**	**0.80**	**0.44**	**0.74**	-0.03	0.00
B2coq2	**0.52**	**0.78**	**0.85**	**0.84**	**0.56**	**0.79**	-0.02	0.01
B2sh1	0.16	0.05	0.18	0.23	0.06	0.20	-0.02	-0.02
B2sh2	**0.39**	0.12	**0.43**	**0.56**	0.17	**0.49**	-0.01	-0.02
Bblkech	0.15	0.05	0.07	0.12	0.10	0.02	-0.02	-0.02
Bblk1	**0.36**	**0.70**	**0.66**	**0.60**	**0.46**	**0.55**	-0.02	0.00
Bblk2	**0.51**	**0.83**	**0.81**	**0.73**	**0.57**	**0.72**	-0.01	0.01
Bblk3	**0.46**	**0.87**	**0.80**	**0.73**	**0.59**	**0.70**	0.00	0.02
Bblk4	0.16	0.27	0.24	0.22	0.16	0.20	-0.02	-0.01
Bblk5	**0.37**	**0.55**	**0.51**	**0.46**	**0.37**	**0.48**	-0.02	-0.01
Bblk6	**0.43**	**0.79**	**0.75**	**0.69**	**0.53**	**0.64**	-0.01	0.01
B22	0.15	0.08	0.29	0.24	0.09	0.20	-0.03	-0.02
B22A	0.21	0.28	**0.38**	**0.33**	0.19	0.31	-0.04	-0.02
B23	0.30	**0.53**	**0.53**	**0.48**	**0.41**	**0.42**	-0.03	-0.02
B24	0.01	0.07	0.07	0.03	0.18	0.01	-0.02	-0.04
Bsh34A	**0.51**	0.12	**0.45**	**0.58**	0.21	**0.56**	-0.02	-0.01
Bsh34B	**0.55**	0.13	**0.44**	**0.55**	0.22	**0.57**	-0.02	-0.02
Bconcr	**0.49**	0.29	**0.53**	**0.61**	0.29	**0.60**	-0.04	-0.02
B25	0.16	0.04	0.10	0.05	0.06	0.12	-0.04	-0.04
B26	0.10	0.30	**0.33**	0.19	0.17	0.17	-0.03	-0.02
B27	-0.02	0.05	0.10	-0.04	0.00	-0.04	-0.03	-0.02
B27A	-0.02	0.03	0.08	-0.04	-0.01	-0.04	-0.03	-0.03
B27B	0.12	0.20	0.21	0.11	0.11	0.13	-0.02	-0.02
B28	0.03	0.11	0.14	0.02	0.05	0.01	-0.03	-0.02
Bsh45	0.13	0.31	0.27	0.26	0.19	0.23	-0.01	-0.03
B28A	**0.37**	**0.46**	**0.63**	**0.58**	**0.35**	**0.53**	-0.03	-0.01
B28B	0.22	**0.50**	**0.50**	**0.43**	**0.32**	**0.39**	-0.02	0.00
Bsh56A	-0.05	-0.07	-0.08	-0.04	-0.06	-0.07	-0.03	-0.05
Bsh56B	-0.03	-0.04	-0.05	-0.01	-0.03	-0.05	-0.04	-0.04
B29	-0.04	-0.03	-0.03	-0.03	**0.48**	-0.03	**1.00**	**1.00**
B30	-0.04	-0.03	-0.03	-0.03	**0.48**	-0.03	**0.99**	**0.99**
	P1	*P2*	*P3*	*P4*	*P5*	*P6*	*P7*	*P8*

	Psh2	*Psh3*	*R2*	*R1*	*F1*	*M1*	*M2*	*M3*
P1								
P2								
P3								
P4								
P5								
P6								
P7								
P8								
Psh2	1.00							
Psh3	0.17	1.00						
R2	0.00	0.05	1.00					
R1	0.14	0.00	**0.94**	1.00				
F1	0.01	0.05	**0.86**	**0.90**	1.00			
M1	0.10	0.24	0.14	0.18	0.29	1.00		
M2	0.01	0.09	0.06	0.08	**0.45**	**0.32**	1.00	
M3	0.02	0.06	0.03	0.06	0.12	**0.46**	0.13	1.00
M4	0.02	0.08	-0.02	0.01	0.02	**0.58**	0.12	**0.35**
S1	0.13	0.22	**0.85**	**0.91**	**0.90**	**0.44**	0.20	0.20
S2	0.11	0.21	**0.33**	**0.39**	**0.53**	**0.90**	**0.42**	**0.42**
PL1	0.14	**0.36**	0.20	0.18	0.30	**0.82**	0.27	0.33
PL2	0.10	**0.44**	0.14	0.05	0.20	**0.34**	**0.34**	0.11
PL3	0.09	**0.48**	0.04	-0.05	0.13	0.03	**0.41**	-0.02
PL4	-0.04	0.09	-0.01	-0.03	0.18	-0.03	**0.56**	-0.03
PL5	**0.63**	0.11	0.03	0.05	0.03	-0.06	0.11	-0.04
PLsh	0.02	0.08	0.01	-0.03	0.05	-0.06	0.12	-0.06
HC	-0.01	0.13	0.07	-0.03	0.10	-0.05	0.12	-0.06
B1	0.00	-0.01	0.24	0.02	0.07	0.19	0.17	0.06
B2	0.04	0.09	0.26	0.09	0.21	**0.48**	**0.36**	0.19
B3	-0.02	-0.04	0.23	0.00	0.07	0.14	0.22	0.03
B4	0.02	0.00	0.26	0.07	0.10	**0.40**	0.11	0.16
B5	0.04	0.03	0.26	0.03	0.07	0.22	0.13	0.07
B6	-0.02	-0.05	0.22	-0.01	0.03	0.10	0.16	0.02
B7	0.01	0.05	0.16	0.07	0.20	**0.41**	**0.32**	0.19
B8	-0.02	0.01	0.18	0.00	0.18	0.11	**0.50**	0.02
B9	0.05	0.11	0.27	0.12	0.26	**0.56**	**0.37**	0.22
B10	-0.03	-0.05	0.03	-0.02	-0.03	0.04	-0.02	-0.01
B11	0.17	0.05	0.13	0.13	0.16	**0.54**	0.16	0.20
Bsh12A	0.12	0.29	0.04	0.00	-0.01	0.13	0.01	0.03
Bsh12B	0.12	**0.34**	0.03	-0.02	-0.03	0.07	-0.01	0.01
Bcoq1	0.20	**0.67**	0.07	0.03	0.05	0.33	0.06	0.12
B12	0.12	**0.34**	0.22	0.17	0.25	**0.78**	0.24	**0.32**

B13	0.18	**0.38**	0.19	0.04	0.02	0.29	0.05	0.11
	Psh2	*Psh3*	*R2*	*R1*	*F1*	*M1*	*M2*	*M3*
B14	-0.03	0.01	-0.02	-0.02	-0.02	0.09	0.03	0.00
B15	0.18	**0.62**	0.13	0.06	0.10	**0.41**	0.12	0.15
B16	0.12	**0.39**	0.16	0.00	-0.02	0.19	0.01	0.05
B17	0.22	**0.34**	0.16	0.20	0.30	**0.82**	0.30	**0.37**
B18	0.13	**0.32**	0.25	0.05	0.04	**0.35**	0.07	0.11
B19	-0.03	-0.05	0.14	-0.01	-0.02	0.14	0.03	0.03
B20	0.00	0.06	0.15	0.05	0.09	**0.42**	0.18	0.15
B21	-0.01	-0.01	0.23	0.00	0.01	0.18	0.09	0.05
B2coq1	0.17	**0.62**	0.11	0.08	0.13	**0.49**	0.13	0.19
B2coq2	0.14	**0.45**	0.12	0.15	0.24	**0.71**	0.22	0.30
B2sh1	0.03	0.27	0.00	-0.02	-0.03	0.03	-0.02	-0.01
B2sh2	0.12	**0.40**	0.03	-0.02	-0.03	0.09	-0.01	0.02
Bblkech	0.06	0.14	0.19	0.00	0.09	0.03	0.06	-0.01
Bblk1	0.05	0.15	0.13	0.16	**0.46**	**0.66**	0.78	0.29
Bblk2	0.09	0.24	0.16	0.18	**0.42**	**0.78**	**0.65**	**0.37**
Bblk3	0.09	0.20	0.14	0.21	**0.47**	**0.79**	**0.67**	**0.35**
Bblk4	0.00	0.06	0.03	0.07	**0.42**	0.31	**0.94**	0.12
Bblk5	0.06	0.22	0.08	0.12	**0.47**	**0.50**	**0.91**	0.21
Bblk6	0.07	0.20	0.15	0.18	**0.47**	**0.72**	**0.77**	0.31
B22	0.03	0.13	0.19	-0.02	-0.04	0.09	0.00	0.00
B22A	0.06	0.11	0.14	0.03	0.06	0.25	0.11	0.08
B23	0.12	0.13	0.12	0.11	**0.35**	**0.65**	**0.71**	0.25
B24	-0.05	-0.07	0.01	-0.01	0.10	0.22	**0.36**	0.08
Bsh34A	0.11	**0.45**	0.06	-0.02	0.00	0.09	0.08	0.04
Bsh34B	0.10	**0.47**	0.06	-0.02	0.02	0.11	0.17	0.02
Bconcr	0.08	**0.36**	0.05	0.01	0.04	0.23	0.08	0.16
B25	-0.02	0.05	0.06	-0.03	0.04	0.03	0.23	0.01
B26	0.01	0.02	0.24	0.06	0.21	0.31	**0.45**	0.11
B27	-0.02	-0.03	0.20	0.00	0.14	0.09	**0.43**	0.01
B27A	-0.03	-0.03	0.18	0.00	0.20	0.07	**0.57**	0.01
B27B	0.00	0.05	0.15	0.04	**0.33**	0.20	**0.82**	0.07
B28	-0.01	0.01	0.23	0.01	0.18	0.13	**0.45**	0.03
Bsh45	0.04	0.04	0.02	0.04	0.14	0.27	0.20	0.08
B28A	**0.59**	0.24	0.21	0.15	0.12	**0.43**	0.18	0.16
B28B	**0.84**	0.07	0.12	0.22	0.15	**0.46**	0.14	0.19
Bsh56A	-0.03	**0.48**	-0.04	-0.05	0.02	-0.08	0.10	-0.03
Bsh56B	-0.03	0.52	-0.02	-0.04	-0.02	-0.04	-0.03	-0.04
B29	-0.03	-0.05	**0.93**	**0.96**	**0.84**	-0.03	-0.01	-0.03
B30	-0.03	-0.05	**0.92**	**0.95**	**0.87**	-0.03	0.08	-0.03
	Psh2	*Psh3*	*R2*	*R1*	*F1*	*M1*	*M2*	*M3*

	M4	*S1*	*S2*	*PL1*	*PL2*	*PL3*	*PL4*
P1							
P2							
P3							
P4							
P5							
P6							
P7							
P8							
Psh2							
Psh3							
R2							
R1							
F1							
M1							
M2							
M3							
M4	1.00						
S1	0.07	1.00					
S2	0.25	**0.63**	1.00				
PL1	0.13	**0.47**	**0.88**	1.00			
PL2	-0.01	0.23	**0.36**	**0.52**	1.00		
PL3	-0.03	0.13	0.02	0.13	**0.68**	1.00	
PL4	-0.06	0.04	0.03	-0.01	0.23	**0.52**	1.00
PL5	-0.06	0.05	-0.02	0.03	0.19	0.31	0.31
PLsh	-0.06	0.06	-0.04	0.03	0.24	0.17	0.25
HC	-0.05	-0.01	-0.03	0.04	0.23	0.22	0.03
B1	-0.02	0.04	0.19	0.27	0.04	0.03	0.05
B2	0.08	0.20	**0.50**	**0.54**	0.26	0.10	0.08
B3	-0.03	0.02	0.14	0.21	0.03	0.08	0.09
B4	0.02	0.16	**0.41**	**0.48**	0.06	-0.06	-0.06
B5	-0.01	0.07	0.22	**0.33**	0.12	0.07	-0.01
B6	-0.03	-0.01	0.09	0.18	-0.01	0.05	0.08
B7	0.02	0.18	**0.47**	**0.45**	0.24	0.17	0.04
B8	-0.04	0.02	0.16	0.18	0.17	0.29	0.29
B9	0.04	0.27	**0.62**	**0.66**	0.31	0.14	0.07
B10	-0.03	-0.03	0.03	0.05	-0.04	-0.05	-0.03
B11	0.04	0.24	**0.58**	**0.57**	0.19	0.00	-0.06
Bsh12A	-0.02	0.06	0.10	0.18	**0.42**	0.31	0.01
Bsh12B	-0.03	0.04	0.03	0.12	**0.47**	**0.41**	0.06
Bcoq1	0.07	0.26	0.28	**0.42**	**0.63**	**0.59**	-0.01
B12	0.13	**0.39**	**0.80**	**0.83**	**0.57**	**0.19**	-0.04

B13	-0.01	0.13	0.25	**0.39**	**0.58**	**0.42**	0.00
	M4	*S1*	*S2*	*PL1*	*PL2*	*PL3*	*PL4*
B14	0.03	-0.02	0.06	0.08	0.15	0.10	0.07
B15	0.08	0.26	**0.38**	**0.50**	**0.68**	**0.54**	-0.03
B16	0.00	0.08	0.12	0.26	**0.56**	**0.46**	-0.06
B17	0.12	**0.46**	**0.87**	**0.87**	**0.57**	0.22	0.00
B18	0.03	0.14	0.31	**0.46**	**0.48**	**0.33**	0.09
B19	-0.04	-0.01	0.13	0.20	0.03	0.04	-0.04
B20	0.09	0.15	**0.39**	**0.42**	0.26	0.13	0.09
B21	0.06	0.00	0.13	0.23	0.05	0.03	0.00
B2coq1	0.09	0.31	**0.48**	**0.57**	**0.59**	**0.43**	-0.06
B2coq2	0.11	**0.41**	**0.74**	**0.75**	**0.50**	0.23	-0.05
B2sh1	-0.03	0.00	0.01	0.04	0.19	0.14	-0.05
B2sh2	-0.02	0.06	0.03	0.16	**0.55**	**0.50**	0.05
Bblkech	-0.02	0.02	0.02	0.18	**0.37**	**0.35**	-0.04
Bblk1	0.11	**0.37**	**0.77**	**0.65**	**0.40**	0.22	0.30
Bblk2	0.18	**0.42**	**0.86**	**0.77**	**0.48**	0.22	0.24
Bblk3	0.12	**0.46**	**0.92**	**0.81**	**0.44**	0.15	0.22
Bblk4	0.14	0.18	**0.40**	0.23	0.28	**0.34**	**0.52**
Bblk5	0.06	**0.33**	**0.62**	**0.50**	**0.43**	**0.41**	**0.52**
Bblk6	0.10	**0.42**	**0.85**	**0.74**	**0.45**	0.22	0.29
B22	-0.04	-0.01	0.05	0.17	0.22	0.18	-0.07
B22A	-0.01	0.09	0.25	0.30	0.20	0.09	-0.03
B23	**0.36**	0.26	**0.63**	**0.52**	**0.38**	0.29	0.29
B24	0.28	0.00	0.15	0.08	0.05	0.12	0.18
Bsh34A	-0.01	0.08	0.02	0.12	**0.67**	**0.66**	0.10
Bsh34B	0.03	0.07	0.03	0.13	**0.68**	**0.67**	0.18
Bconcr	0.02	0.12	0.20	0.25	**0.54**	**0.40**	0.00
B25	0.00	-0.03	0.02	0.04	0.14	0.17	0.20
B26	0.00	0.13	**0.36**	**0.38**	0.16	0.12	0.18
B27	-0.03	0.01	0.12	0.15	0.05	0.15	0.25
B27A	-0.04	0.01	0.13	0.13	0.08	0.22	**0.35**
B27B	-0.01	0.12	0.30	0.23	0.23	**0.35**	**0.51**
B28	-0.03	0.04	0.17	0.22	0.13	0.20	0.25
Bsh45	0.00	0.12	**0.32**	**0.38**	0.13	0.02	0.21
B28A	0.02	0.23	**0.43**	**0.50**	**0.41**	0.24	-0.01
B28B	0.05	0.26	**0.51**	**0.49**	0.17	-0.05	-0.07
Bsh56A	-0.06	-0.05	-0.06	-0.05	0.06	0.12	0.12
Bsh56B	-0.03	-0.04	-0.05	-0.03	0.03	0.01	-0.02
B29	-0.02	**0.81**	0.16	-0.04	-0.05	-0.05	-0.03
B30	-0.03	**0.81**	0.16	-0.05	-0.03	0.00	0.03
	M4	*S1*	*S2*	*PL1*	*PL2*	*PL3*	*PL4*

	PL5	*PLsh*	*HC*	*B1*	*B2*	*B3*	*B4*	*B5*
P1								
P2								
P3								
P4								
P5								
P6								
P7								
P8								
Psh2								
Psh3								
R2								
R1								
F1								
M1								
M2								
M3								
M4								
S1								
S2								
PL1								
PL2								
PL3								
PL4								
PL5	1.00							
PLsh	**0.40**	1.00						
HC	0.17	0.21	1.00					
B1	0.03	-0.02	-0.03	1.00				
B2	0.01	-0.03	-0.03	**0.91**	1.00			
B3	0.04	-0.01	0.00	**0.99**	**0.89**	1.00		
B4	-0.01	-0.05	-0.05	**0.94**	**0.92**	**0.92**	1.00	
B5	0.06	-0.01	0.05	**0.98**	**0.91**	**0.97**	**0.94**	1.00
B6	0.04	-0.02	-0.03	**0.98**	**0.86**	**0.98**	**0.88**	**0.96**
B7	0.02	0.02	0.06	**0.52**	**0.63**	**0.58**	**0.65**	**0.56**
B8	0.07	0.03	0.03	**0.86**	**0.81**	**0.90**	**0.77**	**0.84**
B9	0.05	0.01	0.10	**0.82**	**0.92**	**0.82**	**0.90**	**0.86**
B10	-0.03	-0.05	-0.04	0.22	0.18	0.23	0.22	0.21
B11	0.03	-0.07	-0.06	**0.37**	**0.51**	**0.37**	**0.53**	**0.41**
Bsh12A	-0.03	-0.02	-0.05	0.04	0.12	0.00	0.03	0.06
Bsh12B	0.00	-0.01	-0.05	0.01	0.08	-0.02	-0.01	0.03
Bcoq1	-0.04	-0.05	-0.06	0.04	0.20	0.00	0.07	0.08
B12	-0.04	-0.05	-0.06	**0.41**	**0.69**	**0.35**	**0.57**	**0.46**

B13	0.07	-0.05	-0.07	**0.55**	**0.61**	**0.50**	**0.52**	**0.58**
	PL5	*PLsh*	*HC*	*B1*	*B2*	*B3*	*B4*	*B5*
B14	-0.04	-0.06	-0.08	0.05	0.13	0.05	0.04	0.05
B15	-0.01	-0.05	-0.05	0.18	**0.36**	0.12	0.21	0.22
B16	-0.03	-0.06	-0.06	**0.48**	**0.53**	**0.44**	**0.43**	**0.51**
B17	0.07	-0.05	-0.03	0.16	**0.49**	0.10	**0.36**	0.22
B18	0.14	-0.03	-0.05	**0.70**	**0.74**	**0.66**	**0.69**	**0.73**
B19	-0.04	-0.08	-0.09	**0.73**	**0.65**	**0.74**	**0.73**	**0.73**
B20	0.01	-0.06	-0.09	**0.59**	**0.72**	**0.60**	**0.65**	**0.59**
B21	0.03	-0.04	-0.05	**0.98**	**0.90**	**0.96**	**0.91**	**0.97**
B2coq1	-0.06	-0.07	-0.04	0.12	**0.32**	0.06	0.20	0.16
B2coq2	-0.04	-0.07	-0.03	0.08	**0.36**	0.02	0.26	0.12
B2sh1	-0.06	-0.06	0.01	-0.01	0.03	-0.03	-0.02	0.00
B2sh2	-0.07	-0.06	-0.06	0.02	0.11	-0.01	-0.01	0.05
Bblkech	0.20	0.14	**0.58**	**0.33**	0.29	**0.37**	0.30	**0.46**
Bblk1	0.02	0.02	0.02	0.29	**0.56**	0.28	**0.37**	0.28
Bblk2	0.03	0.01	-0.01	0.28	**0.58**	0.25	**0.41**	0.29
Bblk3	0.02	0.02	0.01	0.17	**0.50**	0.14	**0.33**	0.18
Bblk4	0.08	0.08	0.06	0.13	0.31	0.17	0.07	0.08
Bblk5	0.11	0.07	0.09	0.13	**0.39**	0.16	0.16	0.11
Bblk6	0.03	0.02	0.04	0.27	**0.57**	0.25	**0.38**	0.27
B22	-0.03	-0.06	-0.05	**0.76**	**0.69**	**0.72**	**0.68**	**0.76**
B22A	-0.02	-0.07	-0.05	**0.51**	**0.54**	**0.48**	**0.51**	**0.52**
B23	0.05	-0.01	0.00	**0.44**	**0.68**	**0.46**	**0.50**	**0.43**
B24	-0.04	-0.03	-0.03	0.30	0.30	0.32	0.30	0.27
Bsh34A	0.03	-0.02	-0.02	0.04	0.13	0.02	-0.02	0.07
Bsh34B	0.06	-0.01	-0.03	0.04	0.14	0.02	-0.03	0.05
Bconcr	-0.03	-0.07	-0.04	0.02	0.15	-0.03	0.03	0.04
B25	0.06	-0.02	-0.05	**0.39**	**0.35**	**0.40**	**0.37**	**0.35**
B26	0.05	0.00	-0.01	**0.93**	**0.97**	**0.93**	**0.88**	**0.91**
B27	0.09	0.03	0.01	**0.94**	**0.85**	**0.96**	**0.82**	**0.90**
B27A	0.10	0.05	0.03	**0.87**	**0.80**	**0.90**	**0.73**	**0.82**
B27B	0.14	0.09	0.05	**0.66**	**0.71**	**0.70**	**0.56**	**0.61**
B28	0.13	0.06	0.11	**0.93**	**0.86**	**0.95**	**0.82**	**0.91**
Bsh45	0.04	0.07	0.17	0.03	0.14	0.01	0.10	0.06
B28A	**0.33**	-0.03	-0.06	**0.63**	**0.72**	**0.58**	**0.66**	**0.67**
B28B	**0.48**	-0.04	-0.05	**0.32**	**0.45**	0.28	**0.43**	**0.36**
Bsh56A	0.13	0.24	0.17	-0.04	-0.05	0.00	-0.05	-0.01
Bsh56B	0.03	0.11	0.25	-0.05	-0.06	-0.03	-0.05	-0.01
B29	-0.05	-0.04	-0.03	-0.01	-0.02	-0.02	-0.02	-0.02
B30	-0.03	-0.03	-0.02	-0.01	-0.01	0.00	-0.03	-0.02
	PL5	*PLsh*	*HC*	*B1*	*B2*	*B3*	*B4*	*B5*

	B6	*B7*	*B8*	*B9*	*B10*	*B11*	*Bsh12A*	*Bsh12B*
P1								
P2								
P3								
P4								
P5								
P6								
P7								
P8								
Psh2								
Psh3								
R2								
R1								
F1								
M1								
M2								
M3								
M4								
S1								
S2								
PL1								
PL2								
PL3								
PL4								
PL5								
PLsh								
HC								
B1								
B2								
B3								
B4								
B5								
B6	1.00							
B7	**0.48**	1.00						
B8	**0.87**	**0.63**	1.00					
B9	**0.77**	**0.77**	**0.77**	1.00				
B10	0.30	0.17	0.20	0.24	1.00			
B11	**0.38**	**0.68**	**0.38**	**0.66**	**0.67**	1.00		
Bsh12A	-0.01	0.03	0.04	0.08	-0.03	0.05	1.00	
Bsh12B	-0.03	-0.01	0.03	0.02	-0.04	-0.01	**0.98**	1.00
Bcoq1	-0.02	0.09	0.05	0.15	-0.03	0.13	**0.58**	**0.64**
B12	**0.32**	**0.49**	**0.32**	**0.71**	0.20	**0.64**	0.37	**0.34**

B13	**0.52**	**0.33**	**0.50**	**0.54**	0.24	**0.42**	**0.50**	**0.54**
	B6	*B7*	*B8*	*B9*	*B10*	*B11*	*Bsh12A*	*Bsh12B*
B14	0.15	0.07	0.13	0.12	**0.77**	**0.60**	0.05	0.04
B15	0.10	0.21	0.18	0.30	0.01	0.24	**0.58**	**0.62**
B16	**0.43**	0.29	**0.43**	**0.41**	0.11	0.23	**0.55**	**0.61**
B17	0.07	**0.41**	0.12	**0.57**	0.17	**0.64**	**0.34**	0.30
B18	**0.68**	**0.41**	**0.59**	**0.68**	**0.34**	**0.51**	**0.37**	**0.39**
B19	**0.77**	**0.53**	**0.72**	**0.66**	**0.63**	**0.68**	0.04	0.01
B20	**0.62**	**0.56**	**0.58**	**0.67**	**0.54**	**0.72**	0.06	0.05
B21	**0.97**	**0.49**	**0.82**	**0.78**	0.26	**0.37**	0.06	0.03
B2coq1	0.03	0.21	0.09	0.30	-0.01	0.27	**0.50**	**0.53**
B2coq2	-0.02	0.30	0.03	0.42	-0.01	**0.43**	**0.32**	0.31
B2sh1	-0.03	-0.02	-0.01	-0.01	-0.04	-0.02	0.31	**0.34**
B2sh2	-0.02	0.00	0.05	0.02	-0.04	0.00	**0.81**	**0.85**
Bblkech	**0.32**	0.29	0.31	**0.44**	0.05	0.11	0.09	0.07
Bblk1	0.22	**0.46**	**0.45**	**0.61**	0.02	**0.43**	0.11	0.06
Bblk2	0.19	**0.47**	**0.37**	**0.63**	0.03	**0.50**	0.24	0.18
Bblk3	0.08	**0.46**	0.26	**0.60**	0.02	**0.52**	0.15	0.08
Bblk4	0.12	0.27	**0.46**	0.31	-0.03	0.13	-0.01	-0.03
Bblk5	0.09	**0.35**	**0.40**	**0.42**	-0.02	0.27	0.13	0.11
Bblk6	0.19	**0.48**	**0.40**	**0.63**	0.02	**0.48**	0.15	0.09
B22	**0.72**	**0.34**	**0.62**	**0.57**	0.14	0.21	0.27	0.29
B22A	**0.47**	0.30	**0.42**	**0.49**	0.08	0.25	0.19	0.18
B23	**0.39**	**0.64**	**0.65**	**0.67**	0.09	**0.52**	0.09	0.05
B24	0.31	0.25	**0.52**	0.30	0.09	0.23	-0.05	-0.07
Bsh34A	0.00	0.02	0.11	0.03	-0.03	-0.01	**0.64**	**0.74**
Bsh34B	0.00	0.02	0.15	0.03	-0.03	-0.03	**0.67**	**0.76**
Bconcr	-0.04	0.13	0.06	0.10	0.04	0.19	**0.46**	**0.52**
B25	**0.38**	0.16	**0.51**	0.28	**0.42**	0.24	0.07	0.08
B26	**0.90**	**0.60**	**0.89**	**0.87**	0.18	**0.40**	0.04	0.00
B27	**0.94**	**0.52**	**0.93**	**0.76**	0.19	0.27	-0.01	-0.03
B27A	**0.87**	**0.52**	**0.94**	**0.72**	0.16	0.24	0.00	-0.02
B27B	**0.65**	**0.55**	**0.86**	**0.66**	0.11	0.28	0.07	0.06
B28	**0.92**	**0.53**	**0.92**	**0.81**	0.18	0.29	-0.01	-0.03
Bsh45	-0.01	0.15	0.03	0.21	-0.03	0.17	**0.42**	**0.35**
B28A	**0.56**	**0.43**	**0.53**	**0.67**	0.11	**0.47**	**0.34**	**0.34**
B28B	0.26	0.31	0.22	**0.48**	0.05	**0.48**	0.08	0.04
Bsh56A	-0.04	0.07	0.03	0.03	-0.06	-0.05	0.12	0.12
Bsh56B	-0.05	-0.04	-0.06	0.00	-0.05	-0.07	-0.02	-0.02
B29	-0.02	-0.04	-0.02	-0.03	-0.03	-0.04	-0.03	-0.03
B30	0.00	-0.02	0.03	-0.01	-0.03	-0.04	-0.03	-0.03
	B6	*B7*	*B8*	*B9*	*B10*	*B11*	*Bsh12A*	*Bsh12B*

	Bcoq1	*B12*	*B13*	*B14*	*B15*	*B16*	*B17*	*B18*
P1								
P2								
P3								
P4								
P5								
P6								
P7								
P8								
Psh2								
Psh3								
R2								
R1								
F1								
M1								
M2								
M3								
M4								
S1								
S2								
PL1								
PL2								
PL3								
PL4								
PL5								
PLsh								
HC								
B1								
B2								
B3								
B4								
B5								
B6								
B7								
B8								
B9								
B10								
B11								
Bsh12A								
Bsh12B								
Bcoq1	1.00							
B12	**0.58**	1.00						

B13	**0.70**	**0.73**	1.00					
	Bcoq1	*B12*	*B13*	*B14*	*B15*	*B16*	*B17*	*B18*
B14	0.08	0.27	**0.32**	1.00				
B15	**0.95**	**0.72**	**0.82**	0.12	1.00			
B16	**0.78**	**0.61**	**0.93**	0.14	**0.87**	1.00		
B17	**0.56**	**0.93**	**0.54**	0.25	**0.66**	**0.42**	1.00	
B18	**0.53**	**0.72**	**0.92**	**0.34**	**0.67**	**0.80**	**0.53**	1.00
B19	0.06	**0.39**	**0.56**	**0.53**	0.18	**0.42**	0.21	**0.65**
B20	0.14	**0.61**	**0.54**	**0.66**	0.25	**0.36**	**0.48**	**0.66**
B21	0.06	0.41	**0.59**	0.15	0.20	**0.52**	0.14	**0.74**
B2coq1	**0.86**	**0.75**	**0.70**	0.08	**0.88**	**0.70**	**0.69**	**0.54**
B2coq2	**0.60**	**0.83**	**0.50**	0.07	**0.66**	**0.42**	**0.85**	**0.40**
B2sh1	0.30	0.25	**0.34**	0.00	0.31	**0.32**	0.14	0.17
B2sh2	**0.80**	**0.42**	**0.67**	0.06	**0.80**	**0.79**	**0.36**	**0.46**
Bblkech	0.04	0.13	0.20	-0.03	0.09	0.20	0.06	0.28
Bblk1	0.22	**0.64**	0.25	0.05	**0.32**	0.16	**0.68**	0.29
Bblk2	**0.34**	**0.77**	**0.36**	0.08	**0.45**	0.25	**0.82**	**0.41**
Bblk3	0.25	**0.75**	0.23	0.07	**0.36**	0.10	**0.84**	0.27
Bblk4	0.04	0.22	0.01	0.02	0.09	-0.02	0.27	0.03
Bblk5	0.23	**0.45**	0.14	0.04	0.27	0.07	**0.54**	0.17
Bblk6	0.28	**0.72**	0.28	0.06	**0.38**	0.18	**0.77**	**0.32**
B22	**0.36**	**0.43**	**0.71**	0.04	**0.47**	**0.73**	0.19	**0.73**
B22A	0.27	**0.45**	**0.49**	0.01	**0.37**	**0.47**	**0.32**	**0.52**
B23	0.21	**0.62**	**0.37**	0.25	**0.33**	0.29	**0.56**	**0.41**
B24	-0.05	0.14	0.18	0.28	0.03	0.07	0.08	0.19
Bsh34A	**0.85**	**0.43**	**0.74**	0.10	**0.86**	**0.85**	**0.37**	**0.54**
Bsh34B	**0.83**	**0.41**	**0.72**	0.11	**0.83**	**0.81**	**0.36**	**0.54**
Bconcr	**0.69**	**0.49**	**0.61**	0.21	**0.73**	**0.66**	**0.46**	**0.47**
B25	0.10	0.20	**0.35**	**0.43**	0.17	0.27	0.11	**0.41**
B26	0.07	**0.51**	**0.50**	0.08	0.21	**0.44**	0.30	**0.65**
B27	-0.03	0.27	**0.43**	0.00	0.09	**0.39**	0.05	**0.58**
B27A	-0.03	0.23	**0.37**	0.00	0.08	**0.34**	0.04	**0.50**
B27B	0.03	0.30	0.29	0.02	0.13	0.25	0.20	**0.40**
B28	-0.02	0.31	**0.43**	0.00	0.11	**0.38**	0.10	**0.59**
Bsh45	0.05	0.24	0.01	-0.01	0.07	-0.03	0.31	0.04
B28A	**0.50**	**0.71**	**0.78**	0.06	**0.62**	**0.72**	**0.60**	**0.76**
B28B	0.17	0.52	**0.36**	0.02	0.26	0.23	**0.55**	**0.37**
Bsh56A	-0.07	-0.06	-0.07	-0.11	-0.08	-0.07	-0.06	-0.10
Bsh56B	-0.06	-0.03	-0.05	-0.08	-0.06	-0.06	-0.05	-0.07
B29	-0.03	-0.03	-0.04	-0.04	-0.03	-0.03	-0.03	-0.04
B30	-0.04	-0.04	-0.04	-0.03	-0.03	-0.03	-0.03	-0.04
	Bcoq1	*B12*	*B13*	*B14*	*B15*	*B16*	*B17*	*B18*

	B19	*B20*	*B21*	*B2coq1*	*B2coq2*	*B2sh1*	*B2sh2*	*Bblkech*
B14								
B15								
B16								
B17								
B18								
B19	1.00							
B20	**0.74**	1.00						
B21	**0.76**	**0.66**	1.00					
B2coq1	0.10	0.22	0.12	1.00				
B2coq2	0.07	0.28	0.05	**0.89**	1.00			
B2sh1	-0.01	-0.01	0.00	**0.64**	**0.58**	1.00		
B2sh2	0.04	0.04	0.05	**0.67**	**0.39**	**0.36**	1.00	
Bblkech	0.21	0.15	**0.32**	0.05	0.01	0.01	0.07	1.00
Bblk1	0.16	**0.35**	0.20	**0.37**	**0.56**	0.02	0.07	0.05
Bblk2	0.16	**0.41**	0.21	**0.49**	**0.68**	0.06	0.17	0.06
Bblk3	0.09	**0.36**	0.08	**0.45**	**0.70**	0.03	0.06	0.01
Bblk4	0.00	0.14	0.05	0.10	0.20	-0.02	-0.02	-0.01
Bblk5	0.01	0.25	0.04	0.31	**0.45**	0.02	0.09	-0.01
Bblk6	0.15	**0.37**	0.18	**0.44**	**0.65**	0.03	0.10	0.04
B22	**0.56**	**0.41**	**0.77**	**0.34**	0.15	0.13	**0.38**	0.27
B22A	**0.35**	**0.32**	**0.50**	0.31	0.26	0.07	0.23	0.16
B23	**0.41**	**0.64**	**0.43**	**0.34**	**0.45**	0.05	0.08	0.13
B24	**0.56**	**0.37**	0.30	-0.01	0.01	-0.06	-0.06	0.04
Bsh34A	0.05	0.11	0.07	**0.70**	**0.40**	**0.34**	**0.89**	0.09
Bsh34B	0.04	0.12	0.07	**0.68**	**0.38**	**0.35**	**0.88**	0.05
Bconcr	0.03	0.11	0.03	**0.62**	**0.44**	0.24	**0.66**	0.01
B25	**0.57**	**0.46**	**0.39**	0.08	0.01	0.02	0.09	0.09
B26	**0.63**	**0.65**	**0.90**	0.17	0.19	-0.01	0.02	0.29
B27	**0.64**	**0.51**	**0.90**	0.02	-0.02	-0.02	-0.03	0.30
B27A	**0.58**	**0.46**	**0.81**	0.01	-0.03	-0.03	-0.02	0.27
B27B	**0.42**	**0.43**	**0.58**	0.09	0.11	-0.01	0.02	0.19
B28	**0.62**	**0.51**	**0.88**	0.04	0.02	-0.03	-0.03	**0.44**
Bsh45	-0.04	0.05	-0.01	0.12	0.24	0.06	**0.34**	0.16
B28A	**0.46**	**0.46**	**0.62**	**0.55**	**0.48**	0.15	**0.43**	0.21
B28B	0.22	0.30	0.29	0.29	**0.40**	0.01	0.06	0.08
Bsh56A	-0.06	-0.10	-0.06	0.00	0.02	0.16	0.00	0.23
Bsh56B	-0.09	-0.10	-0.05	0.03	0.05	0.17	-0.05	0.21
B29	-0.04	-0.05	-0.02	-0.04	-0.03	-0.02	-0.03	-0.02
B30	-0.04	-0.04	-0.02	-0.04	-0.04	-0.03	-0.03	-0.02
	B19	*B20*	*B21*	*B2coq1*	*B2coq2*	*B2sh1*	*B2sh2*	*Bblkech*

	Bblk1	*Bblk2*	*Bblk3*	*Bblk4*	*Bblk5*	*Bblk6*	*B22*	*B22A*
B14								
B15								
B16								
B17								
B18								
B19								
B20								
B21								
B2coq1								
B2coq2								
B2sh1								
B2sh2								
Bblkech								
Bblk1	1.00							
Bblk2	**0.96**	1.00						
Bblk3	**0.93**	**0.96**	1.00					
Bblk4	**0.84**	**0.71**	**0.66**	1.00				
Bblk5	**0.90**	**0.84**	**0.84**	**0.90**	1.00			
Bblk6	**0.96**	**0.95**	**0.97**	**0.76**	**0.90**	1.00		
B22	0.12	0.15	0.02	-0.03	-0.01	0.11	1.00	
B22A	0.27	0.30	0.24	0.08	0.16	0.28	**0.85**	1.00
B23	**0.75**	**0.73**	**0.71**	**0.66**	0.70	**0.76**	0.25	0.28
B24	0.28	0.23	0.21	**0.33**	0.27	0.25	0.14	0.08
Bsh34A	0.10	0.20	0.07	0.05	0.16	0.13	**0.42**	0.26
Bsh34B	0.15	0.25	0.11	0.14	0.25	0.18	**0.39**	0.25
Bconcr	0.29	**0.38**	0.25	0.16	0.23	0.27	0.29	0.21
B25	0.17	0.16	0.09	0.20	0.19	0.16	0.29	0.17
B26	**0.52**	**0.49**	**0.40**	**0.39**	**0.41**	**0.51**	**0.66**	**0.50**
B27	**0.38**	0.30	0.20	**0.37**	**0.32**	**0.33**	**0.67**	**0.45**
B27A	**0.45**	**0.34**	0.25	**0.51**	**0.43**	**0.40**	**0.59**	**0.40**
B27B	**0.66**	**0.55**	**0.50**	**0.75**	**0.73**	**0.63**	**0.40**	**0.33**
B28	**0.41**	**0.34**	0.25	**0.39**	**0.35**	**0.38**	**0.65**	**0.45**
Bsh45	0.29	**0.34**	**0.37**	0.18	0.29	**0.34**	-0.05	0.04
B28A	**0.41**	**0.49**	**0.40**	0.14	0.26	**0.44**	**0.64**	**0.51**
B28B	**0.39**	**0.45**	**0.45**	0.12	0.25	**0.43**	0.23	0.28
Bsh56A	0.01	-0.01	0.00	0.07	0.04	0.01	-0.08	-0.09
Bsh56B	-0.06	-0.06	-0.04	-0.05	-0.06	-0.05	-0.06	-0.08
B29	-0.02	-0.03	-0.02	-0.01	-0.02	-0.02	-0.03	-0.03
B30	0.03	0.01	0.02	0.08	0.05	0.03	-0.03	-0.03
	Bblk1	*Bblk2*	*Bblk3*	*Bblk4*	*Bblk5*	*Bblk6*	*B22*	*B22A*

	B23	*B24*	*Bsh34A*	*Bsh34B*	*Bconcr*	*B25*	*B26*	*B27*
B14								
B15								
B16								
B17								
B18								
B19								
B20								
B21								
B2coq1								
B2coq2								
B2sh1								
B2sh2								
Bblkech								
Bblk1								
Bblk2								
Bblk3								
Bblk4								
Bblk5								
Bblk6								
B22								
B22A								
B23	1.00							
B24	**0.60**	1.00						
Bsh34A	0.14	-0.02	1.00					
Bsh34B	0.20	0.05	**0.98**	1.00				
Bconcr	0.16	-0.05	**0.74**	**0.72**	1.00			
B25	**0.45**	**0.64**	0.17	0.25	0.11	1.00		
B26	**0.64**	0.31	0.05	0.07	0.05	**0.38**	1.00	
B27	**0.51**	**0.33**	0.02	0.05	-0.03	**0.40**	**0.95**	1.00
B27A	**0.56**	**0.36**	0.03	0.08	-0.03	**0.40**	**0.92**	**0.98**
B27B	**0.70**	**0.39**	0.08	0.16	0.04	**0.38**	**0.82**	**0.85**
B28	**0.52**	**0.32**	0.02	0.05	-0.02	**0.39**	**0.95**	**0.98**
Bsh45	0.18	-0.01	-0.01	0.04	0.11	-0.05	0.11	0.03
B28A	**0.49**	0.13	**0.47**	**0.44**	**0.41**	0.24	**0.63**	**0.53**
B28B	**0.41**	0.06	0.05	0.04	0.12	0.05	**0.36**	0.24
Bsh56A	0.01	-0.03	-0.03	-0.03	-0.09	-0.06	-0.01	0.02
Bsh56B	-0.07	-0.08	-0.05	-0.07	-0.08	-0.09	-0.06	-0.05
B29	-0.04	-0.04	-0.02	-0.03	-0.04	-0.03	-0.02	-0.01
B30	0.01	0.00	-0.02	-0.01	-0.04	-0.01	0.01	0.03
	B23	*B24*	*Bsh34A*	*Bsh34B*	*Bconcr*	*B25*	*B26*	*B27*

	B27A	*B27B*	*B28*	*Bsh45*	*B28A*	*B28B*	*Bsh56A*	*Bsh56B*	*B29*
B14									
B15									
B16									
B17									
B18									
B19									
B20									
B21									
B2coq1									
B2coq2									
B2sh1									
B2sh2									
Bblkech									
Bblk1									
Bblk2									
Bblk3									
Bblk4									
Bblk5									
Bblk6									
B22									
B22A									
B23									
B24									
Bsh34A									
Bsh34B									
Bconcr									
B25									
B26									
B27									
B27A	1.00								
B27B	**0.92**	1.00							
B28	**0.97**	**0.84**	1.00						
Bsh45	0.06	0.17	0.08	1.00					
B28A	**0.49**	**0.42**	**0.55**	0.09	1.00				
B28B	0.20	0.21	0.26	0.13	**0.81**	1.00			
Bsh56A	0.05	0.09	0.06	0.14	-0.07	-0.08	1.00		
Bsh56B	-0.05	-0.06	-0.01	0.02	-0.07	-0.05	**0.90**	1.00	
B29	-0.01	-0.01	-0.01	-0.04	-0.03	-0.03	-0.04	-0.04	1.00
B30	0.04	0.06	0.02	-0.03	-0.03	-0.03	-0.03	-0.04	**0.99**
	B27A	*B27B*	*B28*	*Bsh45*	*B28A*	*B28B*	*Bsh56A*	*Bsh56B*	*B29*

All Taxa	*phyll*	*fus*	*foram*	*crinoid*	*echinoid*	*Crania*	*Entelet*
phylloid	1.00						79 d. f.
fusulinid	-0.01	1.00					r =0.28
foraminifera	-0.04	-0.02	1.00				p=0.01
crinoid	-0.11	-0.01	-0.06	1.00			
echinoid	-0.13	-0.06	0.16	-0.20	1.00		
Crania	-0.04	-0.03	-0.02	0.18	-0.09	1.00	
Enteletes	-0.05	0.08	-0.05	-0.04	-0.08	-0.05	1.00
Wellerella	-0.04	-0.03	-0.02	-0.05	-0.09	-0.03	-0.05
Composita	0.07	-0.09	-0.06	-0.04	**0.56**	-0.01	-0.09
Phricodothyris	0.05	-0.04	-0.04	**0.33**	-0.06	-0.04	0.25
Hustedia	-0.03	0.06	-0.03	-0.11	-0.09	0.00	0.23
Dielasma	-0.02	0.06	-0.03	0.21	0.12	-0.03	0.26
Crurithyris	-0.05	0.02	-0.04	-0.14	0.08	0.01	0.02
Neospirifer	0.01	-0.05	-0.05	-0.13	-0.04	-0.05	-0.07
Neospir. t.	-0.05	-0.04	-0.03	-0.09	-0.11	**0.28**	-0.06
Punctospirifer	-0.08	-0.02	-0.05	-0.07	-0.06	0.05	0.06
Rhipidomella	-0.04	0.00	-0.02	-0.10	-0.07	-0.02	0.15
Derbyia	-0.06	0.05	-0.07	0.00	-0.08	-0.05	**0.37**
Meekella	-0.05	0.05	-0.04	-0.13	-0.09	-0.04	**0.41**
Chonetinella	-0.04	-0.04	-0.03	0.07	-0.08	0.00	-0.06
Mesolobus	-0.05	-0.02	-0.03	-0.03	0.15	-0.03	-0.06
Neochonetes	0.00	**0.55**	-0.03	-0.04	-0.10	-0.03	**0.28**
Fimbrinia	0.13	-0.02	-0.02	0.07	-0.06	-0.02	-0.04
Desmoinsea	-0.01	-0.05	-0.04	0.14	-0.11	0.16	-0.08
Hystriculina	-0.05	-0.05	-0.04	0.05	-0.11	-0.04	**0.61**
Kozlowskia	-0.05	-0.03	-0.03	0.02	0.27	-0.03	0.14
Retaria	-0.05	-0.04	-0.03	-0.13	0.00	0.19	0.00
Antiquatonia	-0.12	-0.08	-0.08	-0.13	**0.40**	0.04	-0.10
Reticulatia	-0.07	-0.05	-0.04	-0.03	0.07	-0.04	-0.08
Echinaria	-0.08	-0.06	-0.05	-0.17	-0.03	-0.05	-0.08
Parajuresania	-0.05	-0.04	-0.03	0.16	-0.09	**0.32**	-0.05
Linoproductus	-0.07	-0.06	-0.05	0.16	-0.09	0.00	-0.07
Minilya	-0.11	-0.04	0.01	**0.40**	-0.14	**0.34**	-0.10
Fenestrellina	-0.06	0.10	-0.04	**0.52**	-0.10	0.06	-0.04
Septopora	-0.04	-0.01	-0.03	**0.49**	-0.07	0.14	-0.06
Polypora	-0.09	-0.03	-0.05	**0.38**	-0.14	0.13	-0.05
Rhombopora	-0.13	0.06	-0.06	0.27	-0.22	**0.51**	0.21
Leioclema	-0.05	-0.04	-0.03	-0.06	-0.09	-0.03	-0.04
Sheet Tub	-0.07	-0.03	-0.05	-0.03	-0.14	-0.05	0.16
Tubulipuliporate	-0.06	0.00	-0.03	-0.02	-0.09	-0.04	-0.08
Treptostome	0.20	0.06	-0.02	0.00	-0.05	-0.03	-0.05
All Taxa	*phyll*	*fus*	*foram*	*crinoid*	*echinoid*	*Crania*	*Entelet*

Nucula	-0.03	-0.02	-0.02	0.20	-0.06	**0.94**	-0.04
Nuculana	-0.05	-0.03	-0.03	0.25	-0.05	**0.33**	0.01
Myalina	-0.04	-0.03	-0.02	0.19	-0.07	**0.92**	-0.05
Aviculopinna	-0.06	-0.04	-0.04	-0.05	-0.04	0.06	-0.08
Aviculopecten	-0.05	-0.04	-0.03	0.25	-0.08	**0.87**	-0.06
Acanthopecten	-0.05	0.06	-0.03	0.05	-0.10	**0.53**	**0.28**
Astartella	-0.02	-0.03	-0.03	0.15	-0.10	**0.76**	-0.04
Allorisma	-0.03	-0.02	-0.02	0.20	-0.06	**0.94**	-0.04
Bellerophon	0.19	-0.04	0.25	-0.12	-0.06	-0.05	-0.07
Pharkodonotus	-0.03	-0.02	-0.02	-0.09	-0.06	-0.02	-0.04
Trepospira	-0.04	-0.04	0.02	-0.10	-0.09	0.06	-0.06
LgHS	-0.03	-0.02	-0.02	-0.02	-0.06	-0.02	-0.04
Leptozyga	0.16	-0.03	**0.61**	0.10	0.05	-0.05	0.05
Goniasma	-0.03	-0.02	-0.02	-0.04	-0.06	-0.02	-0.04
Straparollus	-0.03	0.00	**0.82**	0.00	0.08	-0.02	-0.04
lg conisp	-0.03	-0.01	-0.02	-0.05	0.01	-0.02	-0.04
nautiloid	-0.05	-0.03	-0.03	-0.09	-0.12	**0.39**	0.02
Lophophyllidium	-0.02	-0.02	-0.04	-0.08	-0.06	-0.04	0.16
Caninia	-0.01	-0.02	-0.02	**0.28**	-0.05	-0.02	-0.05
coral sp.	0.06	-0.02	-0.02	-0.05	-0.02	-0.02	-0.04
Syringopora	-0.03	0.00	-0.02	-0.07	-0.07	-0.02	0.19
sponge	-0.03	-0.02	-0.02	0.11	-0.02	-0.02	0.16
trilobite	-0.07	-0.05	0.13	0.27	-0.05	-0.04	-0.09
shark	-0.05	-0.04	0.04	-0.10	0.00	-0.03	-0.06
All Taxa	*phyll*	*fus*	*foram*	*crinoid*	*echinoid*	*Crania*	*Entelet*

All Taxa	*Wellerel*	*Compos*	*Phric*	*Husted*	*Dielasm*	*Cruri*	*Neospir*
phylloid							
fusulinid							
foraminifera							
crinoid							
echinoid							
Crania							
Enteletes							
Wellerella	1.00						
Composita	-0.04	1.00					
Phricodothyris	-0.04	0.01	1.00				
Hustedia	-0.01	0.03	-0.02	1.00			
Dielasma	-0.03	0.09	**0.58**	0.03	1.00		
Crurithyris	-0.04	-0.02	-0.02	0.17	-0.02	1.00	
Neospirifer	-0.03	-0.09	-0.08	0.00	-0.06	-0.07	1.00
Neospir. t.	-0.03	-0.06	-0.05	0.08	-0.04	0.13	-0.05
Punctospirifer	0.01	0.01	-0.08	**0.52**	0.00	0.09	-0.07
Rhipidomella	-0.02	0.04	-0.04	**0.98**	-0.02	0.14	0.01
Derbyia	0.01	0.01	-0.04	0.27	**0.38**	0.06	-0.09
Meekella	-0.04	-0.07	-0.04	0.05	0.27	0.01	-0.04
Chonetinella	-0.03	-0.08	-0.04	-0.02	-0.03	-0.03	-0.06
Mesolobus	-0.03	0.04	-0.05	-0.04	-0.04	-0.05	-0.01
Neochonetes	-0.03	-0.03	0.04	**0.61**	-0.04	0.09	-0.04
Fimbrinia	-0.02	0.11	**0.44**	0.01	-0.02	0.03	-0.04
Desmoinsea	-0.04	-0.03	-0.03	0.04	-0.05	0.13	-0.07
Hystriculina	0.01	-0.09	0.34	-0.03	-0.04	0.00	-0.05
Kozlowskia	-0.03	0.27	-0.05	0.18	-0.03	0.02	-0.02
Retaria	-0.03	-0.05	0.00	0.05	-0.03	0.09	-0.03
Antiquatonia	-0.08	**0.29**	0.01	-0.07	0.08	-0.09	0.08
Reticulatia	-0.04	-0.02	-0.06	-0.05	-0.05	-0.07	**0.77**
Echinaria	-0.05	-0.04	-0.06	-0.06	-0.06	-0.08	**0.58**
Parajuresania	-0.03	-0.06	0.00	-0.03	0.01	-0.05	-0.07
Linoproductus	-0.05	0.01	0.03	-0.05	0.05	-0.05	0.04
Minilya	-0.05	-0.14	-0.08	-0.07	-0.08	-0.07	-0.09
Fenestrellina	-0.04	-0.10	-0.01	0.00	-0.01	-0.02	-0.08
Septopora	-0.03	-0.07	-0.04	-0.03	-0.03	-0.04	-0.06
Polypora	-0.01	-0.08	-0.05	-0.04	-0.03	-0.07	-0.12
Rhombopora	0.08	-0.12	0.03	0.19	0.05	-0.03	0.04
Leioclema	0.05	-0.07	-0.05	-0.02	-0.03	-0.02	-0.06
Sheet Tub	**0.48**	-0.09	0.09	-0.01	0.12	-0.06	**0.47**
Tubulipuliporate	-0.04	-0.08	-0.06	-0.04	-0.04	0.00	-0.08
Treptostome	-0.03	-0.07	-0.04	-0.01	-0.03	0.00	-0.04

All Taxa	*Wellerel*	*Compos*	*Phric*	*Husted*	*Dielasm*	*Cruri*	*Neospir*
Nucula	-0.02	0.01	-0.03	-0.02	-0.02	-0.03	-0.04
Nuculana	-0.03	0.09	0.06	-0.04	-0.04	-0.06	-0.01
Myalina	-0.02	0.00	-0.04	-0.03	-0.03	-0.04	0.13
Aviculopinna	-0.04	-0.10	-0.06	-0.05	-0.05	-0.07	**0.82**
Aviculopecten	-0.03	0.08	-0.05	-0.03	-0.03	-0.05	-0.07
Acanthopecten	-0.03	-0.04	-0.05	0.03	**0.28**	-0.02	-0.06
Astartella	-0.03	0.03	0.08	0.02	0.01	0.14	-0.07
Allorisma	-0.02	0.01	-0.03	-0.02	-0.02	-0.03	-0.04
Bellerophon	-0.05	-0.01	-0.07	0.09	-0.05	0.03	**0.71**
Pharkodonotus	-0.02	-0.01	-0.03	0.06	-0.02	**0.29**	-0.04
Trepospira	-0.03	-0.02	-0.04	0.10	-0.03	**0.31**	-0.05
LgHS	-0.02	-0.03	-0.03	-0.01	-0.02	0.01	-0.04
Leptozyga	-0.05	0.12	0.13	-0.03	0.13	-0.06	-0.05
Goniasma	-0.02	0.08	-0.03	-0.02	-0.02	-0.03	-0.04
Straparollus	-0.02	-0.03	-0.03	-0.02	-0.02	-0.03	-0.04
lg conisp	-0.02	-0.06	-0.03	-0.02	-0.02	-0.02	0.04
nautiloid	-0.03	-0.03	-0.06	**0.53**	-0.04	0.16	-0.03
Lophophyllidium	-0.04	0.24	-0.07	**0.79**	-0.02	0.22	-0.03
Caninia	-0.02	-0.02	**0.66**	-0.02	**0.71**	-0.03	-0.05
coral sp.	-0.02	-0.05	-0.03	-0.01	-0.02	0.01	-0.04
Syringopora	-0.02	0.03	-0.04	**0.95**	-0.03	0.13	0.01
sponge	-0.02	-0.06	-0.03	-0.01	-0.02	0.01	0.00
trilobite	-0.04	-0.01	-0.07	-0.05	-0.05	-0.07	-0.09
shark	-0.03	-0.01	-0.04	-0.03	-0.03	-0.05	**0.32**
All Taxa	*Wellerel*	*Compos*	*Phric*	*Husted*	*Dielasm*	*Cruri*	*Neospir*

All Taxa	*Neo t.*	*Puncto*	*Rhipido*	*Derbyia*	*Meek*	*Chonetin*	*Mesolob*
phylloid							
fusulinid							
foraminifera							
crinoid							
echinoid							
Crania							
Enteletes							
Wellerella							
Composita							
Phricodothyris							
Hustedia							
Dielasma							
Crurithyris							
Neospirifer							
Neospir. t.	1.00						
Punctospirifer	0.27	1.00					
Rhipidomella	0.05	**0.52**	1.00				
Derbyia	0.14	**0.40**	0.23	1.00			
Meekella	-0.05	-0.02	-0.04	**0.36**	1.00		
Chonetinella	0.05	0.01	-0.02	0.09	-0.05	1.00	
Mesolobus	-0.04	-0.07	-0.03	-0.09	-0.05	-0.03	1.00
Neochonetes	-0.04	0.27	**0.56**	0.04	0.06	-0.03	-0.04
Fimbrinia	-0.02	-0.02	-0.02	0.01	-0.03	-0.02	-0.02
Desmoinsea	**0.48**	0.16	-0.01	0.02	0.00	0.01	-0.05
Hystriculina	-0.05	-0.07	-0.03	-0.08	-0.01	-0.04	-0.05
Kozlowskia	-0.03	0.10	0.17	0.08	-0.05	-0.03	-0.03
Retaria	**0.71**	0.16	0.02	0.07	-0.05	0.03	-0.03
Antiquatonia	0.00	0.01	-0.04	-0.02	0.25	-0.07	0.10
Reticulatia	-0.05	-0.09	-0.04	-0.10	-0.03	-0.04	**0.33**
Echinaria	-0.06	-0.11	-0.04	-0.12	-0.08	-0.05	0.04
Parajuresania	0.00	-0.05	-0.02	-0.05	-0.03	-0.03	-0.04
Linoproductus	-0.04	-0.09	-0.04	-0.11	-0.08	-0.05	0.01
Minilya	-0.03	**0.35**	-0.05	0.11	-0.11	0.22	0.00
Fenestrellina	0.17	0.13	-0.02	-0.01	-0.04	0.03	-0.04
Septopora	-0.02	0.10	-0.02	-0.04	-0.05	0.02	-0.03
Polypora	-0.03	**0.37**	-0.03	0.21	-0.05	0.03	-0.06
Rhombopora	0.13	**0.46**	0.16	0.24	-0.02	0.08	-0.11
Leioclema	-0.04	0.04	0.01	0.11	-0.05	0.00	-0.04
Sheet Tub	-0.07	-0.03	-0.05	0.07	0.11	-0.06	-0.01
Tubulipuliporate	-0.02	**0.75**	-0.02	0.25	-0.06	0.18	-0.05
Treptostome	-0.03	-0.05	-0.02	-0.07	-0.04	-0.03	-0.03

All Taxa	*Neo t.*	*Puncto*	*Rhipido*	*Derbyia*	*Meek*	*Chonetin*	*Mesolob*
Nucula	-0.02	-0.02	-0.02	-0.05	-0.03	-0.02	-0.02
Nuculana	-0.04	-0.06	-0.03	-0.10	-0.06	-0.03	-0.04
Myalina	-0.03	-0.03	-0.02	-0.05	-0.03	-0.03	-0.03
Aviculopinna	-0.05	-0.08	-0.04	-0.09	-0.06	-0.04	-0.03
Aviculopecten	-0.04	-0.05	-0.03	-0.08	-0.05	-0.03	-0.04
Acanthopecten	-0.04	-0.01	-0.03	**0.34**	**0.29**	-0.03	-0.04
Astartella	-0.04	0.00	-0.02	0.02	-0.03	-0.02	-0.04
Allorisma	-0.02	-0.02	-0.02	-0.05	-0.03	-0.02	-0.02
Bellerophon	-0.06	0.02	0.09	0.00	-0.01	-0.04	-0.06
Pharkodonotus	-0.02	0.04	-0.02	0.06	-0.03	0.00	-0.02
Trepospira	0.20	0.09	0.01	0.07	-0.05	0.00	-0.04
LgHS	-0.02	0.02	0.05	0.18	-0.03	-0.02	-0.02
Leptozyga	-0.07	-0.10	-0.05	-0.01	0.02	-0.06	-0.07
Goniasma	-0.02	-0.04	-0.02	-0.05	-0.03	-0.02	-0.02
Straparollus	-0.02	-0.04	-0.02	-0.05	-0.03	-0.02	-0.02
lg conisp	-0.02	-0.04	-0.02	-0.05	-0.03	-0.02	-0.02
nautiloid	**0.77**	**0.42**	**0.48**	0.13	-0.06	0.03	-0.04
Lophophyllidium	-0.05	**0.38**	**0.75**	0.18	-0.03	-0.04	-0.05
Caninia	-0.03	-0.04	-0.02	-0.02	0.05	-0.03	-0.03
coral sp.	-0.02	-0.04	-0.02	-0.05	-0.03	-0.02	-0.02
Syringopora	-0.03	**0.47**	**0.95**	0.16	-0.02	-0.03	-0.03
sponge	-0.02	-0.02	-0.02	0.01	-0.03	-0.02	-0.02
trilobite	-0.05	-0.03	-0.04	0.15	-0.07	**0.36**	-0.05
shark	-0.01	-0.05	-0.02	-0.04	-0.05	-0.03	-0.04
All Taxa	*Neo t.*	*Puncto*	*Rhipido*	*Derbyia*	*Meek*	*Chonetin*	*Mesolob*

All Taxa	*Neoch*	*Fimbrin*	*Desm*	*Hystric*	*Kozlow*	*Retaria*	*Antiquit*
phylloid							
fusulinid							
foraminifera							
crinoid							
echinoid							
Crania							
Enteletes							
Wellerella							
Composita							
Phricodothyris							
Hustedia							
Dielasma							
Crurithyris							
Neospirifer							
Neospir. t.							
Punctospirifer							
Rhipidomella							
Derbyia							
Meekella							
Chonetinella							
Mesolobus							
Neochonetes	1.00						
Fimbrinia	-0.02	1.00					
Desmoinsea	-0.05	0.04	1.00				
Hystriculina	-0.05	0.04	-0.05	1.00			
Kozlowskia	0.08	-0.02	-0.04	0.18	1.00		
Retaria	-0.03	-0.02	-0.04	-0.04	-0.03	1.00	
Antiquatonia	-0.10	-0.05	-0.08	-0.11	0.16	0.06	1.00
Reticulatia	-0.05	-0.03	-0.06	-0.06	-0.05	-0.03	-0.02
Echinaria	-0.06	-0.03	-0.06	-0.07	-0.06	-0.02	0.15
Parajuresania	-0.03	-0.01	-0.03	-0.05	-0.04	-0.01	-0.03
Linoproductus	-0.06	-0.03	-0.04	-0.03	-0.05	-0.04	-0.03
Minilya	-0.06	-0.05	**0.34**	-0.05	-0.07	-0.08	-0.11
Fenestrellina	0.08	-0.02	**0.62**	-0.04	0.00	-0.05	-0.11
Septopora	-0.02	-0.02	**0.40**	-0.04	-0.03	-0.03	-0.06
Polypora	0.00	-0.04	**0.37**	-0.08	-0.05	-0.05	-0.08
Rhombopora	0.11	-0.07	**0.46**	0.22	0.00	-0.11	-0.14
Leioclema	-0.04	-0.02	-0.04	-0.01	0.06	-0.03	-0.09
Sheet Tub	-0.01	-0.04	-0.09	0.07	-0.06	-0.06	-0.12
Tubulipuliporate	-0.02	-0.03	-0.01	-0.05	-0.03	-0.02	-0.02
Treptostome	-0.03	-0.02	-0.04	-0.04	-0.03	-0.03	-0.08

All Taxa	*Neoch*	*Fimbrin*	*Desm*	*Hystric*	*Kozlow*	*Retaria*	*Antiquit*
Nucula	-0.02	-0.01	-0.03	-0.03	-0.02	-0.02	0.07
Nuculana	-0.04	-0.02	-0.05	0.06	-0.04	-0.04	-0.06
Myalina	-0.03	-0.02	-0.04	-0.03	-0.03	-0.03	0.08
Aviculopinna	-0.05	-0.03	-0.06	-0.06	-0.05	-0.04	0.14
Aviculopecten	-0.04	-0.02	-0.05	-0.04	-0.03	-0.03	0.03
Acanthopecten	-0.04	-0.02	-0.05	-0.05	-0.03	-0.03	-0.02
Astartella	-0.04	0.19	0.12	-0.03	-0.03	-0.03	0.01
Allorisma	-0.02	-0.01	-0.03	-0.03	-0.02	-0.02	0.07
Bellerophon	0.01	-0.03	0.00	-0.07	-0.03	-0.04	-0.07
Pharkodonotus	-0.02	-0.01	0.26	-0.03	-0.02	-0.02	-0.05
Trepospira	-0.02	0.00	**0.38**	-0.04	-0.03	0.13	-0.08
LgHS	-0.02	-0.01	-0.03	-0.03	-0.02	-0.02	-0.05
Leptozyga	0.02	0.10	-0.08	-0.07	-0.06	-0.01	-0.07
Goniasma	-0.02	-0.01	-0.03	-0.03	-0.02	-0.02	-0.05
Straparollus	-0.02	-0.01	-0.03	-0.03	-0.02	-0.02	-0.05
lg conisp	-0.02	-0.01	-0.03	-0.03	-0.02	-0.02	-0.05
nautiloid	0.24	-0.02	0.22	-0.05	0.06	**0.75**	-0.05
Lophophyllidium	**0.41**	-0.03	0.08	0.03	**0.42**	-0.05	-0.09
Caninia	-0.03	-0.02	-0.04	0.03	-0.03	-0.03	0.04
coral sp.	-0.02	-0.01	-0.03	-0.03	-0.02	-0.02	-0.05
Syringopora	**0.54**	-0.02	-0.04	0.04	**0.35**	-0.03	-0.07
sponge	-0.02	-0.01	-0.03	0.26	**0.78**	-0.02	-0.05
trilobite	-0.05	-0.03	-0.07	-0.06	-0.05	-0.05	-0.13
shark	-0.04	-0.02	-0.05	-0.04	-0.03	-0.02	0.19
All Taxa	*Neoch*	*Fimbrin*	*Desm*	*Hystric*	*Kozlow*	*Retaria*	*Antiquit*

All Taxa	*Reticul*	*Echinar*	*Parajur*	*Lino*	*Minilya*	*Fenestr*	*Sept*
phylloid							
fusulinid							
foraminifera							
crinoid							
echinoid							
Crania							
Enteletes							
Wellerella							
Composita							
Phricodothyris							
Hustedia							
Dielasma							
Crurithyris							
Neospirifer							
Neospir. t.							
Punctospirifer							
Rhipidomella							
Derbyia							
Meekella							
Chonetinella							
Mesolobus							
Neochonetes							
Fimbrinia							
Desmoinsea							
Hystriculina							
Kozlowskia							
Retaria							
Antiquatonia							
Reticulatia	1.00						
Echinaria	**0.36**	1.00					
Parajuresania	-0.05	0.03	1.00				
Linoproductus	0.04	0.12	**0.28**	1.00			
Minilya	-0.06	-0.10	0.08	-0.07	1.00		
Fenestrellina	-0.07	-0.08	-0.01	0.03	**0.65**	1.00	
Septopora	-0.05	-0.05	0.03	-0.04	**0.74**	**0.91**	1.00
Polypora	-0.09	-0.08	0.11	0.01	**0.88**	**0.65**	**0.71**
Rhombopora	0.03	-0.06	0.09	-0.07	**0.73**	**0.47**	**0.47**
Leioclema	-0.05	-0.06	-0.02	-0.05	0.12	-0.01	-0.01
Sheet Tub	**0.44**	0.20	0.03	0.04	-0.10	-0.07	-0.06
Tubulipuliporate	-0.06	-0.07	-0.04	-0.06	**0.50**	0.05	0.08
Treptostome	-0.04	-0.05	-0.03	-0.05	-0.06	-0.04	-0.03

All Taxa	*Reticul*	*Echinar*	*Parajur*	*Lino*	*Minilya*	*Fenestr*	*Sept*
Nucula	-0.03	-0.03	**0.34**	0.01	**0.36**	-0.01	0.15
Nuculana	-0.06	-0.05	0.11	-0.02	0.10	-0.05	0.03
Myalina	0.13	0.03	**0.32**	0.02	**0.34**	-0.02	0.14
Aviculopinna	**0.70**	**0.39**	-0.01	0.02	-0.03	-0.06	-0.03
Aviculopecten	-0.05	-0.06	**0.31**	0.01	**0.31**	-0.03	0.13
Acanthopecten	-0.05	-0.06	**0.28**	**0.48**	0.15	0.01	0.07
Astartella	-0.05	-0.06	0.26	-0.01	0.25	-0.03	0.11
Allorisma	-0.03	-0.03	**0.34**	0.01	**0.36**	-0.01	0.15
Bellerophon	**0.64**	0.25	-0.06	-0.01	-0.07	-0.07	-0.05
Pharkodonotus	-0.03	-0.03	-0.02	-0.03	-0.05	-0.03	-0.02
Trepospira	-0.05	-0.04	-0.03	-0.05	-0.06	0.02	-0.03
LgHS	-0.03	-0.03	-0.02	-0.03	-0.05	-0.03	-0.02
Leptozyga	-0.08	-0.05	-0.04	-0.07	-0.10	-0.07	-0.04
Goniasma	-0.03	-0.03	-0.02	0.01	-0.05	-0.03	-0.02
Straparollus	-0.03	-0.03	-0.02	-0.03	-0.01	-0.03	-0.02
lg conisp	-0.03	-0.03	-0.02	-0.02	-0.02	-0.03	-0.02
nautiloid	-0.06	-0.07	0.04	-0.04	0.00	0.06	0.00
Lophophyllidium	-0.07	-0.07	-0.05	-0.02	-0.09	-0.04	-0.04
Caninia	-0.03	-0.05	0.02	0.06	-0.06	-0.01	-0.03
coral sp.	-0.03	-0.03	-0.02	-0.03	-0.04	-0.03	-0.02
Syringopora	-0.04	-0.05	-0.03	-0.05	-0.06	-0.02	-0.03
sponge	-0.03	-0.03	-0.02	-0.03	-0.04	0.03	-0.02
trilobite	-0.07	-0.08	-0.05	-0.07	0.07	0.00	0.01
shark	0.00	**0.73**	-0.04	0.10	-0.06	-0.04	-0.03
All Taxa	*Reticul*	*Echinar*	*Parajur*	*Lino*	*Minilya*	*Fenestr*	*Sept*

All Taxa	*Polypora*	*Rhomb*	*Leiocl*	ShTub	Tubulip	Treptost	*Nucula*
phylloid							
fusulinid							
foraminifera							
crinoid							
echinoid							
Crania							
Enteletes							
Wellerella							
Composita							
Phricodothyris							
Hustedia							
Dielasma							
Crurithyris							
Neospirifer							
Neospir. t.							
Punctospirifer							
Rhipidomella							
Derbyia							
Meekella							
Chonetinella							
Mesolobus							
Neochonetes							
Fimbrinia							
Desmoinsea							
Hystriculina							
Kozlowskia							
Retaria							
Antiquatonia							
Reticulatia							
Echinaria							
Parajuresania							
Linoproductus							
Minilya							
Fenestrellina							
Septopora							
Polypora	1.00						
Rhombopora	**0.64**	1.00					
Leioclema	0.08	-0.08	1.00				
Sheet Tub	-0.03	0.11	0.02	1.00			
Tubulipuliporate	**0.47**	**0.38**	0.18	-0.08	1.00		
Treptostome	-0.06	-0.03	-0.03	0.01	-0.04	1.00	

All Taxa	*Polypora*	*Rhomb*	*Leiocl*	ShTub	Tubulip	Treptost	*Nucula*
Nucula	0.14	**0.47**	-0.02	-0.04	-0.03	-0.02	1.00
Nuculana	-0.01	0.16	-0.04	0.00	-0.05	-0.03	**0.36**
Myalina	0.12	**0.48**	0.01	0.06	-0.03	-0.02	**0.98**
Aviculopinna	-0.07	0.11	-0.05	**0.41**	-0.06	-0.04	0.08
Aviculopecten	0.10	**0.40**	-0.03	-0.06	-0.04	-0.03	**0.93**
Acanthopecten	0.04	**0.31**	-0.04	0.04	-0.05	-0.03	**0.57**
Astartella	0.08	**0.34**	-0.02	-0.06	-0.04	-0.03	**0.81**
Allorisma	0.14	**0.47**	-0.02	-0.04	-0.03	-0.02	1.00
Bellerophon	-0.10	0.05	0.08	**0.38**	-0.01	-0.05	-0.03
Pharkodonotus	-0.04	-0.05	-0.02	-0.04	-0.03	-0.02	-0.01
Trepospira	-0.06	-0.01	0.02	-0.06	-0.03	-0.01	-0.02
LgHS	-0.04	-0.05	0.57	-0.04	0.07	-0.02	-0.01
Leptozyga	-0.09	-0.13	-0.06	-0.06	-0.07	-0.05	-0.04
Goniasma	-0.04	-0.07	-0.02	-0.04	-0.03	-0.02	-0.01
Straparollus	-0.03	-0.02	-0.02	-0.04	-0.02	-0.02	-0.01
lg conisp	-0.04	0.06	-0.02	0.15	-0.03	-0.02	-0.01
nautiloid	-0.02	0.20	-0.04	-0.07	-0.04	-0.03	0.14
Lophophyllidium	-0.05	0.11	-0.01	-0.07	-0.05	0.07	-0.03
Caninia	-0.02	-0.03	-0.03	0.03	-0.04	-0.02	-0.02
coral sp.	-0.04	0.00	-0.02	0.06	-0.03	**0.70**	-0.01
Syringopora	-0.04	0.16	0.00	-0.05	-0.04	0.02	-0.02
sponge	-0.03	0.01	0.10	-0.04	-0.02	-0.02	-0.01
trilobite	0.02	-0.07	-0.04	-0.09	0.08	-0.04	-0.03
shark	-0.07	-0.10	-0.04	-0.03	-0.04	-0.03	-0.02
All Taxa	*Polypora*	*Rhomb*	*Leiocl*	ShTub	Tubulip	Treptost	*Nucula*

All Taxa	*Nuculan*	*Myalina*	*Avicpin*	*Avicpec*	*Acanpc*	*Astart*	*Alloris*
Nucula							
Nuculana	1.00						
Myalina	**0.35**	1.00					
Aviculopinna	0.01	0.24	1.00				
Aviculopecten	**0.58**	**0.91**	0.05	1.00			
Acanthopecten	0.19	**0.55**	0.01	**0.52**	1.00		
Astartella	**0.30**	**0.79**	0.04	**0.76**	**0.47**	1.00	
Allorisma	**0.36**	**0.98**	0.08	**0.93**	**0.57**	**0.81**	1.00
Bellerophon	-0.06	0.13	**0.61**	-0.05	-0.06	0.08	-0.03
Pharkodonotus	-0.02	-0.02	-0.03	-0.02	-0.02	**0.53**	-0.01
Trepospira	-0.04	-0.02	-0.04	-0.03	-0.04	**0.51**	-0.02
LgHS	-0.02	0.04	-0.03	-0.02	-0.02	0.01	-0.01
Leptozyga	**0.36**	-0.05	-0.06	0.14	0.02	-0.01	-0.04
Goniasma	-0.02	-0.02	-0.03	0.11	-0.02	-0.02	-0.01
Straparollus	-0.02	-0.02	-0.03	-0.02	-0.02	-0.02	-0.01
lg conisp	-0.02	-0.02	0.02	-0.02	-0.02	-0.02	-0.01
nautiloid	0.02	0.13	-0.04	0.11	0.05	0.09	0.14
Lophophyllidium	-0.06	-0.04	-0.07	-0.05	-0.02	0.18	-0.03
Caninia	-0.03	-0.02	-0.04	-0.03	-0.03	0.00	-0.02
coral sp.	-0.02	-0.02	-0.03	-0.02	-0.02	-0.02	-0.01
Syringopora	-0.03	-0.02	-0.04	-0.03	-0.03	-0.03	-0.02
sponge	-0.02	-0.02	-0.03	-0.02	-0.02	-0.02	-0.01
trilobite	0.17	-0.04	-0.07	0.08	-0.05	-0.04	-0.03
shark	0.01	-0.02	0.07	-0.01	-0.04	-0.03	-0.02
All Taxa	*Nuculan*	*Myalina*	*Avicpin*	*Avicpec*	*Acanpc*	*Astart*	*Alloris*

All Taxa	*Bellero*	*Phark*	*Treposp*	LgHS	*Leptoz*	*Gonias*	*Strap*
Nucula							
Nuculana							
Myalina							
Aviculopinna							
Aviculopecten							
Acanthopecten							
Astartella							
Allorisma							
Bellerophon	1.00						
Pharkodonotus	0.20	1.00					
Trepospira	0.21	**0.96**	1.00				
LgHS	0.20	-0.01	0.07	1.00			
Leptozyga	0.26	-0.04	-0.02	-0.04	1.00		
Goniasma	-0.03	-0.01	-0.02	-0.01	-0.04	1.00	
Straparollus	**0.32**	-0.01	0.03	-0.01	**0.66**	-0.01	1.00
lg conisp	0.09	-0.01	-0.02	-0.01	-0.04	-0.01	-0.01
nautiloid	0.00	-0.02	0.18	-0.02	-0.07	-0.02	-0.02
Lophophyllidium	0.13	**0.39**	**0.38**	-0.03	-0.07	-0.03	-0.03
Caninia	-0.04	-0.02	-0.03	-0.02	0.07	-0.02	-0.02
coral sp.	-0.03	-0.01	0.00	-0.01	-0.04	-0.01	-0.01
Syringopora	0.07	-0.02	0.00	-0.02	-0.05	-0.02	-0.02
sponge	-0.03	-0.01	-0.02	-0.01	-0.04	-0.01	-0.01
trilobite	-0.04	-0.03	-0.03	-0.03	**0.28**	-0.03	-0.03
shark	0.00	-0.02	-0.01	-0.02	0.05	-0.02	-0.02
All Taxa	*Bellero*	*Phark*	*Treposp*	LgHS	*Leptoz*	*Gonias*	*Strap*

All Taxa	lgconisp	naut	*Lopho*	*Caninia*	coral sp	*Syring*	sponge	tril
Nucula								
Nuculana								
Myalina								
Aviculopinna								
Aviculopecten								
Acanthopecten								
Astartella								
Allorisma								
Bellerophon								
Pharkodonotus								
Trepospira								
LgHS								
Leptozyga								
Goniasma								
Straparollus								
lg conisp	1.00							
nautiloid	-0.02	1.00						
Lophophyllidium	-0.03	0.33	1.00					
Caninia	-0.02	-0.03	-0.02	1.00				
coral sp.	-0.01	-0.02	0.13	-0.02	1.00			
Syringopora	-0.02	**0.44**	**0.82**	0.03	0.04	1.00		
sponge	-0.01	-0.02	**0.29**	-0.02	-0.01	0.21	1.00	
trilobite	-0.03	-0.06	-0.07	-0.04	-0.03	-0.04	-0.03	1.00
shark	-0.02	-0.03	-0.05	-0.03	-0.02	-0.03	-0.02	0.00
All Taxa	lgconisp	naut	*Lopho*	*Caninia*	coral sp	*Syring*	sponge	tril

BwdTaxa	phyll	fusul	foram	crin	ech	*Crania*	*Entelet*
phylloid	1.00						
fusulinid	-0.03	1.00					52 d. f.
foraminifera	-0.04	0.01	1.00				r= 0.35
crinoid	-0.14	0.02	-0.05	1.00			p=0.01
echinoid	-0.13	-0.03	0.13	-0.24	1.00		
Crania	-0.03	-0.05	-0.03	0.23	-0.11	1.00	
Enteletes	-0.04	**0.49**	-0.04	-0.04	0.16	-0.03	1.00
Composita	0.11	-0.12	-0.08	-0.13	**0.71**	-0.01	-0.02
Phricodothyris	-0.04	-0.05	-0.04	-0.02	0.10	-0.03	**0.48**
Hustedia	-0.04	-0.06	-0.04	-0.14	-0.15	0.17	-0.04
Dielasma	-0.03	-0.04	-0.03	-0.10	**0.63**	-0.02	-0.03
Crurithyris	-0.03	-0.05	-0.04	-0.12	0.12	-0.01	-0.02
Neospirifer	0.02	-0.05	-0.06	-0.11	-0.10	-0.06	-0.03
Neospirifer t.	-0.04	-0.05	-0.04	-0.14	-0.13	0.17	-0.04
Punctospirifer	-0.06	-0.05	-0.06	0.02	-0.06	0.02	-0.03
Rhipidomella	-0.04	-0.05	-0.04	-0.11	-0.13	-0.03	-0.04
Derbyia	-0.03	-0.04	-0.10	0.19	-0.10	-0.07	-0.04
Meekella	-0.04	-0.05	-0.04	-0.04	-0.05	-0.03	-0.04
Chonetinella	-0.04	-0.06	-0.04	0.11	-0.12	-0.02	-0.04
Mesolobus	-0.05	0.00	-0.05	-0.02	0.12	-0.04	-0.05
Desmoinsea	0.03	-0.08	-0.06	**0.37**	-0.12	-0.05	-0.06
Kozlowskia	-0.03	-0.04	-0.03	-0.10	**0.51**	-0.02	-0.03
Retaria	-0.04	-0.06	-0.04	-0.15	-0.05	0.19	0.18
Antiquatonia	-0.11	-0.07	-0.11	-0.19	0.34	0.03	0.07
Reticulatia	-0.06	-0.07	-0.06	0.00	0.02	-0.06	-0.02
Echinaria	-0.07	-0.09	-0.07	-0.18	-0.10	-0.06	0.00
Parajuresania	-0.04	-0.05	-0.04	0.25	-0.13	**0.96**	-0.04
Linoproductus	-0.10	-0.10	-0.10	-0.05	-0.12	0.13	-0.10
BwdTaxa	phyll	fusul	foram	crin	ech	*Crania*	*Entelet*

Minilya	-0.10	-0.08	-0.01	**0.53**	-0.22	0.33	-0.06
Fenestre	-0.04	-0.06	-0.04	**0.65**	-0.10	-0.02	-0.04
Septopora	-0.04	-0.06	-0.04	**0.63**	-0.11	0.13	-0.04
Polypora	-0.08	-0.08	-0.06	**0.46**	-0.20	0.12	-0.02
Rhombopora	-0.10	-0.10	-0.05	**0.43**	-0.23	**0.53**	-0.09
Leioclema	-0.04	-0.06	-0.04	-0.06	-0.13	-0.03	-0.04
Sheet Tub.	-0.05	-0.03	-0.05	0.00	-0.10	-0.04	-0.05
Tubuliporate	-0.05	-0.08	-0.05	0.00	-0.15	-0.05	-0.06
Nucula	-0.03	-0.04	-0.03	0.26	-0.09	**0.97**	-0.03
Nuculana	-0.04	-0.02	-0.04	0.30	-0.07	**0.37**	-0.04
Myalina	-0.03	-0.04	-0.03	0.25	-0.11	**0.95**	-0.03
Aviculopinna	-0.06	-0.05	-0.06	-0.04	-0.11	0.05	-0.05
Aviculopecten	-0.04	-0.06	-0.04	0.33	-0.13	**0.90**	-0.04
Acanthopecten	-0.03	-0.04	-0.03	0.26	-0.09	**0.97**	-0.03
Astartella	-0.03	-0.04	-0.03	0.27	-0.10	**0.97**	-0.03
Allorisma	-0.03	-0.04	-0.03	0.26	-0.09	**0.97**	-0.03
Bellerophon	0.23	-0.04	0.25	-0.08	-0.10	-0.05	-0.06
Trepospira	-0.05	-0.06	0.19	-0.11	-0.12	0.17	-0.05
LgHS	-0.03	-0.04	-0.03	-0.02	-0.09	-0.02	-0.03
Leptozyga	0.16	-0.03	**0.62**	0.10	0.02	-0.06	0.04
Goniasma	-0.03	-0.04	-0.03	-0.04	-0.09	-0.02	-0.03
Straparollus	-0.03	0.03	**0.82**	0.01	0.05	-0.02	-0.03
lg conisp	-0.03	0.00	-0.03	-0.05	-0.02	-0.02	-0.03
nautiloid	-0.04	-0.05	-0.04	-0.06	-0.13	**0.40**	-0.04
Lophophyllidium	0.18	-0.05	-0.04	-0.16	0.18	-0.04	-0.04
trilobite	-0.06	-0.09	0.11	**0.37**	-0.11	-0.05	-0.06
shark	-0.04	-0.06	0.03	-0.10	-0.04	-0.04	-0.04
BwdTaxa	phyll	fusul	foram	crin	ech	*Crania*	*Entelet*

BwdTaxa	*Compos*	*Phric*	*Husted*	*Dielas*	*Cruri*	*Neo*	*Neo t.*
phylloid							
fusulinid							
foraminifera							
crinoid							
echinoid							
Crania							
Enteletes							
Composita	1.00						
Phricodothyris	-0.03	1.00					
Hustedia	-0.10	-0.04	1.00				
Dielasma	**0.49**	-0.03	-0.03	1.00			
Crurithyris	-0.06	-0.02	0.11	-0.03	1.00		
Neospirifer	-0.11	-0.02	-0.07	-0.05	-0.07	1.00	
Neospirifer t.	-0.08	-0.04	**0.98**	-0.03	0.11	-0.06	1.00
Punctospirifer	-0.02	-0.06	0.25	0.05	-0.01	-0.11	0.26
Rhipidomella	-0.04	-0.04	**0.53**	-0.03	0.07	-0.08	**0.50**
Derbyia	0.02	-0.04	0.29	0.01	-0.02	-0.15	0.27
Meekella	-0.07	-0.04	0.08	-0.03	0.00	-0.04	-0.04
Chonetinella	-0.11	-0.04	0.02	-0.02	-0.03	-0.08	0.03
Mesolobus	0.04	-0.05	-0.05	-0.03	-0.04	-0.04	-0.05
Desmoinsea	-0.06	-0.06	-0.05	-0.04	-0.03	-0.10	-0.06
Kozlowskia	**0.63**	-0.03	-0.03	-0.02	-0.03	-0.05	-0.03
Retaria	-0.08	0.18	**0.90**	-0.03	0.10	-0.05	**0.91**
Antiquatonia	**0.36**	0.07	0.07	0.18	-0.07	0.05	0.01
Reticulatia	-0.04	-0.02	-0.07	-0.05	-0.06	**0.78**	-0.06
Echinaria	-0.06	0.00	-0.08	-0.05	-0.07	**0.58**	-0.07
Parajuresania	0.00	-0.04	0.05	-0.03	-0.02	-0.07	0.06
Linoproductus	0.03	-0.05	-0.06	0.00	-0.02	**0.48**	-0.04

BwdTaxa	*Compos*	*Phric*	*Husted*	*Dielas*	*Cruri*	*Neo*	*Neo t.*
Minilya	-0.18	-0.01	-0.12	-0.07	-0.06	-0.13	-0.10
Fenestre	-0.12	0.04	-0.05	-0.03	-0.04	-0.08	-0.04
Septopora	-0.09	-0.04	-0.05	-0.03	-0.04	-0.08	-0.04
Polypora	-0.10	-0.04	-0.09	-0.05	-0.06	-0.14	-0.08
Rhombopora	-0.10	-0.02	-0.12	-0.03	-0.10	0.06	-0.10
Leioclema	-0.09	-0.04	0.04	-0.03	-0.02	-0.08	-0.04
Sheet Tub.	-0.10	-0.05	-0.06	-0.03	-0.05	**0.84**	-0.05
Tubuliporate	-0.11	-0.06	-0.02	-0.04	0.01	-0.11	-0.02
Nucula	0.01	-0.03	-0.03	-0.02	-0.03	-0.05	-0.03
Nuculana	0.14	-0.04	-0.05	-0.03	-0.05	-0.01	-0.04
Myalina	-0.01	-0.03	-0.03	-0.02	-0.03	0.12	-0.03
Aviculopinna	-0.14	-0.05	-0.07	-0.04	-0.06	**0.83**	-0.06
Aviculopecten	0.09	-0.04	-0.05	-0.03	-0.05	-0.09	-0.04
Acanthopecten	0.01	-0.03	-0.03	-0.02	-0.03	-0.05	-0.03
Astartella	0.01	0.00	-0.03	-0.02	-0.03	-0.06	-0.03
Allorisma	0.01	-0.03	-0.03	-0.02	-0.03	-0.05	-0.03
Bellerophon	-0.03	-0.06	-0.02	-0.04	-0.04	**0.74**	-0.06
Trepospira	-0.11	-0.05	**0.74**	-0.04	0.06	-0.05	**0.68**
LgHS	-0.05	-0.03	0.11	-0.02	0.01	-0.05	-0.03
Leptozyga	0.13	0.04	-0.08	-0.05	-0.06	-0.06	-0.07
Goniasma	0.10	-0.03	-0.03	-0.02	-0.03	-0.05	-0.03
Straparollus	-0.05	-0.03	-0.03	-0.02	-0.03	-0.05	-0.03
lg conisp	-0.08	-0.03	-0.03	-0.02	-0.02	0.03	-0.03
nautiloid	-0.08	-0.04	**0.89**	-0.03	0.09	-0.05	**0.90**
Lophophyllidium	**0.40**	-0.04	-0.05	-0.03	-0.04	-0.06	-0.04
trilobite	-0.02	-0.06	-0.07	-0.04	-0.07	-0.12	-0.06
shark	-0.02	0.00	-0.02	-0.03	-0.04	0.31	-0.01
BwdTaxa	*Compos*	*Phric*	*Husted*	*Dielas*	*Cruri*	*Neo*	*Neo t.*

BwdTaxa	*Puncto*	*Rhipido*	*Derbyia*	*Meek*	*Chon*	*Mesolo*	*Desm*
phylloid							
fusulinid							
foraminifera							
crinoid							
echinoid							
Crania							
Enteletes							
Composita							
Phricodothyris							
Hustedia							
Dielasma							
Crurithyris							
Neospirifer							
Neospirifer t.							
Punctospirifer	1.00						
Rhipidomella	0.21	1.00					
Derbyia	**0.47**	**0.55**	1.00				
Meekella	-0.05	-0.04	-0.10	1.00			
Chonetinella	0.00	-0.01	0.14	-0.04	1.00		
Mesolobus	-0.08	-0.05	-0.13	-0.05	-0.04	1.00	
Desmoinsea	0.05	-0.02	-0.01	0.15	-0.06	-0.07	1.00
Kozlowskia	0.05	-0.03	0.10	-0.03	-0.03	-0.03	-0.04
Retaria	0.19	0.24	0.12	-0.04	0.02	-0.05	-0.06
Antiquatonia	0.03	0.09	-0.01	**0.44**	-0.11	0.07	-0.07
Reticulatia	-0.10	-0.07	-0.14	-0.01	-0.06	0.31	-0.07
Echinaria	-0.12	-0.07	-0.16	-0.07	-0.07	0.02	-0.06
Parajuresania	0.00	0.06	0.00	0.00	-0.04	-0.05	-0.03
Linoproductus	-0.13	-0.07	-0.13	-0.09	-0.09	0.19	0.03

BwdTaxa	*Puncto*	*Rhipido*	*Derbyia*	*Meek*	*Chon*	*Mesolo*	*Desm*
Minilya	**0.43**	-0.05	0.21	-0.09	0.20	-0.03	**0.63**
Fenestre	0.10	-0.04	0.00	-0.04	0.02	-0.04	**0.79**
Septopora	0.12	-0.04	-0.06	-0.04	0.01	-0.05	**0.81**
Polypora	**0.45**	-0.01	0.33	-0.08	0.01	-0.07	**0.73**
Rhombopora	**0.44**	-0.05	0.19	-0.10	0.09	-0.12	**0.49**
Leioclema	0.05	0.20	0.17	-0.04	-0.01	-0.05	-0.05
Sheet Tub.	-0.07	-0.05	-0.08	-0.05	-0.05	0.03	-0.07
Tubuliporate	**0.92**	0.03	**0.39**	-0.05	0.17	-0.07	0.02
Nucula	-0.02	-0.03	-0.07	-0.03	-0.03	-0.03	-0.04
Nuculana	-0.05	-0.04	-0.12	-0.04	-0.04	-0.05	-0.07
Myalina	-0.03	-0.01	-0.08	-0.02	-0.04	-0.04	-0.05
Aviculopinna	-0.09	-0.06	-0.13	-0.05	-0.06	-0.06	-0.09
Aviculopecten	-0.05	-0.04	-0.12	-0.04	-0.05	-0.05	-0.06
Acanthopecten	-0.02	-0.03	-0.07	-0.03	-0.03	-0.03	-0.04
Astartella	-0.02	-0.01	-0.06	-0.03	-0.03	-0.04	-0.04
Allorisma	-0.02	-0.03	-0.07	-0.03	-0.03	-0.03	-0.04
Bellerophon	-0.06	0.04	-0.04	0.04	-0.06	-0.07	-0.07
Trepospira	0.11	0.12	0.08	-0.05	-0.01	-0.07	-0.08
LgHS	0.02	**0.37**	0.27	-0.03	-0.02	-0.03	-0.04
Leptozyga	-0.11	-0.07	-0.15	-0.07	-0.07	-0.08	-0.10
Goniasma	-0.04	-0.03	-0.07	-0.03	-0.03	-0.03	-0.04
Straparollus	-0.04	-0.03	-0.07	-0.03	-0.03	-0.03	-0.04
lg conisp	-0.04	-0.03	-0.07	-0.03	-0.03	-0.03	-0.04
nautiloid	0.19	0.15	0.09	-0.04	0.02	-0.04	-0.05
Lophophyllidium	-0.02	-0.04	0.07	-0.04	-0.04	-0.05	0.29
trilobite	-0.03	-0.06	0.24	-0.06	**0.35**	-0.08	-0.09
shark	-0.06	0.01	-0.05	-0.04	-0.05	-0.06	-0.07
BwdTaxa	*Puncto*	*Rhipido*	*Derbyia*	*Meek*	*Chon*	*Mesolo*	*Desm*

BwdTaxa	*Kozlow*	*Retaria*	*Antiquit*	*Reticul*	*Echinar*	*Parajur*	*Lino*
phylloid							
fusulinid							
foraminifera							
crinoid							
echinoid							
Crania							
Enteletes							
Composita							
Phricodothyris							
Hustedia							
Dielasma							
Crurithyris							
Neospirifer							
Neospirifer t.							
Punctospirifer							
Rhipidomella							
Derbyia							
Meekella							
Chonetinella							
Mesolobus							
Desmoinsea							
Kozlowskia	1.00						
Retaria	-0.03	1.00					
Antiquatonia	0.36	0.02	1.00				
Reticulatia	-0.05	-0.05	-0.08	1.00			
Echinaria	-0.05	-0.05	0.11	0.34	1.00		
Parajuresania	-0.03	0.03	0.06	-0.06	-0.08	1.00	
Linoproductus	-0.07	-0.05	-0.01	**0.38**	**0.68**	0.13	1.00

BwdTaxa	*Kozlow*	*Retaria*	*Antiquit*	*Reticul*	*Echinar*	*Parajur*	*Lino*
Minilya	-0.07	-0.11	-0.18	-0.10	-0.15	0.36	-0.01
Fenestre	-0.03	-0.05	-0.11	-0.07	-0.08	-0.02	-0.09
Septopora	-0.03	-0.04	-0.10	-0.07	-0.07	0.13	-0.06
Polypora	-0.05	-0.07	-0.13	-0.11	-0.12	0.17	0.00
Rhombopora	-0.07	-0.12	-0.12	0.05	-0.03	0.56	0.13
Leioclema	-0.03	-0.04	-0.12	-0.07	-0.07	0.00	-0.09
Sheet Tub.	-0.03	-0.05	-0.11	**0.82**	**0.41**	-0.04	**0.37**
Tubuliporate	-0.03	-0.04	-0.06	-0.09	-0.10	-0.04	-0.11
Nucula	-0.02	-0.03	0.05	-0.05	-0.05	0.99	0.13
Nuculana	-0.03	-0.05	-0.08	-0.08	-0.07	0.43	0.08
Myalina	-0.02	-0.04	0.06	0.11	0.02	0.96	0.18
Aviculopinna	-0.04	-0.06	0.10	**0.69**	**0.37**	0.05	0.23
Aviculopecten	-0.03	-0.05	0.00	-0.08	-0.08	0.93	0.16
Acanthopecten	-0.02	-0.03	0.05	-0.05	-0.05	0.99	0.13
Astartella	-0.02	-0.03	0.04	-0.05	-0.06	0.98	0.13
Allorisma	-0.02	-0.03	0.05	-0.05	-0.05	0.99	0.13
Bellerophon	-0.04	-0.06	-0.11	**0.65**	0.25	-0.06	0.19
Trepospira	-0.04	**0.75**	-0.12	-0.09	-0.02	-0.02	0.00
LgHS	-0.02	-0.03	-0.08	-0.05	-0.05	-0.03	-0.07
Leptozyga	-0.05	-0.02	-0.12	-0.11	-0.07	-0.04	-0.10
Goniasma	-0.02	-0.03	-0.08	-0.05	-0.05	-0.03	0.13
Straparollus	-0.02	-0.03	-0.08	-0.05	-0.05	-0.03	-0.07
lg conisp	-0.02	-0.03	-0.08	-0.05	-0.05	-0.03	0.00
nautiloid	-0.03	**0.92**	-0.04	-0.06	-0.07	0.22	0.01
Lophophyllidium	**0.52**	-0.05	0.11	-0.05	0.00	-0.05	0.11
trilobite	-0.04	-0.07	-0.19	-0.11	-0.12	-0.05	-0.12
shark	-0.03	-0.03	0.17	-0.02	**0.73**	-0.04	**0.59**
BwdTaxa	*Kozlow*	*Retaria*	*Antiquit*	*Reticul*	*Echinar*	*Parajur*	*Lino*

BwdTaxa	*Minilya*	*Fenestr*	*Sept*	*Polypora*	*Rhomb*	*Leiocl*	ShTub
Minilya	1.00						
Fenestre	**0.69**	1.00					
Septopora	**0.74**	**0.97**	1.00				
Polypora	**0.90**	**0.69**	**0.71**	1.00			
Rhombopora	**0.86**	**0.46**	**0.55**	**0.78**	1.00		
Leioclema	0.11	-0.01	-0.02	0.07	-0.08	1.00	
Sheet Tub.	-0.07	-0.05	-0.05	-0.09	0.15	-0.05	1.00
Tubuliporate	**0.49**	0.05	0.06	**0.47**	**0.46**	0.17	-0.07
Nucula	**0.35**	-0.01	0.14	0.14	**0.56**	-0.03	-0.03
Nuculana	0.10	-0.04	0.02	-0.01	0.19	-0.05	-0.06
Myalina	0.33	-0.02	0.13	0.12	**0.57**	0.00	0.13
Aviculopinna	-0.07	-0.06	-0.05	-0.10	0.15	-0.06	**0.76**
Aviculopecten	**0.29**	-0.03	0.12	0.09	**0.49**	-0.04	-0.06
Acanthopecten	**0.35**	-0.01	0.14	0.14	**0.56**	-0.03	-0.03
Astartella	**0.35**	-0.01	0.14	0.13	**0.56**	-0.01	-0.04
Allorisma	**0.35**	-0.01	0.14	0.14	**0.56**	-0.03	-0.03
Bellerophon	-0.10	-0.06	-0.06	-0.11	0.07	0.08	**0.75**
Trepospira	-0.12	-0.06	-0.05	-0.10	-0.12	0.20	-0.07
LgHS	-0.07	-0.03	-0.03	-0.05	-0.05	**0.57**	-0.03
Leptozyga	-0.12	-0.07	-0.05	-0.11	-0.14	-0.07	-0.09
Goniasma	-0.07	-0.03	-0.03	-0.05	-0.07	-0.03	-0.03
Straparollus	-0.02	-0.03	-0.03	-0.04	-0.01	-0.03	-0.03
lg conisp	-0.04	-0.03	-0.03	-0.05	0.08	-0.03	0.28
nautiloid	-0.01	-0.04	0.00	-0.04	0.02	-0.04	-0.05
Lophophyllidium	0.00	-0.04	-0.03	0.07	0.09	-0.02	-0.06
trilobite	0.04	0.00	-0.01	-0.01	-0.06	-0.06	-0.08
shark	-0.09	-0.04	-0.05	-0.09	-0.10	-0.05	0.00
BwdTaxa	*Minilya*	*Fenestr*	*Sept*	*Polypora*	*Rhomb*	*Leiocl*	ShTub

BwdTaxa	Tubulip	*Nucula*	*Nuculan*	*Myalina*	*Avicpin*	*Avicpec*	*Acanpc*
Minilya							
Fenestre							
Septopora							
Polypora							
Rhombopora							
Leioclema							
Sheet Tub.							
Tubuliporate	1.00						
Nucula	-0.04	1.00					
Nuculana	-0.06	**0.39**	1.00				
Myalina	-0.05	**0.98**	**0.38**	1.00			
Aviculopinna	-0.09	0.06	0.00	0.23	1.00		
Aviculopecten	-0.06	**0.93**	**0.62**	**0.91**	0.03	1.00	
Acanthopecten	-0.04	**1.00**	**0.39**	**0.98**	0.06	**0.93**	1.00
Astartella	-0.04	**1.00**	**0.42**	**0.98**	0.06	**0.94**	**1.00**
Allorisma	-0.04	**1.00**	**0.39**	**0.98**	0.06	**0.93**	**1.00**
Bellerophon	-0.03	-0.04	-0.07	0.12	**0.63**	-0.07	-0.04
Trepospira	-0.03	-0.04	-0.06	-0.02	-0.03	-0.05	-0.04
LgHS	0.06	-0.02	-0.03	0.03	-0.04	-0.03	-0.02
Leptozyga	-0.09	-0.05	**0.40**	-0.06	-0.08	0.13	-0.05
Goniasma	-0.04	-0.02	-0.03	-0.02	-0.04	0.10	-0.02
Straparollus	-0.03	-0.02	-0.03	-0.02	-0.04	-0.03	-0.02
lg conisp	-0.04	-0.02	-0.03	-0.02	0.01	-0.03	-0.02
nautiloid	-0.04	0.17	0.04	0.16	-0.04	0.15	0.17
Lophophyllidium	-0.02	-0.03	-0.05	-0.04	-0.07	-0.05	-0.03
trilobite	0.06	-0.04	0.18	-0.06	-0.10	0.06	-0.04
shark	-0.06	-0.03	0.00	-0.03	0.05	-0.03	-0.03
BwdTaxa	Tubulip	*Nucula*	*Nuculan*	*Myalina*	*Avicpin*	*Avicpec*	*Acanpc*

BwdTaxa	*Astart*	*Alloris*	*Bellero*	*Treposp*	LgHS	*Lepto*	*Gonias*
Minilya							
Fenestre							
Septopora							
Polypora							
Rhombopora							
Leioclema							
Sheet Tub.							
Tubuliporate							
Nucula							
Nuculana							
Myalina							
Aviculopinna							
Aviculopecten							
Acanthopecten							
Astartella	1.00						
Allorisma	**1.00**	1.00					
Bellerophon	-0.04	-0.04	1.00				
Trepospira	-0.02	-0.04	0.10	1.00			
LgHS	0.02	-0.02	0.20	**0.41**	1.00		
Leptozyga	-0.03	-0.05	0.28	0.12	-0.05	1.00	
Goniasma	-0.02	-0.02	-0.04	-0.04	-0.02	-0.05	1.00
Straparollus	-0.02	-0.02	0.32	0.18	-0.02	**0.68**	-0.02
lg conisp	-0.02	-0.02	0.08	-0.04	-0.02	-0.05	-0.02
nautiloid	0.17	0.17	-0.06	**0.81**	-0.03	-0.06	-0.03
Lophophyllidium	-0.03	-0.03	0.03	-0.06	-0.03	0.00	-0.03
trilobite	-0.04	-0.04	-0.06	0.01	-0.04	0.28	-0.04
shark	-0.03	-0.03	-0.02	0.05	-0.03	0.03	-0.03
BwdTaxa	*Astart*	*Alloris*	*Bellero*	*Treposp*	LgHS	*Lepto*	*Gonias*

BwdTaxa	*Strap*	lgconisp	naut	*Lopho*	tril	shark
Minilya						
Fenestre						
Septopora						
Polypora						
Rhombopora						
Leioclema						
Sheet Tub.						
Tubuliporate						
Nucula						
Nuculana						
Myalina						
Aviculopinna						
Aviculopecten						
Acanthopecten						
Astartella						
Allorisma						
Bellerophon						
Trepospira						
LgHS						
Leptozyga						
Goniasma						
Straparollus	1.00					
lg conisp	-0.02	1.00				
nautiloid	-0.03	-0.03	1.00			
Lophophyllidium	-0.03	-0.03	-0.04	1.00		
trilobite	-0.04	-0.04	-0.06	-0.07	1.00	
shark	-0.03	-0.03	-0.03	-0.05	-0.02	1.00
BwdTaxa	*Strap*	lgconisp	naut	*Lopho*	tril	shark

Appendix 4: Guilds

GUILDS BASED ON BAMBACH'S (1983) CLASSIFICATION:

Epifaunal, attached, low or erect producer:	phylloid algae
Epifaunal, mobile, microcarnivore (other?):	fusulinid foraminifera
Epifaunal, attached, erect, suspension feeder:	crinoid
Epifaunal, mobile, herbivore:	echinoid
Epifaunal, attached, low, suspension feeder:	*Enteletes* *Composita*
	Phricodothyris *Hustedia*
	Dielasma *Crurithyris*
	Neospirifer *Punctospirifer*
	Derbyia *Meekella*
	Chonetinella *Mesolobus*
	Desmoinsea *Hystriculina*
	Kozlowskia *Retaria*
	Antiquitonia *Reticulatia*
	Echinaria *Parajuresania*
	Linoproductus
Epfaunal, attached, low suspension feeder	*Crania*
Epifaunal, attached, low-erect suspension feeder	*Minilya* *Fenestrellina*
	Polypora *Rhombopora*
	Leioclema
Epifaunal, attached, low suspension feeder	tubuliporate bryozoan
Infaunal, shallow active suspension/deposit feeder	*Nuculana* *Astartella*
	Allorisma
Epifaunal/infaunal, attached, low suspension feeder	*Myalina*
Epifaunal, mobile, suspension feeder	*Aviculopinna* *Acanthopecten*
	Aviculopecten
Epifaunal, mobile, deposit-feeder/herbivore/ carnivore	*Bellerophon* *Glabrocingulum*
	Goniasma *Euomphallus*
	Leptozyga
Nektic carnivore/scavenger	orthocone nautiloid
Epifaunal, attached, low-erect suspension feeder	*Lophophyllidium*
Epifaunal, mobile or infaunal, active deposit feeder	trilobite
Nektic carnivore	shark

GUILDS BASED ON TAXA WITH POTENTIAL FOR INTENSE, INTERSPECIFIC COMPETITION:

Primary producer: phylloid algae
Foraminifera: fusulinids, foraminifera
Crinoids
Echinoids
Crania
Small, brachiopods: *Enteletes, Hustedia, Rhipiodomella*
Composita-like brachiopods: *Composita, Phricodothyris, Dielasma*
Small, attaching brachiopods: *Crurithyris, Punctospirifer*
Neospirifer
Small productids, including chonetidines and marginiferiforms: *Meekella, Chonetinella, Mesolobus, Desmoinsea, Kozlowskia, Retaria*
Large productid brachiopods: *Reticulatia, Antiquitonia, Echinaria, Linoproductus, Parajuresania*
Fenestellid bryozoans: *Minilya, Polypora, Fenestrellina*
Ramose bryozoans: *Rhombopora, Leioclema*
Encrusting bryozoans: tubuliporate bryozoans
Epifaunal to partially infaunal, ?byssate bivalves: *Myalina, Aviculopinna, Aviculopecten, Acanthopecten*
Infaunal bivalves, mode unknown: *Nucula, Nuculana, Astartella, Allorisma*
Gastropods, mode unknown: *Bellerophon, Glabrocingulum, Leptozyga, Goniasma, Euomphallus*
Orthocone nautiloid
Lophophyllidium
Trilobite
Shark

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