Molluscan and brachiopod dominated biofacies in the Platteville Formation (Middle Ordovician), upper Mississippi Valley

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The object of the present investigation was to prepare a map of a taxonomically diverse epeiric sea benthic marine biota in order to determine, in detail, the distribution of the benthic associations. The stratigraphic unit chosen for study was the Mifflin Member of the Platteville Formation (Middle Ordovician) as it outcrops over about 65,000 square km of the upper Mississippi Valley. The Mifflin is a lithologic unit that rarely exceeds six meters in thickness at any one local exposure, yet it is persistent and identifiable over a wide area. Eighty local exposures were sampled extensively for the benthic marine macroinvertebrates and over 100 species-level taxa were identified.

With the help of Q-mode factor analysis seven biofacies were delimited, and maps outlining the distribution of each biofacies were prepared by plotting the loadings of each locality on each of the seven factor axes and contouring the numerical values thus obtained. Five of the seven biofacies are geographically widespread and boundaries among the biofacies are overlapping and gradational. However, localities characterized by pelecypod and gastropod faunas tend to be concentrated along the eastern margins of the study area in south-central Wisconsin, whereas biofacies to the west are characterized by a variety of brachiopods, and bryozoans with ostracodes.

The overlapping of the various biofacies seems to have taken place at the scale of individual 3 to 5 cm carbonate layers, and there was no consistent stratigraphic pattern of biofacies that encompassed the entire Mifflin. However, we cannot point to what seems to have been an ecological separation of the benthic faunas, even within a single carbonate layer, as a case of obligatory biotic succession, although this does seem to be one of the more probable explanations.

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This is the fourth in a series of reports on the distribution and ecology of Middle and Upper Ordovician benthic marine macroinvertebrates from the upper Mississippi valley. Previous investigations by Bretsky and Bermingham (1970), Snyder and Bretsky (1971) and Bretsky and Bretsky (1975) dealt principally with the evolution and ecology of select species of mollusks and brachiopods. The present paper is a broader-based synecological report wherein we map biofacies in the Mifflin or 'middle' Member of the Platteville Formation (fig. 1) in Wisconsin, Iowa, Minnesota and Illinois, based on the distribution of the 35 most numerous Mifflin species. These initial analyses show that the distribution of a particular biofacies in the Mifflin was not haphazard over a collecting area of about 65,000 square km (25,000 square miles); rather, numerically dominant molluscan and brachiopod faunas formed fairly compact taxonomic associations in an environment interpreted as being shallow subtidal. Since this appears to be a normal marine carbonate environment inferred to have been within tropical latitudes, one might have anticipated that the groupings of associated species would have formed ''indistinct spatial associations'' (Stephenson et al. 1974) or have been ''generally large and ill-defined'' (Stephenson et al. 1970). However, we were encouraged by some results of these same investigators (see Stephenson & Williams 1971) who found that in studies where small scale area samples were collected well-defined spatial patterns were obtained. We were able to resolve a taxonomically diverse benthic biota into seven biofacies that are delimited with the help of Q-mode factor

<table>
<tr><th>SYSTEM</th><th>STAGE</th><th>FORMATION</th><th colspan="2">MEMBER</th></tr>
<tr><td rowspan="7">MIDDLE ORDOVICIAN</td><td>TRENTONIAN</td><td>DECORAH</td><td colspan="2">SPECHTS FERRY</td></tr>
<tr><td rowspan="5">BLACKRIVERAN</td><td rowspan="4">PLATTEVILLE</td><td colspan="2">QUIMBYS MILL</td></tr>
<tr><td rowspan="2">McGREGOR</td><td>MAGNOLIA</td></tr>
<tr><td>MIFFLIN</td></tr>
<tr><td colspan="2">PECATONICA</td></tr>
<tr><td>GLENWOOD</td><td colspan="2"></td></tr>
<tr><td>CHAZYAN</td><td>ST. PETER</td><td colspan="2"></td></tr>
</table>

Fig. 1. Generalized stratigraphic column for the Middle Ordovician in south-central and southwestern Wisconsin (modified slightly from Agnew et al. 1956). For details of stratigraphic nomenclature in eastern Iowa, southeastern Minnesota, and north-central Illinois, see Templeton & Willman (1963) and Sloan (1972).

analysis, demonstrating that at least one early Phanerozoic subtidal muddy level-bottom habitat, covering a broad region of epeiric sea, was inhabited by benthic invertebrates that formed some distinct spatial associations. Subsequent studies will examine in detail the probable levels of integrative structure within and among these taxonomic associations, although some speculations are included in the present paper.

Sampling the Middle Ordovician

Initial plans called for the detailed collection of bulk rock samples from each of the Middle Ordovician members comprising the Platteville, Decorah and Galena Formations from exposures only in southern Wisconsin in order to delimit and describe the local evolutionary changes in Middle Ordovician benthic macroinvertebrate epeiric sea communities (see fig. 1 for Platteville members in Wisconsin and Iowa). However, in studying the Platteville the Mifflin or 'middle' Member became the object of a more concentrated collecting effort as we expanded the study geographically away from Wisconsin and into Illinois, Iowa and Minnesota. In this manner we thought we could map the distribution of the benthic communities over a much broader expanse of a shallow subtidal epeiric sea, and determine how taxonomically, and, by inference, ecologically integrated these faunas may have been at any one instant in geologic time.

The location of our collecting area in the lead-zinc district of the upper Mississippi valley (fig. 2) has resulted in the lithostratigraphic setting of the various Middle Ordovician units having been previously explored in considerable detail (see esp. Agnew et al. 1956; Heyl, et al. 1959; Templeton & Willman 1963; Sloan 1972; Fraser 1976). The identification, and subsequent sampling, of the Mifflin Member of the Platteville Formation was facilitated at many local exposures because of its distinctive thin crinkly or wavy limestone and dolomite beds and thin shale partings.

Both micro- and macroinvertebrate fossils seem to indicate faunal equivalence of the Platteville with the Chaumont Formation of the Black River Group in New York State (Wilderness Stage of Fisher, 1962). For further details, the reader is referred to the biostratigraphic studies of Copper (1956) and Webers (1966).

Bedding thickness and the *general character* of the skeletal mud fabric vary little over the area. The average Mifflin carbonate rock is a skeletal wackestone (Dunham 1962), and the average thickness of the Mifflin Member at 41 localities where both its upper and its lower contact are exposed is 4.5 m (14.7 feet). There is no indication that any of the exposed Mifflin carbonates were deposited in supratidal or intertidal environments. Although dolomites are common in the Mifflin in portions of southern Wisconsin and near Minneapolis, Minnesota (Agnew et al. 1956; Sloan 1972), these all appear to have been derived diagenetically after burial from what were originally lime muds (Badiozamani 1972, 1973; fig. 3 herein). However, the thickness of the individual dolomite beds is significantly greater than that of the limestone beds (mean thickness of limestone beds at 44 localities = 3.20 cm, 90% confidence limits = 3.08 to 3.32 cm; mean thickness of dolomite beds at 28 localities = 4.70, 90% confidence limits = 4.73 to 5.03).

Bulk samples of the individual 3 to 5 cm thick carbonate layers were collected and, although many of the samples are stratigraphically localized within one meter vertical collecting intervals within the Mifflin, the present analysis is concerned principally with the geographic distributions of the numerically dominant faunas within the Mifflin as a whole. Herein we are *not* analyzing details of the microstratigraphic distributions of the fossils within the Mifflin Member nor within any one individual 3 to 5 cm carbonate layer, but we, of course, do have some speculations at the end of this study regarding such stratigraphic control on the geographic patterns.

Fossils were collected from over 80 localities (fig. 2), identified and tabulated in the laboratory. Identifications were made of specimens occurring on the top and bottom surfaces of the carbonate beds and of all specimens not imbedded within the matrix; numerous beds were slabbed and polished and identifications were made 'in section' also. Counts of the numbers of fossils ran into the hundreds of thousands; the taxonomic literature used as a guide to identifying the macroinvertebrates occurring on natural surfaces, on cut and polished slabs, and in thin section, has been outlined by Bretsky & Bretsky (1975) and need not be repeated here. These identifications and counts formed the basis for a quantitative recording of the locality-by-locality abundance of various elements of the fauna.

Table 1. Higher taxonomic level distribution of taxa identified from the Mifflin Member and its stratigraphic equivalents. Identifications are to the species level except for the Bryozoa (typically identified to genus) and the organisms in the Miscellany category.

Higher Taxon	No. of taxa included
Trilobita	16
Ostracoda	6
Coelenterata	2
Bryozoa	14
Brachiopoda	16
Gastropoda*	24
Pelecypoda	20
Echinodermata	2
Miscellany (includes conical tubes of unknown affinity; algae; sponges)	7
Total	107

*Includes some species that may belong to the Monoplacophora.

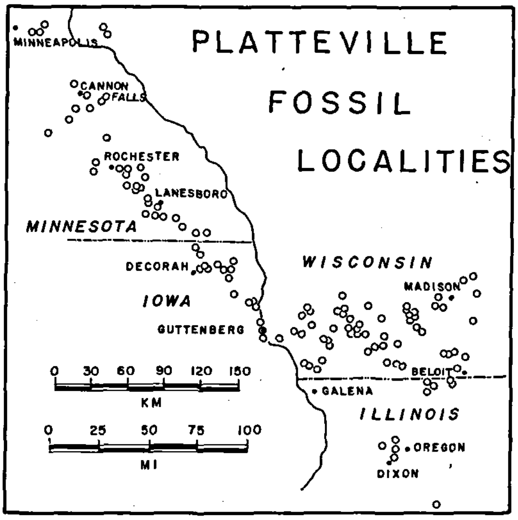

Fig. 2. Location (open circles) of fossiliferous Platteville exposures. About 80 of these sections unequivocally belong to the Mifflin or 'middle' Member of the Platteville Formation. Filled in circles show location of cities and towns mentioned in the text; for purposes of geographic interpretation, these symbols are repeated on each of the succeeding maps.

One hundred and seven taxa were identified in the ecological survey (table 1); details of identification and brief synonymies are available on request from the authors. Of these taxa, only 35 were sufficiently abundant (table 2; 'sufficiently abundant' arbitrarily defined as making up at least 2.5 % by number of the fauna at any one sampling locality) to be included in this initial biofacies analysis in which we decided to concentrate on the distribution of the most numerous benthic invertebrates.

In counting the fossils, whether on bedding planes or in polished section, care was taken to indicate whether a shell was broken or unbroken, and if broken, then whether it was clearly abraded or had undergone rather extensive fragmentation. Fragmentation of skeletal materials was much more pronounced in areas just to the west of the Mississippi River in eastern Iowa and southeastern Minnesota as compared to Illinois and Wisconsin (fig. 3), yet fragmented shell layers could be found at most localities. Complete individuals (i.e. the matching of pedicle and brachial, or left and right valves) of brachiopods

Table 2. Rank ordering by percentage abundance of the 35 most common species (those which constituted at least 2.5% by number of the biota at at least one locality) from the Mifflin Member and its stratigraphic equivalents. Numbers in parentheses are the species code numbers of table 5.

Species	% of Total Fauna
Pionodema conradi (4) (N. H. Winchell)	19.8
Protozyga 'nicolleti' (13) (Winchell & Schuchert)	13.0
Stictopora 'trentonensis' (11) (Ulrich)	10.4
Hesperorthis concava (2) Cooper	8.2
Oepikina minnesotensis (5) (N. H. Winchell)	6.0
Eoleperditia fabulites (14) (Conrad)	5.5
Hormotoma gracilis (1) (Hall)	5.0
Schmidtella 'crassimarginata' (18) Ulrich	4.7
Strophomena plattinensis (9) Fenton	3.9
Campylorthis deflecta (3) (Conrad)	2.7
Leperditella germana (14) (Ulrich)	2.3
Sinuites 'cancellatus' (28) (Hall)	2.2
Vanuxemia spp. (8)	2.2
Holopea spp. (27)	2.1
Lambeophyllum profundum (29) (Conrad)	1.8
Lophospira serrulata (6) (Salter)	1.3
Eurychilina subradiata (16) Ulrich	1.3
Amplexopora minnesotensis (24) (Ulrich)	1.2
Praenucula spp.? (10)	1.2
Skenidioides anthonensis (23) (Sardeson)	0.8
Ceraurus plattinensis (19) Foerste	0.8
Phragmolites triangularis (21) (Ulrich)	0.7
Ruedemannia lirata (26) (Ulrich & Scofield)	0.7
Primitella constricta (33) Ulrich	0.6
Rostricellula minnesotensis (7) (Sardeson)	0.5
Eridotrypa sp. (12)	0.4
Isotelus simplex (20) (Raymond & Narraway)	0.3
Trochonema spp. (30)	0.3
Diplotrypa spp. (31)	0.3
Krausella spp. (17)	0.3
Similodonta sp. (25)	0.2
Escharopora sp. (32)	0.2
Bucanella sp. (22)	0.1
Clathrospira spp. (34)	0.1
Ophiletina sublaxa (35) Ulrich	0.1

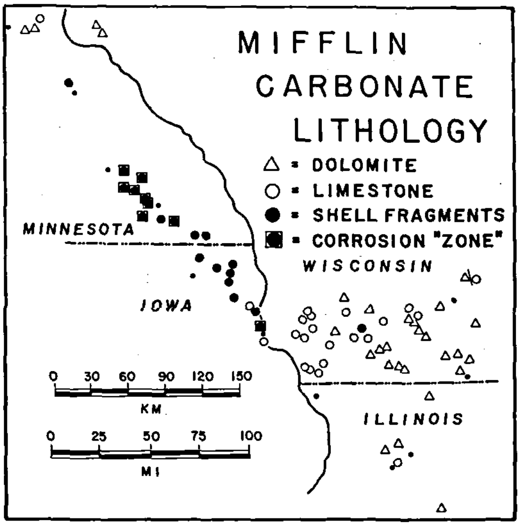

Fig. 3. Locations of and predominant lithologies at the 80 localities from which faunal data have been used in the quantitative analysis. Predominantly limestone sections are indicated by circles, and those which are predominantly dolomite by triangles. Filled-in circles correspond to localities where more then 50% of the total number of skeletal particles were fragmented (limestones only, as fragmentation never exceeded 50% in the dolomites). Filled-in circles enclosed in squares indicate localities (occurring only for sections of highly fragmental limestones) where corrosion 'zones' were observed.

and pelecypods were counted as one specimen, and where one valve outnumbered the other the larger count was recorded. Individual ramose bryozoan stems 1 cm in length or greater were also counted as one. Pelmatozoans, which tended throughout to be extremely disarticulated, were excluded from the statistical analysis. To compensate for the possibility that individual trilobites and ostracodes might be represented in our samples by more than one molt stage, we restricted counts of these within any one sample to a specific size range. This size range varied according to the sample, but we chose that size in each sample that contained the greatest number of individual specimens. In counting disarticulated trilobite specimens, we indicated total abundance by the number of individual pygidia or cephala, whichever was greater. No attempt was made to take into account the differences in size of the various taxa, nor to quantify any articulation/disarticulation ratio for the shells of the bivalved taxa.

Analysis of the Data

Sample sizes varied widely among the localities, and these shell beds, as with many other collections of fossils, represent accumulations of once living animals over variable and typically unknown periods of ecological time (i.e. tens to hundred of years). The use of raw data on absolute numbers of specimens per sample locality would, we believe, be misleading in biological and ecological interpretations. We thus developed a coding for relative abundance. This, while permitting finer distinctions than the traditional 'abundant – common – present – rare' breakdown, remains reasonably consistent with the level of accuracy of identification and counting which is feasible given the nature of fossil materials (see esp. Peterson 1976 and Warme et al. 1976 for recent studies of the ecological significance of 'numbers' in dead versus living populations of marine invertebrates and for a review of the earlier literature).

From the original counts of numbers of individuals of each species from a given locality, we calculated the abundance of each species as a percentage of the total fauna, rounded this figure off to the nearest five percent, and divided the rounded figure by five to yield a species abundance code. (Table 3 illustrates this procedure for the fauna from Locality 1; data on abundance at all localities are available on request from the authors.) This coding has, admittedly, the disadvantage that species making up less than 2.5 percent of the fauna at any locality are treated in the same way as species totally absent; on the other hand, it eliminates the constraint that the species percentages from each locality add up to a fixed sum. In addition, in this initial study we believe that the grouping of abundance values into relative abundance classes represents a sensible compromise between qualitative precision in the definition of the biofacies and the inherent biological and ecological limitations of the fossil materials (see esp. the incisive study by Stanton, 1976, who points up the potential of grossly inaccurate ecological interpretations of 'community structure' from samples of fossil remains; although, as he stresses, the boundaries and distribution of fossil communities can correspond with those of biocoenoses).

Eighty localities yielded usable samples and 35 species occurred at an abundance of "1" in at least one locality (table 2). To process the resulting species abundance matrix we employed the factor analysis program of the BMDP program package (Dixon 1975). Because faunas are highly likely to have been intergradational both within and among localities, we believed it worthwhile to examine the distribution of species through factor analysis, which permits a more flexible ordination of sites or species than the rigid classification of cluster analysis, wherein each species or locality is uniquely assigned to a single cluster. (See Imbrie & Kipp 1971 and Maynard 1976 for detailed examples, with full theoretical discussions, of the use of factor analysis in ecological studies).

The BMDP factor analysis program employed in this study provides a number of options for factor analysis and for rotation of factor axes. In both the Q-mode (similarities among localities) and R-mode (similarities among species) analyses, we extracted the principal components of the matrix of correlations, and performed a varimax rotation of these axes. The most useful results for mapping were obtained from the Q-mode analysis, which will form the basis for the following discussion. The BMDP program, which is basically oriented toward R-mode investigations, could not handle matrices in which the number of variables (80 localities) exceeded the number of cases (35 species). The minimum number of rows or columns in the original data matrix determines the maximum possible num-

Table 3. Illustrative example of the method used to code for species abundances (see text). The locality is New Glarus, Wisconsin (locality 1 of table 4), about halfway between Madison and Beloit (fig. 2).

Species	% of Total Fauna	Rounded %	Abundance Code
Hormotoma gracilis	28.8	30	6
Hesperorthis concava	21.3	20	4
Campylorthis deflecta	8.9	10	2
Pionodema conradi	8.6	10	2
Oepikina minnesotensis	7.2	5	1
Lophospira serrulata	4.1	5	1
Rostricellula minnesotensis	3.8	5	1
Vanuxemia spp.	3.1	5	1
Strophomena plattinensis	3.0	5	1
Praenucula spp?	2.8	5	1

Table 4. Factor loading matrix for the subset of localities discussed in the text, arranged so that the columns appear in decreasing order of variance explained by factors (rotated principal component axes). The rows (localities) are arranged so that for each successive factor, loadings greater than .500 appear first. Loadings less than .250 in absolute magnitude were replaced by zeroes (see text).

Locality	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7
308	.958	.000	.000	.000	.000	.000	.000
224	.954	.000	.000	.000	.000	.000	.000
225	.944	.000	.000	.000	.000	.000	.000
4	.912	.000	.000	.000	.290	.000	.000
231	.894	.000	.000	.000	.000	.000	.000
3	.893	.000	.000	.000	.000	.000	.000
14	.883	.000	.330	.000	.000	.000	.000
221	.854	.000	.294	.000	.000	.254	.000
54	.851	.000	.000	.000	.000	.000	.000
76	.773	.000	.500	.000	.277	.000	.000
2	.674	.000	.333	−.252	.313	.327	.000
64	.536	.000	.000	.000	.748	.000	.000
213	.504	.000	.000	−.260	.601	.354	.000
202	.000	.933	.000	.000	.000	.000	.000
66	.000	.904	.000	.000	.000	.000	.000
39	.000	.815	.000	.000	.000	.000	.000
1	.000	.800	.332	.000	.000	.000	.000
314	.347	.540	.000	−.275	.000	.628	.000
78	.306	.000	.843	.000	.000	.000	.000
307	.000	.348	.799	.000	.000	.000	.000
17	.000	.000	.782	.562	.000	.000	.000
73	.000	.000	.000	.875	.000	.000	.000
58	.000	.000	.440	.866	.000	.000	.000
61	.000	.000	.000	.751	.000	.000	.000
8	.000	.000	.000	.000	.969	.000	.000
63	.000	.000	.000	.000	.925	.000	.000
44	.000	.000	.000	.000	.000	.886	.000
227	.000	.000	−.281	.376	.000	.649	.000
40	.000	.000	.000	.413	.000	.604	.000
50	.000	.000	.000	.000	.000	.000	.822
301	.000	.000	.000	.000	.000	.000	.800
Eigenvalue	9.361	3.625	3.237	3.215	3.138	2.434	1.438

ber of independent dimensions of variation (cf. Jöreskog et al. 1976). Hence, for factor analysis involving correlations among localities, we chose six different subsets of 31 localities each and used an option provided by BMDP to select these localities from the full data matrix of 35 species and 80 localities. The criteria for choice of localities were such that the entire geographic extent of the sampling area was represented in each subset; each locality was included in at least two subsets; and if adjacent localities showed identical coded species abundances, only one of these was included in any given subset.

Table 4 is an example of a factor loading matrix (after varimax rotation) for one of the six subsets, using the first *seven* factors (principal component axes) extracted. The magnitude of each loading indicates the importance of each species assemblage (axis) at each locality. For example locality 308 is strongly dominated by the assemblage corresponding to Axis 1. To emphasize the main features of the pattern of factor loadings, we have employed an output option of the BMDP program that replaces loadings less than 0.250 (an arbitrary cutoff point) in absolute values by zeros. Thus the representation of all other assemblages at Locality 308 is regarded as of negligible importance.

The matrix of factor scores (table 5) gives us the species composition of each axis; that is, those species having high positive factor scores on a certain axis are the ones which characterize the assemblage corresponding to that axis. The results of the six replications of the factor analysis, being quite consistent in terms of the composition of the principal assemblages, provided a good test of the biofacies patterns. This result emphasized the high level of redundancy in the sampling grid. From run to run, however, there were small differences in the percentage of varia-

Table 5. Factor scores on each of the seven axes of Table 4 for each of the 35 species of table 2.

Species	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7
1	–.556	5.093	–.284	–.876	.298	.800	–.042
2	.141	.899	4.875	1.148	–.355	–.980	.003
3	–.303	–.117	.034	1.211	–.164	.036	–.538
4	5.316	.609	–.985	.026	–.177	–.436	–.036
5	–.007	.063	–.291	4.462	.098	.955	.166
6	–.297	.037	–.647	.319	–.301	.746	–.092
7	–.355	–.187	.047	–.304	–.236	–.393	–.382
8	–.497	–.187	–.884	.385	–.448	4.051	–.450
9	.038	–.156	.129	1.843	–.098	–.411	–.412
10	–.483	–.233	.072	–.251	–.286	.882	–.648
11	1.111	–1.028	2.377	–1.889	1.709	2.989	.775
12	–.321	–.416	–.002	–.517	–.102	–.178	–.280
13	–.209	–.162	–.667	.481	5.322	–.970	–.314
14	1.030	–.255	.060	.315	–.764	.365	.389
15	–.407	–.044	–.726	.233	–.141	–.209	4.703
16	.112	–.432	–.043	–.387	–.298	–.393	–.353
17	–.283	–.402	.013	–.518	–.189	–.245	.037
18	.615	–.269	–.269	–.311	–.592	–.548	.206
19	–.083	–.402	–.129	–.418	–.328	–.339	–.409
20	–.064	–.356	–.213	–.345	–.349	–.426	–.406
21	–.255	–.313	–.200	–.355	–.195	–.427	–.366
22	–.359	–.331	–.159	–.362	–.058	–.353	–.346
23	–.243	–.210	–.103	–.258	.159	–.520	–.096
24	–.035	–.533	.502	–.376	–.324	–.353	–.499
25	–.328	–.326	–.168	–.372	–.225	–.365	–.352
26	–.369	–.206	–.144	–.446	–.229	–.142	–.408
27	–.366	1.848	–.358	–.283	–.176	–.693	–.158
28	–.224	–.034	–.251	–.386	–.288	–.429	–.342
29	–.206	–.099	–.515	.168	.111	.011	–.367
30	–.307	–.334	–.291	–.225	–.254	–.123	–.375
31	–.252	–.314	–.203	–.354	–.247	–.412	–.371
32	–.328	–.326	–.168	–.372	–.225	–.365	–.352
33	–.577	–.251	.068	–.364	–.190	–.579	2.739
34	–.321	–.299	–.306	–.249	–.235	–.179	–.272
35	–.328	–.326	–.168	–.372	–.225	–.365	–.352

tion explained by individual axes, and therefore in the rank ordering of the axes from subset to subset. In subsequent discussion, therefore, we shall often identify a particular axis by a name or names of its characteristic species rather than by a number.

Results of the Factor Analyses

In fig. 4 we present the results of plotting the loadings of each locality on the first seven factor axes and contouring the numerical values thus obtained. For the sake of clarity, only the contour intervals of the highest magnitude are included in this initial plot. Fig. 5–8 add further detail, only on the contouring of Axes 1 (*Pionodema – Schmidtella*), 2 (*Hormotoma – Sinuites*), 4 (*Oepikina – Strophomena*), and 6 (*Vanuxemia – Lophospira*). Axis 5 (*Protozyga*) is well enough outlined on fig. 4, and Axes 3 (*Hesperorthis*) and 7 (*Schmidtella – Leperditella*) are of much more limited geographic extent than the other five. Contouring the factor loadings (table 4) for each axis was relatively easy, for the areas of highest loadings on a particular factor axis tend to be geographically contiguous. Thus we can view the taxonomic associations defined by the matrix of factor scores (table 5) as *biofacies*. Herein we assume no ecological integration of the associated faunas; they are purely taxonomic associations (table 6) that exhibit mappable biofacies patterns throughout the upper Mississippi Valley during some portion of the Middle Ordovician.

Again in summary, five of the biofacies (characteristic species for the axes of table 4 are listed in table 6) are geographically widespread; that is, *Pionodema – Schmidtella* (Axis 1, fig. 5),

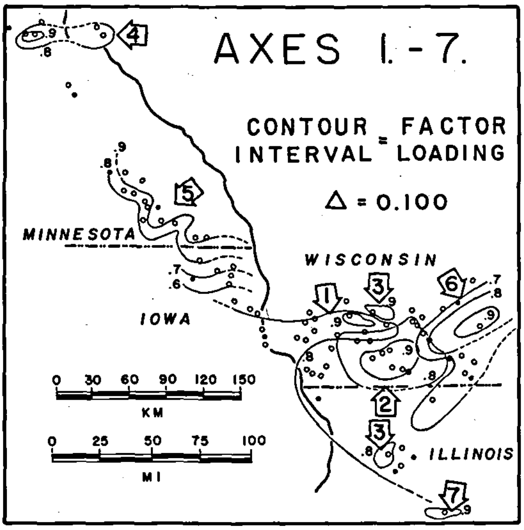

Fig. 4. Summary contour map indicating areas of maximum factor loadings for each of the seven most important factor axes. Numbers within arrows correspond to axes of table 4 (see also text). Contour interval indicates a difference in magnitude of factor loadings of 0.100.

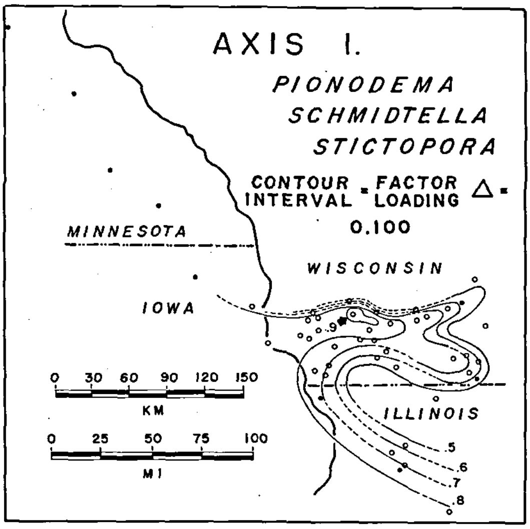

Fig. 5. Contour map of factor loadings for the axis corresponding to the Pionodema-Schmidtella *fauna (Axis 1 of table 4). Table 6 lists diagnostic taxa of this and other major faunas. Compared to plot of Axis 1 in fig. 4, more detail is given herein on the occurrence of localities having lower loadings on this axis. Localities whose loadings are less than the arbitrary cut-off point of 0.250 on this axis are not plotted; a similar convention applies for all subsequent contour maps.*

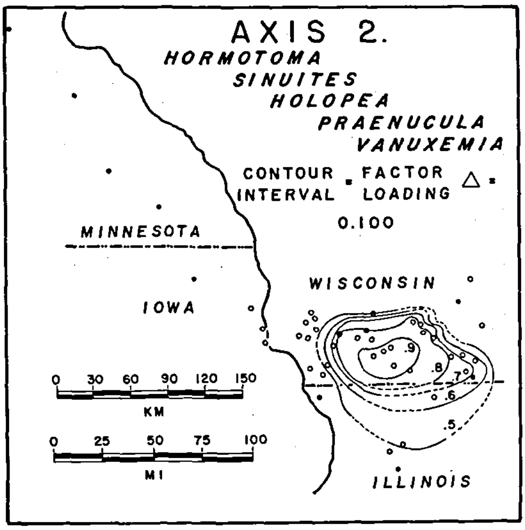

Fig. 6. Contour map of factor loadings for the axis corresponding to the Hormotoma-Sinuites *fauna (Axis 2 of table 4).*

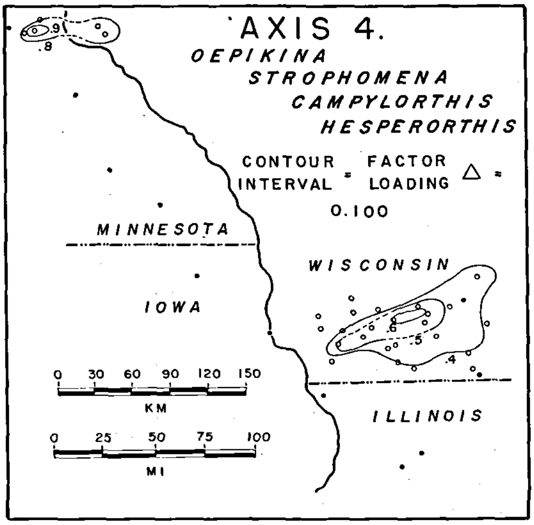

Fig. 7. Contour map of factor loadings for the axis corresponding to the Oepikina-Strophomena *fauna (Axis 4 of table 4).*

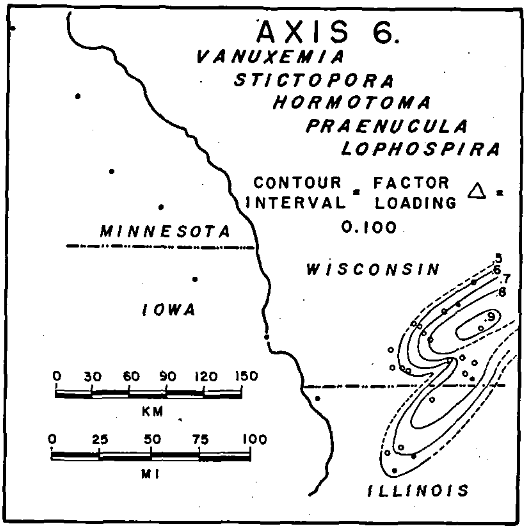

Fig. 8. Contour map of factor loadings for the axis corresponding to the Vanuxemia-Lophospira *fauna (Axis 6 of table 4).*

Hormotoma – Sinuites (Axis 2, fig. 6), *Oepikina – Strophomena* (Axis 4, fig. 7), *Protozyga* (Axis 5, fig. 4), and *Vanuxemia – Lophospira* (Axis 6, fig. 8). The other two biofacies, *Hesperorthis* (Axis 3, fig. 4) and *Schmidtella – Leperditella* (Axis 7, fig. 4), are much more restricted geographically.

Localities characterized by gastropod and pelecypod faunas are concentrated along the eastern margin of the study area. These are the faunas of Axis 6 (fig. 8), characterized by the cyrtodontoid pelecypod *Vanuxemia* spp. (fig. 9-N), the palaeotaxodont pelecypod *Praenucula* spp. and the pleurotomariacean gastropod *Lophospira serrulata* (*sensu lato*) (fig. 9-K, O); and of Axis 2 (fig. 6), containing some of the same molluscan species but dominated by the murchisoniacean gastropod *Hormotoma gracilis* (fig. 9-J), the bellerophontacean gastropod *Sinuites 'cancellatus'* (fig. 9-L) and the platyceratacean gastropod *Holopea* spp. Moving to the west and south of south-central Wisconsin, the faunal composition of the benthos gradually shifts towards domination by brachiopods, ostracodes and bryozoans. The *Pionodema – Schmidtella* biofacies of Axis 1 (fig. 5) is typically composed of the orthid brachiopod *Pionodema conradi* (*sensu lato*) (fig. 9-H), the ostracode *Schmidtella 'crassimarginata'* and the cryptostome bryozoan *Stictopora 'trentonensis'* (fig. 9-M). All are represented on other axes, but not elsewhere in this unique combination. Isolated patches of the Axis 3 fauna, typically dominated by the orthid brachiopod *Hesperorthis concava* (fig. 9-F, I), are found at the margins of the *Pionodema – Schmidtella* biofaces (fig. 4). They also occur at the most southerly exposure of the Mifflin Member where a fauna almost totally dominated by ostracodes, the *Schmidtella – Leperditella* biofacies (Axis 7, fig. 4) is recorded.

Farther to the west of the Mississippi River and at the western margins of the study area, the benthos was composed almost exclusively of low-diversity articulate brachiopod faunas. The fauna occupying much of eastern Iowa and southeastern Minnesota was dominated by the atrypid brachiopod *Protozyga 'nicolleti'* (fig. 9-G) (Axis 5, fig. 4), whereas further to the north near Minnespolis the strophomenoid brachiopods *Oepikina minnesotensis* (fig. 9-D, E) and *Strophomena plattinensis* (fig. 9-G) have high loadings on the fourth axis (fig. 7). The *Oepikina – Strophomena* biofacies is unique among the seven associations in that there appears to be a second non-contiguous concentration of these faunas in south-central Wisconsin, as indicated by the factor loadings on Axis 4 in this more southerly region which, however, are considerably lower than those recorded for the Minneapolis localities.

After this brief description of the geographic display of the seven biofacies and their general faunal content (table 6), we can explore the more probable ecological settings as defined by these biofacies, keeping always in mind that we shall be discussing only those numerically dominant members of the benthos. Hence, this discussion will incorporate all those biases inherent in dealing only with the numerical dominants. Subsequent reports will attempt to integrate the numerically less significant trilobites and trepostomatous bryozoans into the present biofacies scheme in order to develop a more complete picture of the benthic ecology of this shallow, subtidal epeiric sea.

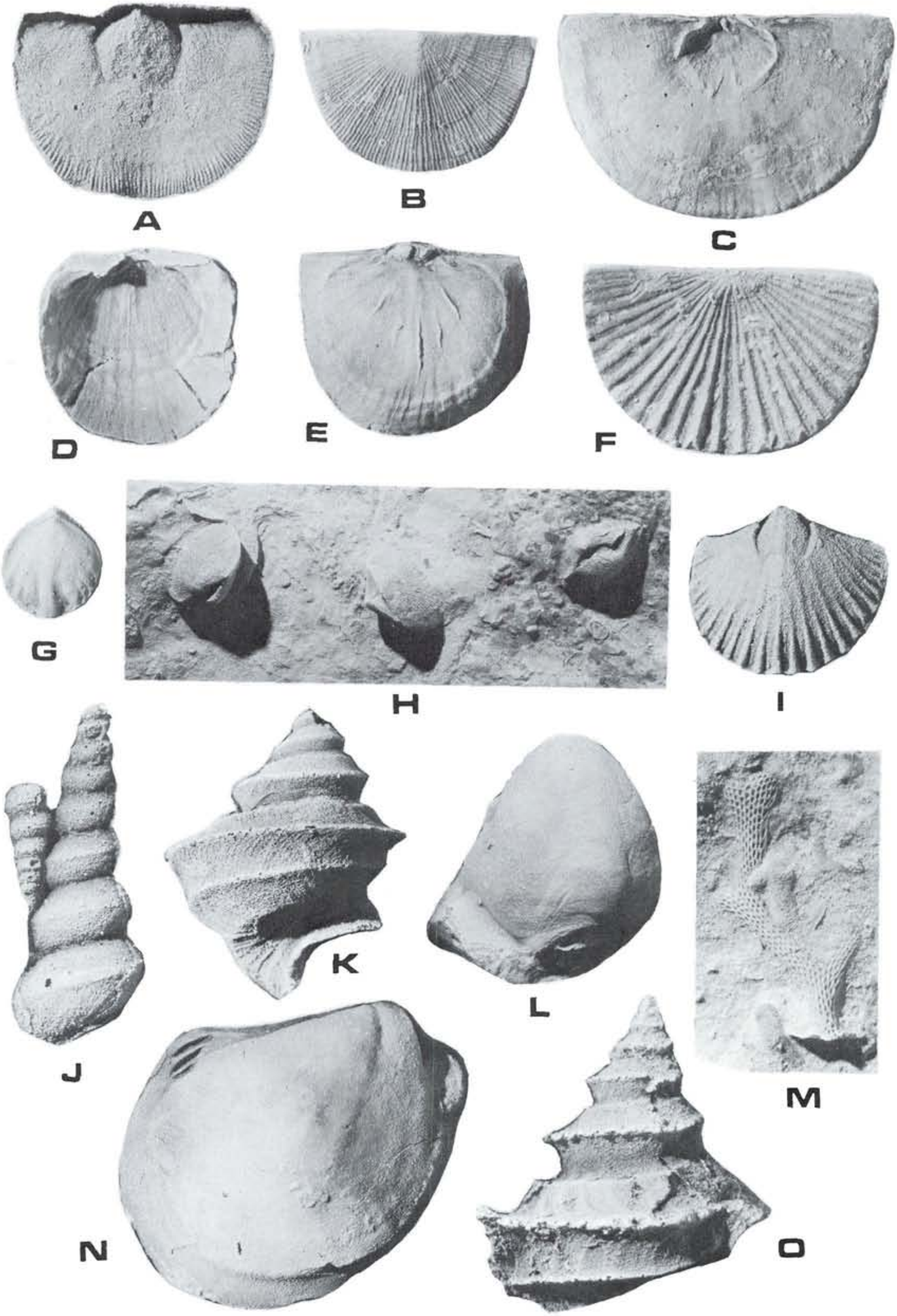
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Table 6. Species, in rank order by magnitude of factor scores, which have factor scores greater than 1.0 on a particular axis. The numbering of the axes corresponds to the order of table 4, but the ranking of species on an axis is based on an averaging over all six replications of the Q-mode analysis. For each axis, the relative positions based on factor scores of the first two species listed were consistent for all six replications, but slight differences existed from replication to replication in the ranking of the other species listed.

AXIS 1.	*Pionodema conradi* (Brachiopoda)
	Schmidtella 'crassimarginata' (Ostracoda)
	Stictopora 'trentonensis' (Bryozoa)
AXIS 2.	*Hormotoma gracilis* (Gastropoda)
	Sinuites 'cancellatus' (Gastropoda)
	Holopea spp. (Gastropoda)
	Praenucula spp? (Pelecypoda)
	Vanuxemia spp. (Pelecypoda)
	Pionodema conradi (Brachiopoda)
	Campylorthis deflecta (Brachiopoda)
AXIS 3.	*Hesperorthis concava* (Brachiopoda)
	Stictopora 'trentonensis' (Bryozoa)
	Hormotoma gracilis (Gastropoda)
	Skenidioides anthonensis (Brachiopoda)
AXIS 4.	*Oepikina minnesotensis* (Brachiopoda)
	Strophomena plattinensis (Brachiopoda)
	Campylorthis deflecta (Brachiopoda)
	Hesperorthis concava (Brachiopoda)
AXIS 5.	*Protozyga 'nicolleti'* (Brachiopoda)
	Stictopora 'trentonensis' (Bryozoa)
AXIS 6.	*Vanuxemia* spp. (Pelecypoda)
	Stictopora 'trentonensis' (Bryozoa)
	Hormotoma gracilis (Gastropoda)
	Praenucula spp? (Pelecypoda)
	Lophospira serrulata (Gastropoda)
AXIS 7.	*Schmidtella 'crassimarginata'* (Ostracoda)
	Leperditella germana (Ostracoda)
	Primitella constricta (Ostracoda)
	Stictopora 'trentonensis' (Bryozoa)
	Eoleperditia fabulites (Ostracoda)

Ecological Interpretations of the Biofacies

The Eastern Molluscan-Dominated Biofacies

The pelecypod constituents of the molluscan faunas that dominated the eastern portions of the study area (*Vanuxemia – Lophospira* biofacies, Axis 6, fig. 8) were predominantly shallow infaunal or semi-infaunal in life habit. We can infer this for the pelecypods both from analogies with their modern taxonomic or morphological counterparts, and from observations of numerous specimens preserved in what appears to have been life position. In the former case we refer specifically to the palaeotaxodont, and presumed protobranchiate pelecypod *Praenucula* spp?; in modern waters nuculoid pelecypods are mobile shallow infaunal deposit feeders. In the latter instance (i.e. semi-infaunal), the larger-size *Vanuxemia* spp. (fig. 9-N) appears to be preserved time and again as a member of the shallow infauna, and was presumably a suspension feeder (see also Pojeta 1971 for reconstruction of life habits of close relatives of *Vanuxemia* from fossil materials preserved in situ).

Interpretations of the life habits of the gastropods characterizing the *Vanuxemia – Lophospira* biofacies are tenuous, but the pleurotomariacean gastropod *Lophospira serrulata (sensu lato)* (fig. 9-K, O), by direct analogy to modern pleurotomariids, was probably an archaeogastropod. As such it may have been restricted to detritus feeding or perhaps suspension feeding very near or at the surface of a substratum that experienced only limited turbidity; a high con-

Fig. 9. A representative sampling of some of the more common benthic marine invertebrates to be found in the Mifflin Member of the Platteville Formation.

A. Campylorthis deflecta *(Conrad), pedicle valve internal mold natural, × 2,0, SUSB 385003, locality 1 (New Glarus, Wisconsin). B.* Campylorthis deflecta *(Conrad), brachial valve external, × 2.0, SUSB 385004, locality 213 (Adeline, Illinois). C.* Strophomena plattinensis *Fenton, pedicle valve internal, × 1.5, SUSB 400047, locality 52 (Ellenboro, Wisconsin). D.* Oepikina minnesotensis *(N. H. Winchell), pedicle valve internal, × 2.0, SUSB 400048, locality 14 (Fennimore, Wisconsin). E.* Oepikina minnesotensis *(N. H. Winchell), brachial valve internal, × 2.0, SUSB 400049, locality 69 (Mineral Point, Wisconsin). F.* Hesperorthis concava, *Cooper, brachial valve external, × 4.0, SUSB 385005, locality 2 (Potosi, Wisconsin). G.* Protozyga 'nicoletti' *(Winchell and Scuchert), articulated valves, × 4.0, SUSB 430015, locality 63 (Chatfield, Minnesota). H.* Pionodema conradi *(N. H. Winchell), in situ specimens preserved on upper surface of limestone bed, × 2.0, SUSB 385007 (left), 385008 (middle), 385009 (right), locality 15 (Mt. Ida, Wisconsin). I.* Hesperorthis concava *Cooper, pedicle valve internal mold natural (articulated specimen), × 2.0, SUSB 385006, locality 1 (New Glarus, Wisconsin). J.* Hormotoma gracilis *(Hall), latex impression of external mold, × 4.0, SUSB 507047 (left), 507048 (right), locality 202 (Darlington, Wisconsin). K.* Lophospira serrulata *(Salter), latex impression of external mold, × 2.0, SUSB 507049, locality 40 (Madison, Wisconsin). L.* Sinuites 'cancellatus' *(Hall), oblique anterior view showing broad sinus, × 2.0, SUSB 505009, locality 2 (Potosi, Wisconsin). M.* Stictopora "trentonensis" *(Ulrich), external view showing width and branching pattern of the zoarium, × 4.0, SUSB 330014, locality 14 (Fennimore, Wisconsin). N.* Vanuxemia *sp., internal mold natural, right valve, × 1.5, SUSB 525032, locality 219 (Mt. Horeb, Wisconsin). O.* Lophospira serrulata *(Salter). latex impression of external mold, × 4.0, SUSB 507050, locality 32 (Skinner Creek, Green County, Wisconsin).*

centration of clay-size particles tends to clog the delicate gill structures of archaeogastropods (Yonge 1947). The higher spired murchisoniacean gastropod *Hormotoma gracilis* (fig. 9-J) which appears in the *Vanuxemia – Lophospira* biofacies but is the dominant member of the adjacent *Hormotoma – Sinuites* biofacies (Axis 2, fig. 6), may also have been a detritus feeder. These organisms may have been caenogastropods rather than archaeogastropods, and hence may have possessed gill structures that were more tolerant to suspensions of fine-grained sediment. In conjunction with the high-spired shell form, this assignment to the caenogastropods permits one a bit more latitude in assigning the murchisoniaceans to a shallow infaunal life habit. In neither instance, however, are life habits assigned to the pleurotomariaceans or the murchisoniaceans without trepidation.

The epifaunal suspension-feeding life habit seems to have been dominated by the delicate, branching cryptostome bryozoan *Stictopora 'trentonensis'* (fig. 9-M). There were, of course, other less numerous benthic invertebrates that inhabitated these waters, indeed there was a most diverse gastropod and pelecypod fauna with lesser numbers of brachiopods and ostracodes. However, we wish at present to summarize our ecological interpretations of the biofacies based *only* on those data resulting from the foregoing analysis. In summary, the eastern margin of the study area exhibits a broadly diverse association of life habits; however, taxonomically, the mollusks are clearly the numerically dominant members of this portion of a shallow epeiric sea.

Moving slightly to the west of the Madison-Beloit area (fig. 2), the molluscan composition of the benthos begins to undergo a gradual change from a biofacies characterized by the cyrtodontoid pelecypod *Vanuxemia* spp. (fig. 9-N) to one characterized by higher concentrations of the murchisoniacean gastropod *Hormotoma gracilis* (fig. 9-J). The taxonomic change is accompanied by a significant increase in the numbers of the platyceratacean gastropod *Holopea* spp. (the *Hormotoma – Sinuites* biofacies; Axis 2, figs 4 & 6). The faunas of the *Vanuxemia – Lophospira* biofacies are most certainly not abruptly terminated but grade very gradually into the *Hormotoma – Sinuites* – dominated one (note the taxonomic overlap between the Axis 2 and Axis 6 faunas as listed in table 6). The pleurotomariaceans, however, do appear to be more restricted to the easternmost facies than do some of the pelecypods. Furthermore, in the murchisoniacean – dominated portions of the benthos (central portions of Axis 2 distribution on fig. 6), there are added significant numbers of the bellerophontacean gastropod *Sinuites 'cancellatus'* (fig. 9-L) and the orthid brachiopods *Pionodema conradi* (fig. 9-H) and *Campylorthis deflecta* (fig. 9-A, B). All three were probably surface dwellers. The bellerophontacean gastropod was most likely an archaeogastropod and an epifaunal detritus feeder. The latter two brachiopods were more than likely strictly limited to epifaunal suspension feeding, although the broad, flattened strophomenoid-like valves of *C. deflecta* may have permitted a very shallow infaunal life habit.

Thus, as was the case further to the east, this biofacies exhibits good ecological diversity both infaunally and epifaunally. The additions of large numbers of the small-size platyceratacean gastropod may indeed indicate some expansion of the preserved molluscan fauna into the realm of surface scavenging, but, unfortunately, any interpretation of the life habits of *Holopea* sp. must remain as tentative as those for the other gastropods in these shallow seas. It is clear, However, that the dominant taxonomic members in these two eastern facies have remained molluscan, but in the transition from east to west, that is from Axis 6 to Axis 2 faunas, the benthos has come under the domination of gastropods as pelecypods have assumed a numerically less strong position.

The Western Brachiopod-Dominated Biofacies

To the west and south of the areas characterized by the molluscan faunas of Axes 2 and 6, the benthos is dominated by a variety of epifaunal suspension-feeding brachiopods, and bryozoans, with ostracodes whose life habit was probably also a suspension-feeding one. The *Schmidtella – Leperditella* faunas of Axis 7 (table 6 and fig. 4) delimit a biofacies in north-central Illinois in which these ostracodes had become the dominant benthic taxa. It seems, however, to have been more characteristic for the bottom fauna to have been dominated not by ostracodes alone but by a mixture of ostracodes, orthid brachiopods and cryptostome bryozoans (*Pionodema – Schmidtella* fauna of Axis 1, table 6 and figs 4 and 4; and the *Hesperorthis* fauna of Axis 3, table 6 and fig. 4). Mollusks had not been completely lost from the sea floor, and, in fact, the murchisoniacean gastropod *Hormotoma gracilis* (fig. 9-J) is found in association with the orthid brachiopods *Hesperorthis concava* (fig. 9-F, I) and *Skenidioides anthonensis* on Axis 3; this biofacies is located immediately along the northern and southern margins of the Axis 1 and Axis 2 biofacies.

Tracing this benthic fauna into Iowa and southeastern Minnesota, we have noted that specimens of the *Pionodema-Schmidtella* biofacies (fig. 5) are substantially more fragmented than in Wisconsin, and broken skeletal wackestones and packstones are the predominant rock type containing these fragments (fig. 3). Carbonate lithologies to the east, whether dolomites or limestones, are characterized by skeletal wackestones that show much lesser degrees of breakage wherein cyrtodontoid pelecypods and orthid brachiopods are preserved in living position. Because the plotting of loadings on factor axes is derived from information on complete specimens only, the apparently abrupt termination west of the Mississippi River of the fauna corresponding to Axis 1 does not indicate the actual extent of the distribution of the fragmentary remains of its component taxa. To the east the geographic attenuation of the *Pionodema – Schmidtella* biofacies, again based on the occurrence of entire specimens, appears to be much more gradual than its western termination.

Occurring among the fragmented remains of the *Pionodema* – dominated Axis 1 fauna to the west is a very low diversity atrypid brachiopod-dominated fauna, one essentially *in situ,* or at least in unbroken condition. The species *Protozyga 'nicolleti'* (fig. 9-G) (usually 5 mm or less in width) defines the fifth axis on our exemplar run (Axis 5 in table 6 and fig. 4). Patches of nearly monospecific associations of this small epifaunal suspension feeder are scattered all along the western and southwestern margins of the outcrop area. However, only in southeastern Minnesota and northeastern Iowa is *Protozyga* the numerically dominant constituent, and there it makes up between 90 to 95 percent of the *Protozyga* biofacies.

At the northern edge of the study area, that is in the vicinity of Minneapolis, Minnesota, the degree of skeletal fragmentation is low and dolomites are as common as they were along the southeastern margins of the area in central Wisconsin (fig. 3). However, the fauna in the north is characterized by the strophomenoid brachiopods *Oepikina minnesotensis* (fig. 9-D,E) and *Strophomena plattinensis* (fig. 9-C) (Axis 4 biofacies in table 6, figs 4 and 7). Both strophomenoids were presumably epifaunal or very shallow infaunal suspension feeders (see Bretsky & Bretsky 1975 for more details on the distribution and morphological variation of these strophomenoids). The non-contiguous secondary concentrations of this strophomenoid-dominated biofacies in south-central Wisconsin (fig. 7) is, of course, taxonomically very similar to those more highly concentrated patches in Minnesota, but the faunas to the south tend to incorporate more numerous individuals of the orthid brachiopod *Hesperorthis concava* (fig. 9-F, I) and *Campylorthis deflecta* fig. 9-A, B), hence their high loadings on Axis 4 (table 6). In the south the geographic discreteness of the *Oepikina – Strophomena* biofacies is lost in the tangled overlapping of faunas from Axis 1, 2 and 6; yet the strophomenoids appear to form a discrete faunal association of remarkably low life-habit diversification over a broad geographic area, one that is ecologically quite distinct from the obvious higher diversity of the molluscan-dominated faunas.

Discussion

In summary, it does appears as if there was a preferential geographic localization of the benthic faunas in this Middle Ordovician shallow subtidal sea. The eastern biofacies appear not only to be numerically dominated by mollusks but seem, in the present analysis, to be more diverse ecologically; however this may prove to be false as the less numerous faunal components are integrated into the ecological interpretations. Most certainly mollusks are less characteristic of the Mifflin bottom faunas to the west and south of south-central Wisconsin. Furthermore, the molluscan fauna appears to have undergone a change in taxonomic composition gradually from east to west as it lost its pelecypod component and the gastropods underwent a taxonomic shift away from the dominant pleurotomariaceans in the east to the murchisoniaceans and bellerophontaceans in the west.

Also, there does seem to be a positive association between the predominance of mollusks (fig. 4), the dolomitization of the carbonates (fig. 3) and a significantly greater thickness of the individual carbonate layers (page 116–7). This relationship between the presence of mollusks and the subsequent dolomitization of the rocks may be entirely coincidential, but the occurrence of large numbers of mollusks, especially infaunal pelecypods, in association with an increased bedding thickness may indicate some common factors affecting both the physical and biological realms. However, we do not know what this 'common factor' could be.

The fact that skeletal fragmentation increases west of the Mississippi River and appears to be positively correlated with a change in the taxonomic composition of the benthic fauna (that is, from Axis 1 biofacies to Axis 5) emphasizes the fact that substratum type was, at least in this one instance, presumably of some importance with regard to the composition of the bottom fauna. Lesser amounts of skeletal debris are common east of the Mississippi River, but characteristically associated with the limestone layers and only rarely with the dolomites. If the fragmentation of the skeletal remains were, in large part, the result of physical breakage (and indeed sharp contacts between wackestones and overlying grainstones are common), then one would have to feel that higher energy conditions must have prevailed in the west and diminished eastward. Whether this means that epeiric sea currents moved across the area preferentially from west to east carrying variable loads of shell debris and lime mud must remain for the final most speculative section of this report.

Speculations Concerning the Ecological Setting

If we venture away from the more obvious interpretations of the factor analysis, one readily enters into the field of paleocological speculation; there are, however, some findings, mentioned below, that deserve further scrutiny. Of considerable interest were those localities which loaded rather strongly on two or more of the seven principal axes (see for example localities 2 and 213 on table 4). These should be local Mifflin exposures in which, in the most general terms, some type of 'mixing' of benthic associations had taken place. Had this 'mixing' taken place within a single 3–5 cm carbonate layer, or had it occurred among beds over the entire 5–7 m interval of the Mifflin Member at any one exposure? Also, might the 'mixing' between faunas be essentially between *in situ* associations or between those that had undergone significant transport? Because we had eliminated all broken and abraded fossil shells from the quantitative analysis, we believed that some of these localities should represent areas of transition between biofacies. Thus the faunal data from 25 localities, ranging from ones quite central to a particular biofacies to ones which were highly 'marginal' or 'mixed', were examined visually in detail, though not subjected to further quantitative treatment.

What we did was to display the fossil data from each of the 25 exposures in 1 m stratigraphic increments, and over these 1 m intervals record the rank order, by abundance, of the fossil species. Then we categorized the numerically ranked fauna within each 1 m interval as belonging to one of the seven biofacies as defined by the principal components analysis. In no case could it be unequivocally demonstrated that there was any consistent stratigraphic pattern of biofacies that encompassed the entire Mifflin Member. Most simply, over any given 5–7 m interval, the geographic position of the locality was a much more accurate indication of the benthic fauna than was the stratigraphic position of any particular bed within it.

Another possible explanation for 'mixing' is that it had taken place at the scale of the individual carbonate layers; in other words, the faunas that defined the axes may occur preferentially either on one or the other surface, or within the carbonate bed itself. Again this hypothesis needs much more rigorous testing, but we shall point out some of our observations. The molluscan-dominated faunas of Axes 2 and 6 tend to be concentrated within the individual carbonate mud beds, and the basal portions of these beds, on occasion, tend to be dominated by valves of the large flat strophomenoid or orthid brachiopods of Axis 4. Recall that there is a secondary concentration of these flattened brachiopods with loadings of about 0.4 to 0.6 on Axis 4 in south-central Wisconsin (fig. 7). Hence we are led to the speculation in this instance that the terrigenous fine mud bottoms, now preserved in the rock record as thin and unfossiliferous shale intercalations between the carbonate layers, were colonized by the larvae of these flattened strophomenoid and orthid brachiopods. Subsequent colonizations of the carbonate mud environments seems to have preferentially involved other brachiopods, bryozoans, ostracodes and, of course, mollusks. Furthermore, the upper portions of some of the easternmost lime mud beds occasionally contain essentially untransported remains of some brachiopod, ostracode and bryozoan species scoring in the range of 0.5 to 0.7 on Axis 1 (*Pionodema – Schmidtella* biofacies, see fig. 5 for the geographic spread of this facies into the molluscan-dominated eastern regions of the study area).

Therefore, it may be that within any given carbonate layer there were at least three temporally separated biotic associations, and that the separation of these was principally on an ecological rather than an evolutionary time scale. We feel, however, that at the present time we cannot point to this ecological separation as a case of obligatory biotic succession (sensu Horn 1976) for it seems as if there is little in the way of actual documentable biotic integration among the various 'successional' faunas. (However the reader is referred to a paper by Walker & Alberstadt, 1975, wherein obligatory succession toward a common taxonomic convergence is more vigorously argued). Our impression is that in the upper Mississippi Valley there may have been greater physical than biotic control on the taxonomic composition of the bottom fauna and that this may have been critically involved with rates of sedimentation dependent upon the local production or influx of carbonate mud. The 'successional' patterns are not easily generalized.

Furthermore, as shell fragmentation increased to the west, the fragments appear to be concentrated at the base of the individual carbonate layers. This is not invariably so, but the best preserved specimens of the *Pinodema – Schmidtella* biofacies in the heart of its distribution in southwestern Wisconsin occur within the layers and at the tops of the carbonate beds, rarely at the base of the beds. It appears as if the orthid brachiopods, ostracodes and cryptostome bryozoans may have been unable to successfully colonize the bottom until the terrigenous muds were covered over by shell debris.

To the west of the Mississippi River shell fragmentation is spread throughout the carbonate layers (fig. 3), and, in fact, the fragmented remains of the *Pionodema*-dominated Axis 1 fauna seems to have provided, in part, substratum attachment sites for those faunas of the Axis 5 *Protozyga*-dominated fauna.

In order to pursue the physical control of the benthic faunal composition further, let us assume that each of the thin shale partings represent a widespread depositional event when, for some reason, terrigenous muds were deposited across a predominantly carbonate depositional basin. We cannot correlate any particular terrigenous mud event among localities, but in looking at the general compositional properties of the Mifflin carbonates between these layers, we note that there is a decrease in thickness of the individual carbonate layers from the eastern dolomites to the western limestones. Accompanying this decrease in thickness is an increase in the degree and amount of shell fragmentation. Furthermore, in south-eastern Minnesota, commonly occurring with the broken skeletal wackestones and packstones, are irregular mounds of shell debris on the surface of the beds, associated with iron-rich pods and lenses that previously (see Weiss 1953) have been called 'corrosion zones' or 'corrosion surfaces' (see fig. 3). The bedding planes of the carbonates are quite irregular and the surfaces take on the appearance of a 'hummocky hardground', as discussed by Bromley (1975). The corrosion zones appear to have been pyritic and to have subsequently undergone extensive chemical weathering at the exposed outcrop surfaces. They have been recognized only in the 'middle' portions of the Platteville formation west of the Mississippi River (fig. 3), where bedding is overall thinner and the skeletal debris comprising the carbonate rock is a good deal more fragmented than to the east of the river. Pending a more detailed petrographic study, however, any explanation of the depositional significance of the corrosion surfaces must remain tentative.

We suggest, however, that lime muds may

have been washed preferentially from west to the east and the more regular physical reworking of the shelly beds in the west permitted the buildup of higher concentrations of shell fragments. Regular movement of fines away from the west also permitted the development of possible hardgrounds in those areas of southeastern Minnesota where sedimentation must have been negligible for relatively long periods of time. The preferential movement of fine sands and occasionally coarser-grained shell debris eastward could be tested in local sections by documenting a gradient of decreasing numbers of shelly storm layers from west to east, and indeed storm layers are commonly found throughout local sections west of the Mississippi River, but most certainly not exclusively.

If indeed we accept this environmental setting as a working model for the deposition of the Mifflin carbonates, then it appears that the benthic faunas of Axis 5 west of the Mississippi River existed in somewhat more episodically agitated and perhaps shallower waters than those to the east. The carbonate layers throughout the east show very little compaction, and exhibit crisp borings with well preserved fecal pellets that had settled to the bottom of now spar-filled borings. Furthermore, there is very little crushing of the infaunal mollusk shells. Hence it appears as if the sea bottom in the east was not a soupy carbonate mud, but a reasonably firm substratum; that is, the type of environmental setting required for the successful habitation of a sea floor by archaeogastropods, which, indeed, do show high loadings on Axes 2 and 6 in this region.

Two previous studies of Middle Ordovician units from the upper Mississippi Valley add some partial support to the notions suggested herein that there was a gradual shallowing of this Middle Ordovician sea from east to west. Parham & Austin (1967) and Fraser (1976) in studies of the fine-grained terrigenous clastics of the unit (Glenwood Shale, fig. 1) which immediately underlies, and, in some cases, is interbedded with the lower portions of the Platteville Formation have shown that the depositional environments just west of the Mississippi River appear to represent shallower waters than those to the east. Whether Fraser's reconstruction of epeiric sea bathymetry is also in part applicable to the Platteville environments remains to be further explored.

Finally in the Minneapolis region the degree of shell fragmentation is comparable to that seen in south-central Wisconsin and not that seen in southeastern Minnesota. Furthermore, the fauna tends to be dominated by strophomenoid brachiopods of Axis 4, and the rock is typically a dolomite, but the gastropod and pelecypod faunas that are so characteristic to the southeast are, by and large, missing from these northwestern exposures. Certainly there are a few well-preserved specimens of *Vanuxemia* spp., but not nearly in the abundances that characterize south-central Wisconsin. Why the strophomenoid faunas should be so dominant in these northernmost environments presents yet another problem, and at present we have no way of knowing why the molluscan faunas should have been so limited numerically in the north.

Summary

1. With the help of Q-mode factor analysis, we are able to define seven biofacies in the Mifflin or 'middle' Member of the Platteville Formation (Middle Ordovician, upper Mississippi Valley). Maps outlining the distribution of each biofacies can be prepared by plotting the loadings of each locality on each of the seven factor axes and contouring the numerical values thus obtained.

2. Five of the seven biofacies are geographically widespread and boundaries among the biofacies are overlapping and gradational. However, localities characterized by pelecypod and gastropod faunas tend to be concentrated along the eastern margins of the study area in south-central Wisconsin, whereas to the west the faunal composition of the benthos gradually shifts to one more dominated by brachiopods, ostracodes and bryozoans.

3. There does seem to be a positive association between the predominance of mollusks, dolomitization of the Mifflin carbonates, and a significantly greater thickness of the individual carbonate layers. This relationship between the presence of mollusks and what appears to have been the *subsequent* dolomitization of the rocks may be entirely coincidential, but the occurrence

of large numbers of mollusks, especially infaunal pelecypods, in association with an increased bedding thickness may indicate some common factor affecting both the physical and biological realms.

4. *Skeletal fragmentation in the carbonates* increases from east to west and also appears to be positively correlated with a change in the taxonomic composition of the benthic fauna, indicating that substratum type was presumably of some importance in determining the composition of the bottom fauna.

5. The 'mixing' of various biofacies seems to have taken place at the scale of the individual 3 to 5 cm carbonate layers, and there was no consistent stratigraphic pattern of biofacies that encompassed the entire Mifflin. It does appear as if the separation of the benthic faunas was on a very short-term ecological rather than an evolutionary time scale, yet we cannot point to this ecological separation, even within a single carbonate layer, as a case of obligatory biotic succession. It seems as if there is little in the way of actual documentable biotic information among the various 'successional' faunas. The pattern appears to be complex, and at present we believe that the distribution of the biofacies in the Middle Ordovician of the upper Mississippi Valley was more a function of substratum type, rate of sedimentation (especially of the lime muds) and perhaps some unknowable component of benthic larval ecology as it related to these various physical factors.

6. Although we think that we have clearly demonstrated that biofacies can be 'mapped' in shallow subtidal epeiric seas and that these faunal associations may be understable in a general ecological context, whether one wants to call these associations 'communities' or not probably depends more on the predilections of an individual investigator rather than on any information that can be extracted from the fossil marine realm.

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Dansk sammendrag

Et op til 6 cm tykt lag af kalk og dolomit (Mifflin member, Mellem Ordovicium) er blottet over et område dækkende ca. 65 000 km² in Illinois. Mifflin formationen indeholder en artsrig fauna som er analyseret med henblik på en kortlægning af de enkelte faunaselskabers geografiske udbredelse. 80 lokaliteter og over 100 arter udgør analysens basis. Ved hjælp af en »Q-mode« faktor analyse er der udskilt 7 faunaselskaber (faktor akser) som de enkelte lokaliteter er vægtet imod. De derved fremkomne værdier er omsat i kurvebilleder illustrerende de enkelte selskabers udbredelse og relative betydning. 5 af selskaberne har udbredelser med indbyrdes geografisk overlap. Disse overlap mellem forskellige samfund synes at befinde sig inden for 3–5 cm tykke kalklag, antydende at der er tale om økologiske successioner. Der er dog en tendens til at snegle/muslinge selskaber er koncentreret langs området østlige begrænsninger, mens brachiopod/bryozo/ostracod selskaber dominerer mod vest. Der drages ingen endelig konklusion om de økologiske faktorer som må have adskilt de forskellige samfund i den enkelte succession.

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