STRATIGRAPHIC AND GEOGRAPHIC BRYOZOAN ABUNDANCE GRADIENTS IN THE CALCAREOUS SHALES OF THE WREFORD MEGACYCLOTHEM (LOWER PERMIAN, KANSAS)

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Abstract.—Studies of bryozoans from the Wreford Megacyclothem have provided an extensive species-level database with which to examine paleoecologic patterns using multivariate statistical methods. Detrended correspondence (DCA) or gradient analysis was applied to fractional abundances of 17 species across 85 sampling intervals primarily within calcareous lithologies of the Wreford strata of Kansas.

Gradient analysis segregated the single robust trepostome species and all the encrusting-upright cystoporates from mostly small or delicate fenestrates, cryptostomes, and a ctenostome. The distribution of colonial morphologies and sizes suggests that these patterns were ecologically controlled and not the result of hydrodynamic sorting or taphonomic processes.

With minor exceptions involving the uppermost Speiser Shale and Schroyer Limestone Member of the Wreford Limestone, detrended correspondence analysis did not segregate any distinctive groupings of beds or lithologies. Speiser assemblages contain a diverse suite of abundant fenestrates and cryptostomes, whereas assemblages from the Schroyer maintain high fenestrate and cryptostome diversity while adding cystoporates and a trepostome.

The average position of each sampled interval on the first three detrended correspondence analysis axes indicates a general stratigraphic trend within the Wreford. Samples are arrayed in approximate stratigraphic order along axis 1 with axis 3 isolating Schroyer from Havensville samples.

Similar patterns result from gradient analyses of individual stratigraphic sampling intervals. Bryozoan faunas are dominated by fenestrates and cryptostomes, while trepostomes and cystoporates are generally rare or absent.

Regression of detrended correspondence analysis scores on a south-to-north distance of a sample from the Oklahoma-Kansas border indicates onshore-offshore gradients in species abundances within Wreford stratigraphic intervals. Significant trends occur in five of eight stratigraphic intervals, suggesting that gradient strength varied temporally within the uniformly shallow Wreford sea.

INTRODUCTION

The bryozoans of the Lower Permian (Wolfcampian) Wreford Megacyclothem have been examined extensively over the past thirty years (Cuffey, 1967, 1977; Newton, 1971; Warner & Cuffey, 1973; Fry & Cuffey, 1976; Simonsen & Cuffey, 1977, 1980; Lutz-Garrihan & Cuffey, 1979; Cuffey & Hall, 1985; Pachut & Cuffey, 1991; Pachut, Anstey, & Cuffey, 1991). This information and stratigraphic conclusions were thoroughly documented in these previous publications; a detailed survey of all the data and the reasoning supporting these conclusions is far beyond the scope of this paper. Studies of systematics, morphology, patterns of development and heterochrony, and paleoautecology have provided an extensive quantitative database with which to examine possible biotic and spatiotemporal gradients in
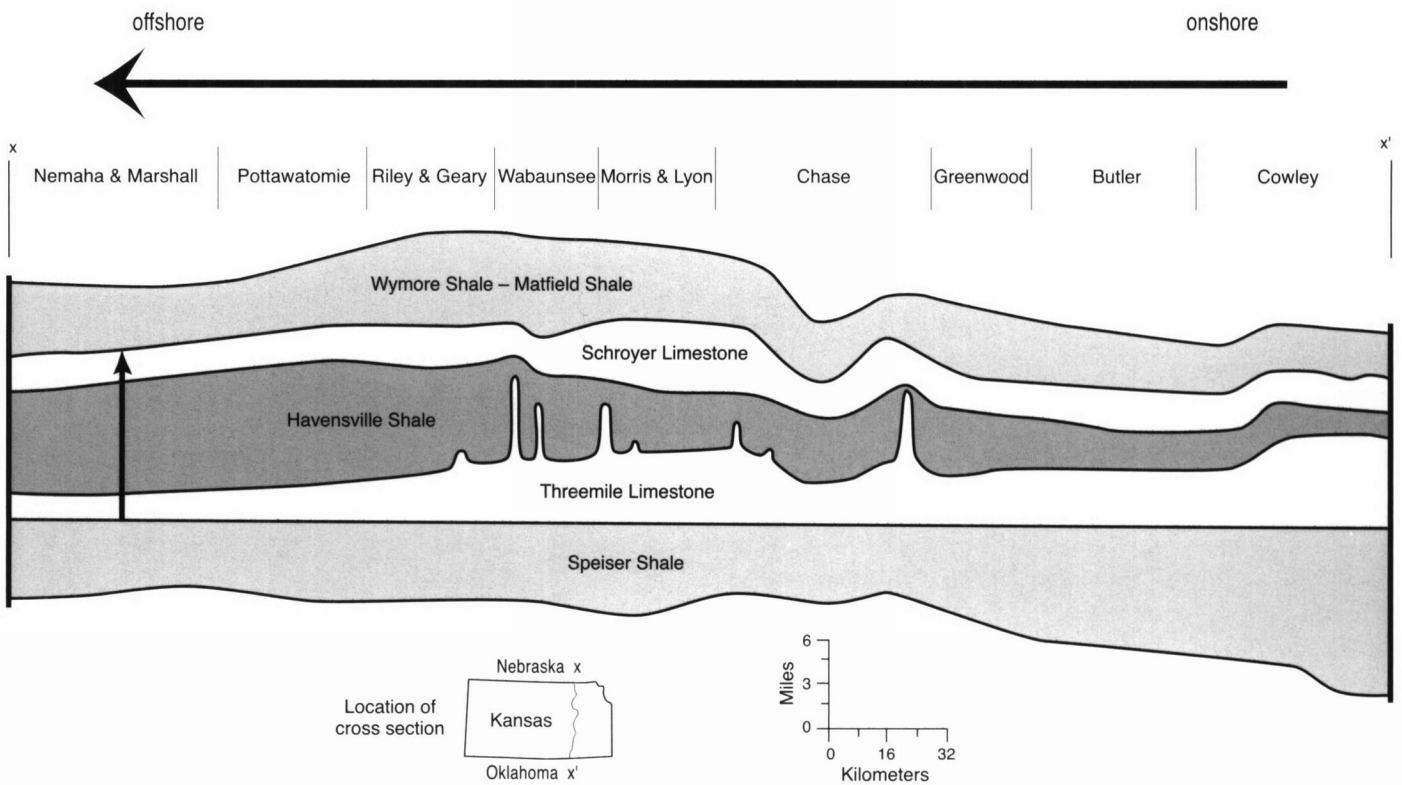
Figure 1. Schematic cross section of the Wreford Megacyclothem across Kansas (adapted from Cuffey, 1967, fig. 2, p. 14–15). County boundaries are indicated along the top, and Wreford stratigraphic units are indicated within the figure; Wreford Limestone indicated by *vertical arrow* (new).

these strata. The delineation of Wreford bryozoan species-level associations has paleosynecological significance in potentially permitting the delineation of paleoecological conditions, community structure, and biogeographic distributions that may ultimately be useful in establishing patterns of organism and community evolution.

General stratigraphic setting.—Rocks of the Wreford Megacyclothem (Fig. 1) are exposed along a south-to-north trending outcrop belt extending from northern Oklahoma across east-central Kansas into southernmost Nebraska. The Wreford Megacyclothem includes, in ascending order, the Speiser Shale of the Council Grove Group; the Threemile Limestone, Havensville Shale, and Schroyer Limestone Members of the Wreford Limestone; and the Wymore Shale Member of the Matfield Formation (Hattin, 1957). These units consist of a succession of 22 very thin beds that are roughly time parallel along the outcrop belt and within each of which may occur facies gradations (Hattin, 1957; Newton, 1971; Lutz-Garihan & Cuffey, 1979). These rocks were deposited in a shallow but extensive shelf sea and consist mostly of micritic limestones and mudstones indicative of paleoenvironments influenced partly by fluctuations in water depth and partly by variations in the supply of fine clastics (Cuffey & Hall, 1985). Some beds have since been recognized as diagenetically overprinted

by soil-forming (pedogenic) processes (Miller & West, 1993).

Previous studies of Wreford bryozoan associations.—Cuffey (1967) made an initial attempt to delineate Wreford paleoenvironmental patterns prior to having a species-level taxonomic framework by examining the relative proportions of bryozoan growth forms present in sampled populations. He recognized that the same species sometimes constructed colonies that had different growth forms, whereas similar growth forms could be generated by different species. He also identified ten different colony growth forms among Wreford species (Table 1) but could not detect clear patterns of variation in percentages of growth forms within any of the lithologies across the Kansas outcrop belt. Several aspects of colony growth forms, however, became apparent within facies (Cuffey, 1967, fig. 6–10). 1. Delicate branching, small pinnate, and fenestrate growth forms numerically dominated faunas throughout the Wreford. 2. Bryozoans were most abundant in calcareous shales and cherty limestones presumably representing times of maximum marine submergences (based on the symmetry of the cyclothems around the cherty limestones). 3. Rarer growth forms occurred only in those same maximum-submergence rocks indicative of transgressions, whereas the three dominant colony forms were also found in units

indicative of more extreme ecological conditions associated with nearshore environments. 4. Delicate branching and fenestrate colonies became more abundant than small pinnate forms upward in the uppermost Speiser, probably paralleling environmental changes affecting sediment types, such as deposition of molluscan limestone followed by calcareous shale and then cherty limestone. 5. Bryozoans were far more abundant and widely distributed in more normal-marine, offshore (northern) areas of Kansas than in onshore (southern) areas where clastic input and possibly salinity varied.

Cuffey and Hall (1985) extended the earlier study of growth forms by completing the species-level taxonomy of Wreford bryozoans and examining their distributions qualitatively and quantitatively through Fourier analysis of species abundances. Only one species, the tiny, ramose cystoporate *Filiramoporina kretaphilia*, was environmentally restricted, occurring only in chalky limestones, particularly in carbonate mudbanks in the middle upper part of the upper Threemile Limestone. The other nineteen species were more widely distributed. Some were found only in calcareous shales and cherty limestones and others in varying abundances in most rock types. No mutually exclusive sets of species could be delineated that defined different communities that simultaneously occupied different habitats on the Wreford sea floor. Similarly, no consistent patterns were discernible in species abundances either from bed to bed or from nearshore habitats to offshore habitats (south-to-north) within the five principal calcareous shales of the Wreford: uppermost Speiser, middle Threemile, basal and topmost Havensville, and middle Schroyer. Cuffey and Hall (1985, p. 259) concluded that "no assemblages could be delineated by matching similar abundance variations among the Wreford bryozoans within particular rock types at several horizons."

The bryozoan assemblages they were able to define were based on an examination of overlapping ranges of species within lithologies (Cuffey & Hall, 1985, table 1, p. 258). 1. A full assemblage, containing all species except *Filiramoporina kretaphilia*, occurs in calcareous shale, brachiopod-molluscan limestone interbedded with calcareous shale, cherty limestone, and some algal limestones. 2. A partial assemblage, consisting of eight species, each with at least three zoaria, and single zoaria for each of two species, is found in molluscan limestone, most brachiopod-molluscan limestone, and some algal limestone. 3. A bank assemblage, comprising mostly (44 percent) *Filiramoporina kretaphilia* but with contributions from nine other species (four containing three or fewer zoarial fragments), is found in chalky limestone, especially in buildups. 4. A reduced assemblage containing seven species (three represented by three colony fragments each) occurs in green shale and gray-yellow mudstone. Assemblages 1 and 2 appear to have lived under normal-marine, offshore conditions. Reduced assemblage 4 lived in more nearshore, perhaps periodi-

Table 1. Current taxonomic assignments and colony growth forms of bryozoan species known to occur in the Wreford Megacyclothem of Kansas. The assignment of species of *Condranema* to the Ctenostomata follows Cuffey (1967). We recognize that they may be cyclostomes and require additional study (new).

Order (Suborder) Species	Colony Growth Form
Ctenostomata	
Condranema magna	encrusting threads
Condranema parvula	encrusting threads
Fenestrata	
Acanthocladia guadalupensis	small pinnate
Fenestella spinulosa	delicate fenestrate
Fenestella tenax	delicate fenestrate
Minilya binodata	delicate fenestrate
Penniretepora auernigiana	tiny pinnate
Penniretepora curvula	tiny pinnate
Penniretepora flexistriata	tiny pinnate
Polypora aestacella	robust fenestrate
Polypora nodolinearis	robust fenestrate
Protoretepora elliptica	robust fenestrate
Septopora spinulosa	delicate fenestrate
Cryptostomata (Rhabdomesina)	
Rhombopora lepidodendroides	delicate ramose
Syringoclemis wrefordensis	delicate ramose
Trepostomata	
Tabulipora carbonaria	robust ramose
Cystoporata (Fistuliporina)	
Filiramoporina kretaphilia	tiny ramose
Fistulipora carbonaria	encrusting sheets
Fistulipora incrustans	encrusting sheets
Meekopora prosseri	upright sheet (bifoliate)

cally brackish and turbid waters, and assemblage 3 occurred only in chalky limestone mudbanks that formed, apparently, under conditions that were not conducive to the development of a normal, offshore, faunal association. Finally, 440 Fourier spectra (20 species from 22 samples) were calculated from species abundance profiles. They did not successfully delineate species assemblages, however. This could have resulted from the inability of spectra to delineate meaningful groupings or from random variations in species abundances across facies (Cuffey & Hall, 1985).

Holdener (1997) delineated geographic and clinal morphologic variation among populations of *Rectifenestella* sp. from the upper upper Speiser and middle Threemile of the Wreford. Patterns of variation were complex; morphologic characters that distinguished populations within each of these units generally were not the same, and those that were useful in distinguishing populations from both units did not always exhibit the same patterns of covariation. Populations of *Rectifenestella* sp. became more gracile with time, and patterns of morphologic variation in populations paralleled changes among populations of a Wreford trepostome bryozoan, *Tabulipora carbonaria* (Pachut & Cuffey, 1991). Among *T. carbonaria*, clinal geographic variation, different population growth trajectories, and heterochronic modifications of growth were demonstrated

Table 2. Ordination scores for 17 species calculated across 85 sampling intervals by detrended correspondence analysis (DCA) (DECORANA; Hill, 1979). Taxonomic assignments and growth habits of species are listed in Table 1 (new).

Species	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.42	0.22	0.14	0.12
Fistulipora carbonaria	386	173	-51	126
Tabulipora carbonaria	345	133	132	195
Fistulipora incrustans	321	150	244	254
Meekopora prosseri	314	474	275	291
Protoretepora elliptica	297	334	311	308
Fenestella tenax	279	-43	1	73
Condranema magna	194	153	232	125
Syringoclemis wrefordensis	194	295	-105	246
Rhombopora lepidodendroides	178	201	64	75
Penniretepora curvula	175	27	144	20
Septopora spinulosa	165	35	237	222
Polypora aestacella	117	124	257	456
Minilya binodata	96	87	236	74
Acanthocladia guadalupensis	42	52	78	232
Penniretepora flexistriata	0	42	172	136
Penniretepora auernigiana	-1	97	217	12
Fenestella spinulosa	-33	100	204	-23

in three calcareous shales across an inferred onshore-offshore environmental gradient.

The purpose of this study is to expand on earlier quantitative analyses of colonial growth forms and qualitative attempts to delineate recurring assemblages of bryozoan species within the Wreford Megacyclothem of Kansas. Visual inspection of the relative frequencies of colony growth forms and of overlapping stratigraphic and geographic ranges of species has provided a general framework within which multivariate techniques may be applied to define more rigorously intergrading groups of species and to indicate the geographic and stratigraphic patterns of species occurrences within sampled units. Finally, the presence of clinal variation, previously delineated in *Tabulipora carbonaria* from three calcareous shales, can be evaluated in the entire bryozoan fauna across all calcareous shales of the Wreford.

ANALYSES AND RESULTS

Wreford strata were extensively examined at about 250 localities by Cuffey (1967), Newton (1971), and Lutz-Garihan (1976). We selected the eight most fossiliferous beds for analysis and obtained 509 samples. Limestone samples were mechanically broken; shales were disaggregated using standard kerosene treatment and sieved. The resulting approximately 16,000 bryozoan colony fragments were sorted into species. Table 1 lists the twenty species that occur in Wreford lithologies along with their colony growth forms.

Samples containing three or more species were retained for analysis; those containing fewer than three species provide little information on both the composition of species associations and on geographic groupings of samples.

Included were 85 fossiliferous samples representing collections from units at different localities within the Wreford and encompassing 11,015 colonies or fragments of colonies (hereinafter referred to as colonies). This screening of the data eliminated *Filiramoporina kretaphilia* and *Polypora nodolinearis,* leaving 18 species in the analysis. Numbers of colonies within each sample were transformed by calculating fractional abundances equal to the number of specimens of each species divided by the total number of specimens in the entire data set (Fishbein & Patterson, 1993).

An examination of sampled units across formations and members and across horizons at all localities permits a spatio-temporal analysis that attempts to delineate recurring associations of both species and sampling intervals occurring stratigraphically and geographically across Kansas. Calcareous shales were by far the most commonly sampled lithologic facies (68 samples), followed by calcareous shales interbedded with brachiopod-molluscan limestones (12 samples). Other facies contained locally sufficient numbers of species to justify analytical treatment, including gray-yellow mudstones (3 samples) and cherty limestones (2 samples). The overwhelming predominance of calcareous shales among our samples indicates both preserved abundances of fossils in that rock type and probably also ease of collection and extraction. As a byproduct, this lithologic dominance permits analyses to concentrate upon the detection of biotic variations related to environmental factors operating along onshore-offshore gradients across the shallow Wreford sea that are independent of sediment type.

Cuffey (1967) and Lutz-Garihan and Cuffey (1979) interpreted the depositional environments of these rocks. Calcareous shale appears to have been deposited in normal salinity, low turbulence, shallow-marine waters, perhaps between 3 and 16 meters deep (see also Lane, 1964). Similar conditions prevailed during deposition of cherty limestone, possibly during times of deepest waters in the Wreford sea (but only slightly deeper than 16 m). Brachiopod-molluscan limestone also accumulated under similar conditions that at times were somewhat more turbulent and perhaps of slightly lower salinity than those of calcareous shales. In contrast, gray-yellow mudstone represents very shallow, nearshore, slightly brackish-marine habitats, perhaps shallower than 3 meters (Cuffey, 1967; Lutz-Garrihan & Cuffey, 1979). In places, these rocks have also been overprinted by soil-forming processes, as noted above. In general, each calcareous shale unit has been interpreted as representing an approximately time-parallel deposit that graded from nearshore environments in southern Kansas to progressively more offshore areas northward (Cuffey, 1967, p. 70–71).

Detrended correspondence analysis (DCA).—DCA, also referred to as gradient analysis, is an ordination technique related to principal component analysis. It is based on an eigenvalue algorithm that simultaneously calculates sample

Table 3. Ordination scores calculated for 85 sampling sites across 17 species using DCA (DECORANA; Hill, 1979). A generalized stratigraphic section (Simonsen & Cuffey, 1980, fig. 1) and a locality map (Pachut & Cuffey, 1991, fig. 1) have been published previously. County abbreviations are followed by a sample number and stratigraphic unit code. Abbreviations of Kansas counties are as follows: *BU,* Butler; *CH,* Chase; *CY,* Cowley; *GE,* Geary; *GR,* Greenwood; *LY,* Lyon; *ML,* Marshall; *MS,* Morris; *PT,* Pottawatomie; *RY,* Riley; *WA,* Wabaunsee. Unit codes are: *Sp,* upper upper Speiser Shale; *MTm,* middle Threemile Shale; *LLLH,* lower lower lower Havensville Shale; *ULLH,* upper lower lower Havensville Shale; *MH,* middle Havensville Shale; *UUH,* upper upper Havensville Shale; *LMSh,* lower middle Schroyer Limestone; *UMSh,* upper middle Schroyer Limestone (new).

| Stratigraphic Unit | Axis 1 | Axis 2 | Axis 3 | Axis 4 |
	Eigenvalue 0.42	0.22	0.14	0.12
ML03LLLH	322	141	113	178
GE01UMSh	270	122	161	177
PT09LLLH	267	67	26	118
CY21UUH	256	147	103	159
PT16LMSh	244	176	221	218
WA05LMSh	240	34	101	150
MS05UUH	238	33	61	126
GE18ULLH	234	235	149	167
CH24UUH	231	100	85	130
CH04MH	228	33	61	95
CH56UUH	223	193	64	124
PT04UMSh	221	200	91	151
GE18LMSh	221	161	163	174
GE04UMSh	218	61	165	186
CH22ULLH	216	7	64	102
MS06UUH	213	27	69	127
RY14ULLH	211	144	79	98
BU04UUH	209	103	77	148
GR01MH	203	109	71	121
GE30UMSh	203	162	104	119
CH56LMSh	198	145	52	106
GE30LMSh	197	112	133	141
CH44MH	194	63	70	83
GE18UMSh	193	125	70	74
GE18MTm	192	103	39	104
LY08LLLH	191	216	110	133
CY18Sp	190	231	0	162
GE01LMSh	190	67	193	145
ML03MTm	180	189	51	91
WA04MH	180	0	54	147
CH08UUH	180	58	51	135
CH44UUH	180	42	85	144
CH52LMSh	180	120	147	180
LY08ULLH	179	202	64	82
BU04ULLH	179	131	62	110
GR01LLLH	175	140	68	116
GR01ULLH	175	140	68	116
BU04Sp	170	188	79	81
CY09LMSh	168	123	199	227
RY06UUH	166	61	95	151
CH22MH	165	124	114	135
BU04UMSh	165	63	141	162
CH24ULLH	164	32	98	106
CH52MH	162	38	138	178
MS21LMSh	162	57	55	123
CY14Sp	161	145	95	120
WA04ULLH	159	38	91	162
CH18Sp	156	132	63	115
CH52LLLH	156	146	77	139
BU05Sp	153	181	73	86

Table 3. Continued.

| Stratigraphic Unit | Axis 1 | Axis 2 | Axis 3 | Axis 4 |
	Eigenvalue 0.42	0.22	0.14	0.12
RY14LLLH	143	51	100	168
BU04LMSh	142	103	144	237
CH39MTm	141	177	82	76
GE21Sp	140	152	101	112
BU04MH	140	132	106	111
RY04LMSh	140	124	178	105
RY04Sp	137	159	98	96
GE18UUH	137	39	120	169
GR01Sp	132	74	97	165
GR01UUH	130	152	52	162
ML01MTm	125	152	128	63
WA03Sp	112	130	78	141
ML01Sp	108	55	85	165
CH22UUH	108	74	140	104
PT04MH	105	42	91	205
CH53Sp	96	103	81	176
CH06MTm	91	135	129	34
CH39Sp	90	91	140	94
CH45UMSh	88	97	146	126
CH56Sp	87	102	105	148
PT09Sp	86	90	98	157
PT02Sp	78	77	90	203
CH32Sp	76	90	124	103
PT15Sp	75	83	133	203
CH04Sp	72	112	127	101
CH33Sp	72	111	127	92
LY01Sp	68	74	89	202
CH16Sp	66	76	141	122
ML03Sp	62	73	69	232
GE18Sp	55	75	135	136
LY13Sp	39	79	138	123
WA08Sp	37	81	140	115
MS22Sp	37	80	154	97
WA04LLLH	3	109	208	0
WA08MTm	0	93	161	51

scores (as the means of scores of taxa in the samples) and taxon scores (as the means of scores of the samples within which the taxa occur; Patzkowsky, 1995). DCA focuses on the abundances and distributions of taxa relative to physical environmental gradients that may be established by the interplay of multiple factors (Cisne & Rabe, 1978, p. 347). These factors may not be easily separable, but they parallel variation in some overriding environmental variable. In marine-benthic communities, including reef-dwelling bryozoans (Pachut & Cuffey, 1995), continuous change has been documented along depth-related or onshore-offshore gradients (Sanders & Hessler, 1969; Johnson, 1970, 1971). In fossil applications (Cisne & Rabe, 1978; Patzkowsky, 1995), ordination scores calculated by gradient analysis appear to represent the environment as experienced by the organisms and can be viewed as generalized measures of the environment. The technique has been used to delineate environmental and temporal gradients, to establish correlations, to evaluate sedimentation and sea level changes, and to examine clinal morphologic evolution (Cisne & Rabe, 1978; Cisne & others, 1980; Cisne, Molenock, & Rabe, 1980; Cisne, Chandlee, & others, 1982; Cisne, Karig, & others, 1982; Cisne & Chandlee, 1982;

Table 4. Data matrix illustrating the distribution of Wreford species across samples based upon first axis scores from detrended correspondence analysis (DCA). Values in the matrix represent original rather than fractional species abundances. Species and samples were rearranged to correspond to the scores generated by DCA; Kansas county abbreviations are listed in Table 3, and the eigenvalues for species and samples are listed in Tables 2 and 3. Two species groups and three sample groups are indicated along the top and right side of the figure, respectively, with average abundances also given for the latter (based on abundances per total number of cells in which species could have been found). Shading highlights differences discussed in the text. Average abundances within subsets, defined as combined species group-sample group intervals (number or letter, respectively, indicates shaded or unshaded rectangles), are as follows: 1A = 4.24, 2A = 7.41; 1B < 0.00, 2B = 4.52; 1C = 0.15, 2C = 22.21. Mean Brillouin diversity and evenness within each sample group = 1.23 and 0.72 for Group A, 1.05 and 0.69 for Group B, and 1.20 and 0.67 for Group C; calculations are discussed in the text (new).

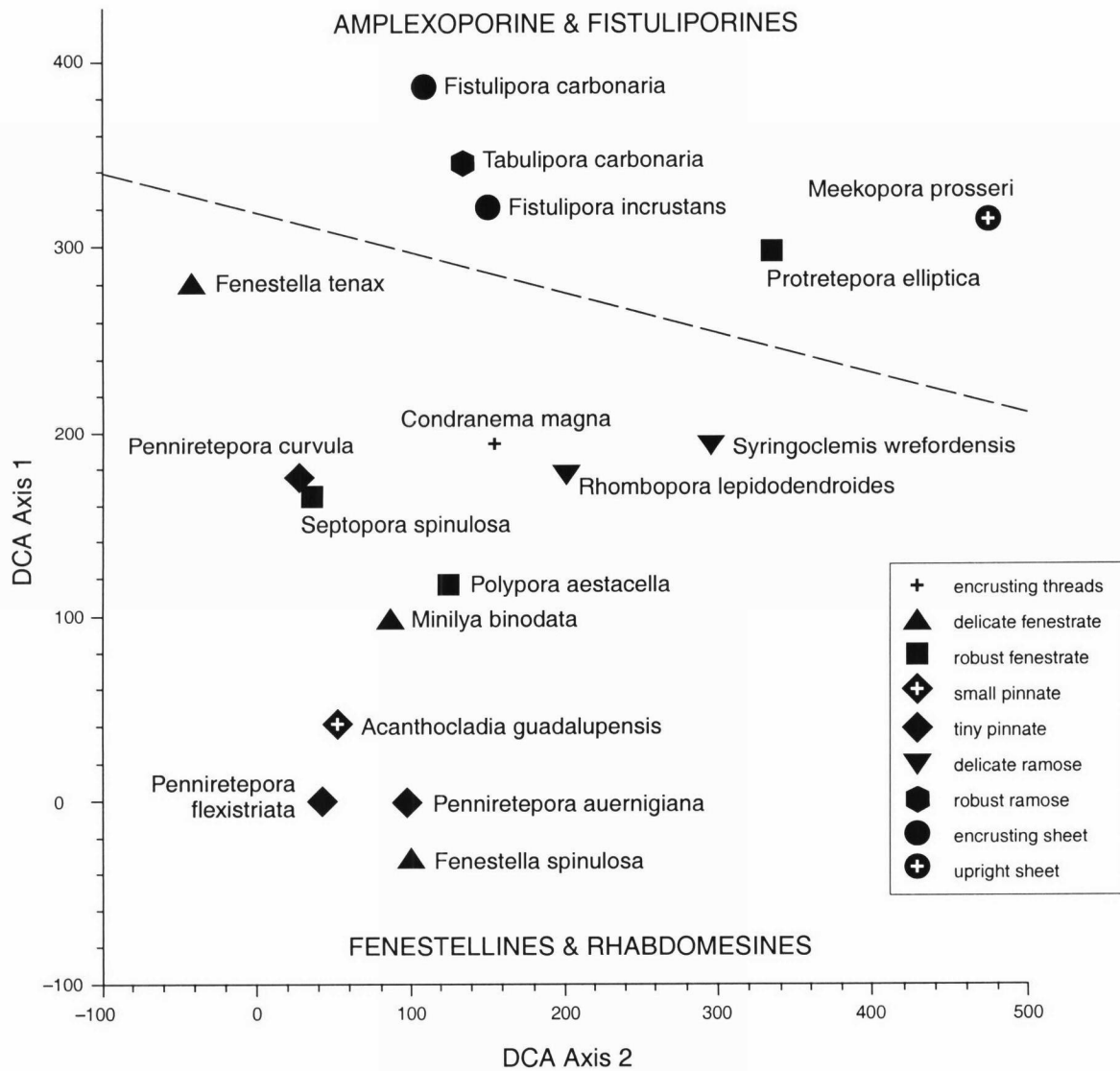Figure 2. Plot of the positions of Wreford species on the first two DCA axes. High values on axis 1 separate a robust trepostome and cystoporates displaying encrusting-upright growth forms from generally small fenestrates, cryptostomes, and a single ctenostome. *Protoretepora elliptica,* a robust fenestrate, is also allied with the trepostome-cystoporate group. Detrended correspondence analysis scores are listed in Table 2 (new).

Table 4. For explanation, see facing page.

SAMPLE	UNIT	SAMPLE SCORE	Fistulipora carbonaria 386	Tabulipora carbonaria 345	Fistulipora incrustans 321	Meekopora prosseri 314	Prasopora elliptica 297	Fenestella tenax 279	Condranema magna 194	Syringoclemis wrefordensis 194	Rhombopora lepidodendroides 178	Penniretepora curnula 175	Fenestella spinulosa 165	Polypora aestacella 117	Minilya binodata 96	Acanthocladia guadalupensis 42	Penniretepora flexistriata 0	Penniretepora avernigiana -1	Septopora spinulosa -33	TOTAL	AVERAGE ABUNDANCE	SAMPLE GROUP
ML03	LLLH	322	7	39	5				1	1	6				1					60		
GE01	UMSh	270		66	8	2	4	9	2	1	3		1	2	20	1			8	127		
PT09	LLLH	267	2	3				8		1	3					1				18		
CY21	UUH	256		5							3					1				9		
PT16	LMSh	244		5			13	2	1		3				2				9	35		
WA05	LMSh	240					2	8											3	14		
MS05	UUH	238		26	7			84		4	8	7	3		1	22			6	168		
GE18	ULLH	234		3	4	2			2	1	9								3	24		
CH24	UUH	231	2	50	8			56	2	4	68		4		4	16			15	229		
CH04	MH	228		1				58	1	23		1	2		2				15	103		
CH56	UUH	223		5						2	12									19		
PT04	UMSh	221			2					1	4									7		
GE18	LMSh	221	1	7	6	1	10	3	1	1	16	1			6	4			7	64	6.47	A
GE04	UMSh	218		9	1		2	11	1	1	3					1			32	61		
CH22	ULLH	216						147			19	8			23	24			25	246		
MS06	UUH	213	4	46	6		1	265		6	40	23	7		7	91	7		62	565		
RY14	ULLH	211		2				3	1		12								1	19		
BU04	UUH	209		23				12		2	20	4				19				80		
GR01	MH	203						6		2	10								5	23		
GE30	UMSh	203		1							4								1	6		
CH56	LMSh	198						2		1	6								1	10		
GE30	LMSh	197	1	18	15	8	33	97	5		166	10		10	44	24	1	5	97	534		
CH44	MH	194						10		2	8	12				3			1	36		
GE18	UMSh	193						2			5			1						8		
GE18	MTm	192						41		5	61					18				125		
LY08	LLLH	191					8		1	1	31					3				44		
CY18	Sp	190		2				1	2	41	41								4	91		
GE01	LMSh	190					1	1					2			1			3	8		
ML03	MTm	180								1	5	1								7		
WA04	MH	180						10								7			2	19		
CH08	UUH	180						30		10	13		5			21			11	90		
CH44	UUH	180		2				26			12				2	18			14	74		
CH52	LMSh	180			1					2	6								10	19		
LY08	ULLH	179							1	1	31									33		
BU04	ULLH	179						6		3	21	3				4			3	40		
GR01	LLLH	175		5				15	2	3	77					20			6	128		
GR01	ULLH	175		5				15	2	3	77					20			6	128		
BU04	Sp	170									60		2						4	66		
CY09	LMSh	168					2				1					2			4	9		
RY06	UUH	166						3			3					3			3	12		
CH22	MH	165						1			11					2			6	20	3.26	B
BU04	UMSh	165		2	2			7	1		11	8				14			25	70		
CH24	ULLH	164						41	1		6		6		21	18			6	99		
CH52	MH	162			1			33		2	10				6	34			71	157		
MS21	LMSh	162						4			3					3	1			11		
CY14	Sp	161						1	1		18					6			4	30		
WA04	ULLH	159						14			6					16			11	47		
CH18	Sp	156						6		1	27				2	11				47		
CH52	LLLH	156		2							9					5				16		
BU05	Sp	153									17		1			2				20		
RY14	LLLH	143						18	1		13	2				34			20	88		
BU04	LMSh	142		3	2				1	1	6			6		13			7	39		
CH39	MTm	141									20		3			2				25		
GE21	Sp	140							2	1	25		2		3	7			3	43		
BU04	MH	140								2	22	5	4			6			7	46		
RY04	LMSh	140		1	1					1	3		1		9				1	17		
RY04	Sp	137							1	1	49		5		8	10			2	76		
GE18	UUH	137						18			6	5	2		3	35			28	97		
GR01	Sp	132					1	21	1	1	30		1		6	56			20	137		
GR01	UUH	130		1	1					10	37				1	32				82		
ML01	MTm	125									33	2	11			3		4	3	56		
WA03	Sp	112									29		2			24			1	56		
ML01	Sp	108					4	157	6	8	88	11	37		2	443	33	11	55	855		
CH22	UUH	108		1	1			22	2	1	17		51	1		26			29	151		
PT04	MH	105										2				9			7	18		
CH53	Sp	96									30					51			4	85		
CH06	MTm	91			1						14	4	12			1				32		
CH39	Sp	90						26	1	1	75	13	72		65	74	13	11	20	371		
CH45	UMSh	88									1		1			1			1	4		
CH56	Sp	87			1						18	1	5		7	32				64		
QF09	Sp	86						7		3	44	1	15		3	94	7	4	12	190	15.72	C
PT02	Sp	78									6					24			3	33		
CH32	Sp	76		1			2	26		5	53	5	97	3	18	97	3		14	324		
PT15	Sp	75					2	24		2	34	1	24		32	161	9		28	317		
CH04	Sp	72								1	16		62		17	68	1	1	10	177		
CH33	Sp	72							1	1	53	8	52		6	48	4	2	6	181		
LY01	Sp	68							1	1	33		7			179			14	235		
CH16	Sp	66						17			29	5	79		87	155		1	14	388		
ML03	Sp	62								22	2					223			11	258		
GE18	Sp	55		1			2	19	6	14	28	11	156	3	52	294	32	17	49	684		
LY13	Sp	39					1	4	1	1	36	5	171		29	242	11	5	27	533		
WA08	Sp	37						6		3	44	3	185		13	202				457		
MS22	Sp	37						20	4	1	49	2	327		48	269	12	31	63	826		
WA04	LLLH	3							4							21				25		
WA08	MTm	0									5				22	55	37		32	151		
TOTAL			17	335	73	13	89	1423	60	208	1933	167	1491	26	554	3369	171	92	975	10996		TOTAL
AVERAGE					1.24									10.26							7.61	AVERAGE

Cisne, Gildner, & Rabe, 1984; Springer & Bambach; 1985; Anstey, Rabbio, & Tuckey, 1987; Anstey & Rabbio, 1990; Patzkowsky, 1995). Results of these studies support the view (Warme & others, 1976) that such taphonomic factors as time averaging may enhance the expression of paleocommunity gradients relative to similar gradients in living communities.

Gradients across formations and members.—Sample- and species-ordination scores for Wreford fractional abundance data were calculated using the program DECORANA (Hill, 1979). An initial DCA analysis indicated that *Condranema parvula* was an outlier distorting gradient structure. Its score on axis 2 was 892, while scores for all other species ranged between 0 and 366. It was essentially behaving like *Filiramoporina kretaphilia* and *Polypora nodolinearis* in forming a dense monotypic accumulation. *C. parvula* was therefore removed, and DCA was computed again using 17 species and 85 sampling intervals, reducing the sample size to 10,996 colonies. Both species and samples (Tables 2 and 3, respectively) were reordered in Table 4 to match the arrangements produced by DCA. This diagram illustrates resulting gradational patterns more clearly than the individual sets of DCA scores. Figure 2 plots scores of each species on the first two DCA axes to illustrate graphically the associations of species.

Two groupings of species are apparent in Table 4 and Figure 2 and form opposite poles of an abundance gradient (most easily seen in Table 4 in the upper left to lower right). Species Group 1 contains only robust and encrusting colonial morphologies that include the single trepostome and all of the cystoporate bryozoans sampled from the Wreford. These include the robust trepostome *Tabulipora carbonaria;* two encrusting cystoporates, *Fistulipora carbonaria* and *Fistulipora incrustans;* and the upright, sheet-forming cystoporate *Meekopora prosseri. Protoretepora elliptica,* a robust fenestrate, also displays an affinity for the trepostome-cystoporate grouping (Fig. 2). Abundances range between 1 and 66 specimens per sample with an average abundance of only 1.24 specimens per sample. Species are not uniformly distributed; most have high DCA scores and occur at the end of the sample gradient.

Species Group 2 contains all of the remaining fenestrate and cryptostome bryozoans, nearly all of which have small or delicate growth forms. *Fenestella spinulosa, F. tenax, Minilya binodata,* and *Septopora spinulosa* are delicate fenestrates, whereas *Acanthocladia guadalupensis* is a small pinnate fenestrate, and *Penniretepora auernigiana, P. curvula,* and *P. flexistriata* are tiny pinnate fenestrate morphotypes. Both of the sampled cryptostomes, *Rhombopora lepidendroides* and *Syringoclemis wrefordensis,* also display delicate ramose growth habits. Finally, one questionable ctenostome, *Condranema magna,* exhibits an encrusting, threadlike growth form. Only the robust fenestrate *Polypora aestacella* deviates from this overall pattern of small and delicate morphologies, but it occurs sporadically in only 7 samples

and at low abundances (26 total specimens with 10 specimens in one sample). Species abundances in Group 2 range between 1 and 443 specimens per sample with a mean abundance of 10.26 specimens per sample. In contrast to Species Group 1, these species become more common as sample DCA scores decrease (Sample Group C in Table 4).

The ordination of samples (the sample gradient) was divided into three groupings (Table 4). The boundary of Sample Group A was placed between samples GE30LMSh and CH44MH, marking the last abundant occurrence of the trepostome and cystoporates of Species Group 1 (see Table 3 for explanation of sample codes). Sample Groups B and C were divided between samples ML01MTm and WA03Sp. This boundary is more arbitrary than the first but was located at a point where a trend of small decreases in sample scores was punctuated by a larger decrease in scores (from 125 to 112). Larger changes occur near the origin of DCA axis 1: a decrease of 16 units occurs between GE18Sp and LY13Sp; and a decrease of 34 units between MS22Sp and WA04LLLH. The first change, however, involves only three samples that contain the same species and have the same abundances as other samples in Sample Group C. The larger change of scores separates two samples, WA04LLLH and WA08MTm, that have only two and five species, respectively. They do not warrant designation as a fourth sample group and were also retained in Sample Group C.

Abundances of specimens vary between sample groups (not only across samples). Raw abundances for Group A range between 1 and 265 specimens with an average abundance of 6.47 specimens per sample (total of 374 possible collections of species within localities), between 1 and 77 specimens with a mean of 3.26 specimens per sample for Group B (663 samples), and between 1 and 443 specimens with an average of 15.72 specimens per sample for Group C (408 samples).

Combining the species and sample gradients illuminates several distributional and abundance patterns. First, representatives of Species Group 1, consisting of a trepostome, all Wreford cystoporates, and one robust fenestrate, occur abundantly only in Sample Group A where their average abundance is 4.24 specimens per sample. These species are virtually absent in the other two sample groups, where average abundances do not exceed 0.15 specimen per sample (in Species Group C). Fenestrates and cryptostomes of Species Group 2 occur even more abundantly within Sample Group A than do species of Group 1, having an average abundance of 7.41 specimens per sample. Of these, *Fenestella tenax, Rhombopora lepidodendroides, Acanthocladia guadalupensis,* and *Septopora spinulosa* are most abundant. These species continue to dominate Sample Group B, having an average abundance of 4.52 specimens per sample. Here, species from Group 1 are very sparsely distributed (average abundance < 0.01),
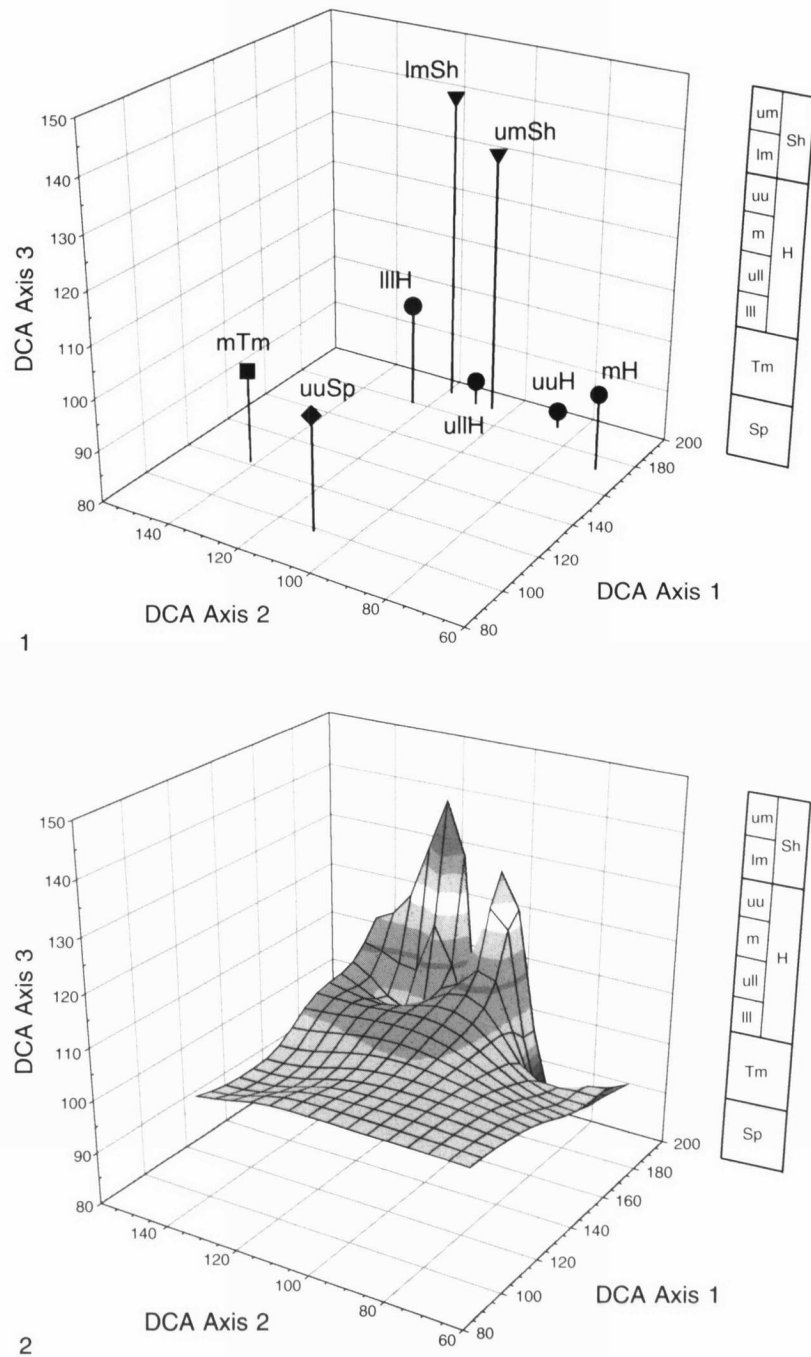
Figure 3. Three-dimensional plots of the mean positions of Wreford stratigraphic sampling intervals on the first three detrended correspondence analysis (DCA) axes. *1,* Raw means and *2,* 3-dimensional fitted surface illustrate a stratigraphic gradient that extends from the Speiser and Threemile (lower left) to Havensville (lower right) to Schroyer (upper right) sampling intervals. The schematic stratigraphic column indicates finer-scale subdivisions of the Havensville and Schroyer Members discussed in the text. DCA scores for each sample across axes are listed in Table 3; the distributions of samples and species on DCA axis 1 are listed in Table 4 (new).

which lowers the mean overall species abundance across samples to 3.26 specimens per sample. Sample Group C has the most abundant and diverse assemblage of fenestrates and cryptostomes. In addition to the dominant species of Groups A and B—*Fenestella tenax, Rhombopora lepidodendroides, Acanthocladia guadalupensis,* and *Septopora spinulosa*—

Group C has large numbers of *Fenestella spinulosa* and *Minilya binodata* along with three nearly ubiquitous species of *Penniretepora* that occurred more sporadically in the other two sample groups: *P. curvula, P. flexistriata,* and *P. auernigiana.* Considering only the portions of samples that include species of Group 2, mean abundance is 22.21

specimens per sample. If Species Group 1 is added (average = 0.15 specimen per sample), the average abundance across samples decreases to 15.72 specimens per sample.

In summary, these Wreford samples are dominated by fenestrates and cryptostomes. Cystoporates and a trepostome contribute, however, at one end of the gradient where DCA scores are high (on axis 1). More abundant and diverse fenestrates and cryptostomes occur at the other end of the gradient when DCA scores are low. A similar taxonomic dichotomy was noted in the Devonian Threeforks Formation (Prezbindowski & Anstey, 1978) and across Upper Ordovician bryozoan biomes or provinces (Anstey, 1986). In the latter, the Cincinnati biome was dominated by trepostomes and cystoporates and the Red River-Stony Mountain province by cryptostomes.

Species diversity shows this pattern well with some interesting caveats. Diversity indices have been interpreted as indicators of important aspects of community organization and structure including niche partitioning, trophic stability, and food chain length (see Pachut & Anstey, 1979, and references therein; Dodd & Stanton, 1990). The Brillouin diversity index (Pielou, 1974) was calculated for each sample and sample group. Unlike the more widely used Shannon-Weaver index, Brillouin's equation was developed to work with samples rather than with infinitely large populations. This and most other dominance diversity measures, however, confound species richness or number with evenness, a measure of the numerical distribution of species within a sample (Pielou, 1974); evenness is maximized (ranges between 0.0 and 1.0) when species have equal numbers of individuals (here, individuals = colonies or colony fragments).

For these Wreford samples, mean diversity and evenness are highest in Sample Group A (1.22 and 0.72, respectively) due to the presence of cystoporates and a trepostome and because the abundances of species are more uniform than in the other two groups. Sample Group B has the lowest diversity (1.05) but the second highest index of evenness (0.69). Although fewer species occur, abundances are similar across species. The mean diversity of samples from Sample Group C is only slightly lower (1.20) than that of Group A, but it is coupled with the lowest value of evenness (0.67). Diversity levels are maintained in spite of the rarity of species from Species Group 1 because species of fenestrates and cryptostomes of Species Group 2 reach their maximum diversity in Group C. Large numbers of approximately one-half of the species, however, create disparities in abundances within the assemblage that lower species evenness. Therefore, the single full assemblage of Cuffey and Hall (1985) has been subdivided based upon subtle, intergradational variations in species numbers and abundances, even within rocks of relatively uniform lithology.

Species assemblages occur across Kansas and do not appear to have been restricted to single time units or to specific formations or members of the Wreford Megacyclothem. This is not surprising because these fossiliferous samples are primarily from calcareous shales, all very similar lithologies that were apparently deposited under relatively similar environmental conditions across a very gentle onshore-offshore (south-to-north) depth gradient. The various species appear to have been responding to spatially patchy paleoenvironmental conditions that did not affect preservable characteristics of the accumulating sediments in different regions of the Wreford sea.

Stratigraphic gradients.—The mean location of each sampled stratigraphic interval on the first three DCA axes is plotted in Figure 3.1 (data in Table 2). Axis 1 arrays samples approximately in ascending stratigraphic order: Speiser, Threemile, Havensville, and Schroyer, with some overlap among samples of the latter two members. Overlap is removed by axis 3, which separates Schroyer samples from all others. This suggests the presence of a complex stratigraphic gradient extending from the Speiser and Threemile toward the Havensville and curving upward to the Speiser, represented by the fitted surface in Figure 3.2. As discussed above, the scarcity of trepostomes and cystoporates sets Speiser, and to a lesser extent, Threemile samples apart from all others. Differing abundances and diversity of fenestrates and cryptostomes differentiate between Havensville and Schroyer samples. Holdener (1997) studied morphologic patterns in populations of *Rectifenestella* sp. from the Wreford. Populations from the Speiser and, to a lesser extent, the Threemile were also distinct morphologically from those of other members. The lack of independent physical evidence preserved in the rocks, however, leaves the sources of these differences unresolvable.

Faunal composition of individual stratigraphic intervals.— Sample and species ordination scores were calculated separately for each of eight Wreford sampling intervals to evaluate possible stratigraphic differences in faunal composition. For each analysis, we omitted species that only occurred within a single sample and sample locations containing fewer than two co-occurring species. As before, both species and samples were reordered in data matrices (Table 5–12) to match the arrangements produced by DCA.

It is not surprising that fenestrates and cryptostomes dominate assemblages across sampling intervals. In fact, after removing single-species occurrences, the middle Threemile and middle Havensville contain no trepostomes or cystoporates at all; and two other intervals, the upper upper Speiser and upper lower lower Havensville, include only one trepostome species (*Tabulipora carbonaria*). The lower lower lower Havensville and upper middle Schroyer include *T. carbonaria* and a single species of *Fistulipora* each (*F. carbonaria* and *F. incrustans,* respectively). Only the upper upper Havensville and the lower middle Schroyer have more than two trepostome and cystoporate species.

Table 5. Distribution of species and sample intervals for the upper upper Speiser. Original abundances have been rearranged to correspond to the placement of species and samples by detrended correspondence analysis. Species occurring in fewer than two samples and samples containing fewer than two species were removed prior to the analysis. Scores = ordination values calculated by detrended correspondence analysis; Kansas county abbreviations listed in Table 3 (new).

Species	Score	ML03	ML01	GR01	GE18	CH18	LY01	PT02	PT09	WA03	CY14	PT15	CH56	GE21	RY04	CH32	CH16	LY13	CH39	CH04	WA08	CH33	MS22	Total
												upper upper Speiser												
Score		113	106	93	88	88	85	84	65	65	57	52	50	45	34	33	22	18	14	14	12	11	0	
F. tenax	272		157	21	19	6			7		1	24				26	17	4	26		6		20	334
S. urcefordensis	253	22	8	1	14	1			3			2			1	5	1		1			1	1	46
P. elliptica	181		4	1	2		1					2		1		2			1	1	1			13
C. magna	116		6	1	6		1				1			2	1			1	1		1		4	25
A. guadalupensis	106	223	443	56	294	11	179	24	94	24	6	161	32	7	10	97	155	242	74	68	202	48	269	2496
R. lepidodendroides	45	2	88	30	28	27	33	6	44	29	18	34	18	25	49	53	29	36	75	16	44	53	49	784
S. spinulosa	-9	11	55	20	49		14	3	12	1	4	28	1	3	2	14	14	27	20	10	32	6	63	377
P. flexistriata	-24		33		32				7							3	11	11	13	1	37	4	12	162
P. curvula	-35		11		11				1			9				5	5	5	13	1	3	8	2	67
T. carbonaria	-56				1							1												2
P. auernigiana	-68		11		17				4					3		1	1		11	1	2	2	31	83
M. binodata	-73		2	6	52	2			3			32	7	2	8	18	87	29	65	17	13	6	48	398
F. spinulosa	-92		37	1	156		7		15	2		24	5	2	5	97	79	171	72	62	185	52	327	1299
Total		258	855	137	681	47	235	33	190	56	30	317	63	43	76	321	388	533	371	177	526	181	826	6086

Table 6. Distribution of species and sample intervals for the Threemile. Original abundances have been rearranged to correspond to the placement of species and samples by detrended correspondence analysis. Species occurring in fewer than two samples and samples containing fewer than two species were removed prior to the analysis. Scores = ordination values calculated by detrended correspondence analysis; Kansas county abbreviations listed in Table 3 (new).

Species	Score	ML03	GE18	CH39	ML01	CH06	WA08	Total
				middle Threemile				
Score		155	134	111	93	60	0	
Syringoclemis urefordensis	310	1	5					5
Rhombopora lepidodendroides	138	5	61	20	33	14		133
Penniretepora curvula	88	1		2		2		6
Acanthocladia guadalupensis	71		18	2	1		22	43
Fenestella spinulosa	-41			3	11	12	55	81
Total		7	84	22	35	19	27	268

Table 7. Distribution of species and sample intervals for the lower lower lower Havensville. Original abundances have been rearranged to correspond to the placement of species and samples by detrended correspondence analysis (DCA). Species occurring in fewer than two samples and samples containing fewer than two species were removed prior to the analysis. Scores = ordination values calculated by DCA; county abbreviations listed in Table 3. Lower lower lower Havensville samples are generally arranged from south to north (ML03 to RY14, except for the last of these; new).

		lower lower lower Havensville						
Species	Score	ML03	PT09	LY08	CH52	GR01	RY14	Total
Score		253	138	96	87	80	0	
Fistulipora carbonaria	286	7	2					9
Tabulipora carbonaria	276	39	3		2	5		49
Syringoclemis wrefordensis	138	1	1	1		3		6
Condranema magna	134	1		1		2	1	5
Rhombopora lepidodendroides	105	6	3	31	9	77	13	139
Fenestella tenax	82		8			15	18	41
Acanthocladia guadalupensis	-20		1	3	5	20	34	63
Septopora spinulosa	-114					6	20	26
Total		54	18	36	16	128	86	338

Table 8. Distribution of species and sample intervals for the upper lower lower Havensville. Original abundances have been rearranged to correspond to the placement of species and samples by detrended correspondence analysis (DCA). Species occurring in fewer than two samples and samples containing fewer than two species were removed prior to the analysis. Scores = ordination values calculated by DCA; county abbreviations listed in Table 3 (new).

		upper lower lower Havensville							
Species	Score	GE18	RY14	GR01	BU04	WA04	CH22	CH24	Total
Score		192	160	150	130	63	1	0	
Tabulipora carbonaria	273	3	2	5					10
Syringoclemis wrefordensis	237	1		3	3				7
Condranema magna	231	2	1	2				1	6
Rhombopora lepidodendroides	192	9	12	77	21	6	19	6	150
Acanthocladia guadalupensis	97			20	4	16	24	18	82
Septopora spinulosa	72	3	1	6	3	11	25	6	55
Penniretepora curvula	24				3		8		11
Fenestella tenax	-36		3	15	6	14	147	41	226
Minilya binodata	-99						23	21	44
Total		0	3	10	3	0	0	1	23

Nonetheless, trepostome-cystoporate subgroups are not found because many samples contain only one to three specimens per species for these two taxa.

Sampling localities are generally arrayed geographically from south-to-north in the lower lower lower Havensville and upper middle Schroyer and from north-to-south in the lower middle Schroyer. Otherwise, DCA scores vary from one location to another across Kansas.

If not simply the result of small sample sizes, these compositional and distributional patterns may represent a paleontological example of the Gleasonian perspective on community ecology (see Roughgarden, 1989). In this model, communities are viewed as mere samples of a regional species pool that co-occur simply because they are capable of tolerating the existing environmental conditions (Jackson, Budd, & Pandolfi, 1996). It is possible that patchy habitats and Gleasonian sampling (i.e., random) of taxa combined to produce no clear-cut compositional distinctions and often no geographic patterns within individual sampling intervals of the Wreford.

Ecological gradients within stratigraphic intervals.—DCA scores of samples were used to evaluate the presence of geographic, onshore-offshore, bryozoan faunal gradients in the Wreford. Many ecological gradients are weakly developed and do not possess sharp discontinuities in species abundances (Cisne & Rabe, 1978). In such instances, results of gradient analysis will show these ecological continua more accurately than will divisive clustering algorithms that force samples into discrete cluster groups. To test for statistically significant ecological or geographic gradients, sample ordination scores were regressed (using SYSTAT; Wilkinson, 1990) on south-to-north (onshore-to-offshore)

Table 9. Distribution of species and sample intervals for the middle Havensville. Original abundances have been rearranged to correspond to the placement of species and samples by detrended correspondence analysis (DCA). Species occurring in fewer than two samples and samples containing fewer than two species were removed prior to the analysis. Scores = ordination values calculated by DCA; county abbreviations listed in Table 3 (new).

| Species | Score | middle Havensville | | | | | | | | |
		CH44	BU04	GR01	CH04	CH22	WA04	CH52	PT04	Total
Score		151	126	114	104	91	40	17	0	
Penniretepora curvula	232	12	5		1				2	20
Fenestella spinulosa	204		4		2					6
Syringoclemis wrefordensis	175	2	2	2	23			2		31
Rhombopora lepidendroides	173	8	22	10		11		10		61
Fenestella tenax	107	10		6	58	1	10	33		118
Septopora spinulosa	-18	1	7	5	15	6	2	71	7	114
Acanthocladia guadalupensis	-37	3	6			2	7	34	9	61
Minilya binodata	-64				2			6		8
Total		36	46	23	101	20	19	156	18	419

Table 10. Distribution of species and sample intervals for the upper upper Havensville. Original abundances have been rearranged to correspond to the placement of species and samples by detrended correspondence analysis (DCA). Species occurring in fewer than two samples and samples containing fewer than two species were removed prior to the analysis. Scores = ordination values calculated by DCA; county abbreviations listed in Table 3 (new).

| Species | Score | upper upper Havensville | | | | | | | | | |
		CH22	GE18	RY06	GR01	CH44	CH08	MS06	BU04	CH24	MS05	Total
Score		133	101	91	87	68	62	27	25	21	0	
Fenestella spinulosa	227	51	2				5	7		4	3	72
Condranema magna	204	2								2		4
Septopora spinulosa	177	29	28	3		14	11	62		15	6	168
Acanthocladia guadalupensis	144	26	35	3	32	18	21	91	19	16	22	283
Rhombopora lepidodendroides	68	17	6	3	37	12	13	40	20	68	8	224
Syringoclemis wrefordensis	18	1			10		10	6	2	4	4	37
Fenestella tenax	-23	22	18	3		26	30	265	12	56	84	516
Minilya binodata	-39		3			2		7		4	1	17
Tabulipora carbonaria	-59	9			1	2		46	23	50	26	157
Penniretepora curvula	-109		5					23	4		7	39
Fistulipora carbonaria	-132							4		2		6
Fistulipora incrustans	-171				1			6		8	7	22
Total		157	97	12	81	74	90	557	80	229	168	1545

distances of sampling localities from the Oklahoma-Kansas border (Cuffey, 1967; Pachut & Cuffey, 1991). This approach is analogous to the ones used to study the effects of environmental gradients on the evolution of Ordovician trilobites (Cisne & others, 1980; Cisne, Molenock, & Rabe, 1980). Significance values in Table 13 suggest that gradients were developed in five of the eight sampled Wreford units on either axis 1 or 2: upper upper Speiser, lower lower lower Havensville, middle Havensville, upper upper Havensville, and the lower middle Schroyer. The geographic development of ecological gradients in the calcareous shales in the middle Threemile, the upper lower lower Havensville Shale, and upper middle Schroyer lacks statistical support; small sample sizes (total of 19 sampling sites across the 3 intervals) and concentrations of sampling sites in relatively small geographic areas may have contrib-

uted to this. In addition, patchy environmental conditions in this shallow epicontinental sea throughout Wreford deposition could also account for variations in the development and strength of gradients. Gradients delineated in virtually all previous studies of other sequences have been much steeper, particularly those studied in the Taconic trench (Cisne & others, 1980; Cisne, Molenock, & Rabe, 1980; Cisne, Chandlee, & others, 1982; Cisne, Karig, & others, 1982), where depths may have reached 500 meters. In stark contrast, Wreford deposition has been estimated to have taken place in shallow waters having depths ranging between 10 or 15 m up to a maximum of only 35 m (Cuffey, 1967; Newton, 1971; Lutz-Garrihan & Cuffey, 1979). Another possible explanation of the variable development of bryozoan abundance gradients, operating independently or together with rather patchy environmental

Table 11. Distribution of species and sample intervals for the lower middle Schroyer. Original abundances have been rearranged to correspond to the placement of species and samples by detrended correspondence analysis (DCA). Species occurring in fewer than two samples and samples containing fewer than two species were removed prior to the analysis. Scores = ordination values calculated by DCA; county abbreviations listed in Table 3. Lower middle Schroyer samples are generally arranged from north to south (BU04 to RY04, but with some reversals; new).

Species	Score	lower middle Schroyer											Total
		BU04	MS21	CH52	CY09	CH56	GE30	GE18	WA05	PT16	GE01	RY04	
Score		181	129	98	88	82	61	55	48	15	1	0	
Polypora aestacella	282	6					10						16
Acanthocladia guadalupensis	260	13	3		2		24	4	1				47
Penniretepora flexistriata	250		1				1						2
Syringoclemis wrefordensis	181	1		2		1		1				1	6
Condranema magna	157	1					5	1		1			8
Fistulipora incrustans	139	2		1			15	6				1	25
Tabulipora carbonaria	89	3					18	7		5		1	34
Septopora spinulosa	88	7		10	4	1	97	7	3	9	3	1	142
Rhombopora lepidodendroides	79	6	3	6	1	6	166	16		3		3	210
Fenestella tenax	38		4			2	97	3	8	2	1		117
Meekopora prosseri	14						8	1					9
Fistulipora carbonaria	-4						1	1					2
Penniretepora curvula	-66						10	1			2		13
Protoretepora elliptica	-78				2		33	10	2	13	1		61
Minilya binodata	-81						44	6		2	1	9	62
Total		39	11	19	9	10	529	64	14	35	8	16	754

Table 12. Distribution of species and sample intervals for the upper middle Schroyer. Original abundances have been rearranged to correspond to the placement of species and samples by detrended correspondence analysis (DCA). Species occurring in fewer than two samples and samples containing fewer than two species were removed prior to the analysis. Scores = ordination values calculated by DCA; county abbreviations listed in Table 3; upper middle Schroyer samples are generally arranged from south to north (GE18 to GE04, except for the last of these; new).

Species	Score	upper middle Schroyer					Total
		GE18	GE30	CH45	BU04	GE04	
Score		139	98	81	52	0	
Rhombopora lepidodendroides	162	5	4	1	11	3	24
Acanthocladia guadalupensis	103			1	14	1	16
Fenestella tenax	83	2			7	11	20
Fistulipora incrustans	80				2	1	3
Septopora spinulosa	-20		1	1	25	32	59
Condranema magna	-28				1	1	2
Tabulipora carbonaria	-99		1		2	9	12
Total		7	6	3	62	58	136

conditions, is that the steepness of environmental gradients may have varied temporally. It is regrettable that gradient steepness may have varied in concert with biotic or abiotic environmental conditions that left no obvious signatures in these rocks. The geographic and stratigraphic patterns discussed above, however, mirror those studied by Pachut and Cuffey (1991) in *Tabulipora carbonaria* from three Wreford units: the lower and upper Havensville Shale and the middle Schroyer Member. In an analysis of clinal morphological variation, multivariate analyses delineated statistically significant differences in morphology between populations of *Tabulipora*, evidence for heterochronic modifications, and an increase in developmental canalization in

an onshore-offshore direction. Additionally, Holdener (1997) found that patterns of morphologic variation in populations of *Rectifenestella* sp. paralleled changes in equivalent characteristics of *Tabulipora carbonaria* examined by Pachut and Cuffey (1991). Nearly identical patterns occurred stratigraphically in this study of Wreford bryozoan species abundances after pooling data within each of the sampled units. These similarities among studies suggest that, in spite of difficulties in identifying specific environmental parameters responsible for establishing them, onshore-offshore ecologic gradients in the Wreford Megacyclothem existed and can be delineated by detrended correspondence analysis.

CONCLUSIONS

1. Detrended correspondence analysis (DCA) of the fractional abundances of bryozoan species from the Wreford Megacyclothem of Kansas permit the recognition of two species and three sample subgroups in the sampled calcareous shales. Subgroupings lack sharp compositional discontinuities and intergrade with one another.

2. The single, full species assemblage of Cuffey and Hall (1985) was partitioned by DCA into two assemblages based upon intergradational differences in the relative abundances of taxa across sampling sites. One assemblage includes moderate abundances of a trepostome and several cystoporates plus a single robust fenestrate, whereas the other generally lacks those species and includes abundant, mainly small fenestrates, cryptostomes, and a ctenostome.

3. No distinctive groupings of beds or lithologies were identified other than a cluster of samples collected mostly from the upper upper Speiser Shale, where trepostomes and cystoporates are nearly absent, and the monospecific assemblages containing either *Filiramoporina kretaphilia*, *Polypora nodolinearis*, or *Condranema parvula*. The three sample subgroups vary in relative species abundances, diversity, and evenness. This suggests environmental patchiness during the deposition of Wreford calcareous lithologies that, otherwise, appear to have been deposited under rather similar environmental conditions.

4. A general stratigraphic trend is indicated by a plot of the average position of each Wreford stratigraphic sampling interval on the first three DCA axes. Factors responsible for the establishment of this trend remain obscure.

5. Analyses of individual stratigraphic sampling intervals indicate similar biotic responses by bryozoan faunas throughout the deposition of Wreford sediments. Fenestrates and cryptostomes dominate, with only the upper upper Havensville and lower middle Schroyer displaying more than two species of trepostomes or cystoporates.

6. Significant geographic trends occurred in five of eight sampled stratigraphic intervals in spite of the shallowness of the onshore-offshore depth gradient across Kansas.

Table 13. Statistical significance of linear regressions of DCA scores for samples on onshore-offshore distances (south-to-north) across Kansas. DCA scores were calculated separately for each sampling interval. Sampled intervals are arranged in stratigraphic order with values representing the calculated level of significance for each regression; *N*, number of samples (new).

Sampling Interval	N	Axis 1	Axis 2
upper middle Schroyer	6	0.25	0.31
lower middle Schroyer	11	0.02**	0.99
upper upper Havensville	10	0.70	0.02**
middle Havensville	8	0.07*	0.28
upper lower lower Havensville	7	0.42	0.34
lower lower lower Havensville	6	0.27	0.05**
middle Threemile	6	0.62	0.59
upper upper Speiser	23	0.09*	0.05**

levels of significance noted by * at $p \leq 0.10$, ** at $p \leq 0.05$.

7. These stratigraphic and geographic abundance gradients parallel onshore-offshore clinal morphologic variation studied in *Tabulipora carbonaria* from the lower and upper Havensville Shale and middle Schroyer Member (Pachut & Cuffey, 1991) and in *Rectifenestella* sp. (Holdener, 1997). This strengthens our interpretation of the existence of an overall onshore-offshore gradient in the Wreford sea.

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