Morphological Diversification of Ptychopariida (Trilobita) from the Marjumiid Biomere (Middle and Upper Cambrian)

Frederick A. Sundberg

Paleobiology, Vol. 22, No. 1 (Winter, 1996), 49-65.

Morphological diversification of Ptychopariida (Trilobita) from the Marjumiid biomere (Middle and Upper Cambrian)

Frederick A. Sundberg

Abstract.—Ptychopariid trilobites from the Marjumiid biomere of Laurentia underwent a statistically significant morphological diversification that is concordant with proposed adaptive radiations of trilobites in each of the Cambrian biomeres. An analysis of a subset consisting of the biomere's most characteristic taxa, the Asaphiscacea, Raymondinacea, and Marjumiacea, also illustrates this morphological diversification. In detail, the total data set and subset show a limited range of morphologies near the base of the biomere and a large increase in range in the upper portion of the biomere.

Regional assemblages from the Appalachians, Great Basin, and Texas were also studied to determine if they too show the larger-scale macroevolutionary patterns of trilobites from Laurentia as a whole. The regional assemblages illustrate similar, but *not identical*, morphological diversifications, which are also similar to the overall Laurentian pattern. Subsets of the characteristic taxa also show this diversification. These results suggest that regional assemblages can be used to investigate these larger-scale macroevolutionary patterns.

Causal mechanisms for the diversification patterns are not clear. Potential mechanisms include: (1) endemic evolution of new morphologies in Laurentia; (2) migration of new morphologies, including intra- and inter-continental migrations; and (3) environmental controls over the distribution of morphologies. Likely causes for the morphological diversification and its similarity among regions probably include aspects of all three mechanisms.

Frederick A. Sundberg. Research Associate, Invertebrate Paleontology Section, Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California 90007

Introduction

Stitt (1975) hypothesized that during the deposition of a biomere, trilobites underwent an "adaptive radiation" represented by an increase in taxonomic diversity. Implicit in this hypothesis is the diversification of trilobite morphologies within the biomere. However, taxonomic diversity need not correlate with morphological diversity (Foote 1993). Taxonomic diversity may result from minor variations on a morphological theme, where taxa have only small morphological differences (i.e., "conservative taxa").

The primary intent of this paper is to determine if one of these purported adaptive radiations is represented by a corresponding morphological diversification. This analysis concentrates on the ptychopariid trilobites from the Middle and Upper Cambrian Marjumiid biomere (Fig. 1) of Laurentia.

The second goal of this paper is to determine if the assemblages from smaller regions of Laurentia also show the larger-scale macroevolutionary pattern. This goal addresses the reliability of analysis of regional assemblages to determine larger macroevolutionary patterns.

Further testing of these hypotheses is achieved through the analysis of a subset consisting of the three superfamilies of the Marjumiid biomere, the Asaphiscacea, Raymondinacea, and Marjumiacea. These taxa represent the most characteristic trilobites of the biomere (Sundberg 1990).

Biomeres

Palmer (1965) introduced the concept "biomere" to designate distinct stratigraphic packages, each containing trilobite assemblages dominated by one or two taxonomic groups. The boundaries between biomeres are abrupt and "non-evolutionary" (Palmer 1965, 1984) in that the shelf fauna in the overlying biomere is not directly derived from the shelf fauna of the underlying biomere. These boundaries represent major extinction events that eliminated the vast majority of trilobites of the underlying biomere. The initial trilo-

Biomere	Biozone
Pterocephaliid Biomere	*Aphelaspis* Biozone
	Coosella perplexa Subzone
Marjumiid Biomere	*Crepicephalus* Biozone
	Cedaria Biozone
	Bolaspidella Biozone
	Ptychagnostus atavus Biozone
	Ptychagnostus gibbus Biozone
	Ehmaniella Biozone
"Corynexochid" Biomere	*Glossopleura* Biozone

FIGURE 1. Trilobite biozones within and adjacent to the Marjumiid biomere (Middle to Upper Cambrian). The Middle and Upper Cambrian boundary falls near the middle of the *Cedaria* Biozone.

FIGURE 2. Trilobite cranidial characters measured for this study. A = cranidial length, B = glabellar length, C = anterior border sagittal width, D = preglabellar sagittal width, E = occipital transverse width, F1 = preoccipital lobes transverse width, F2 = second glabellar lobe transverse width, F3 = frontal lobe transverse width at ocular ridges.

bites of each of the three Middle and Upper Cambrian biomeres, however, have very similar morphologies (Palmer 1965, 1984). The morphologic similarities of these initial trilobites and their absence from the shelf faunas of the underlying biomere have led to the hypothesis that the initial taxa of each biomere were derived iteratively from the same, slowly evolving "basic stock" of trilobites of deeper-water origin (Palmer 1965, 1984). Stitt (1975) has suggested that after this initial invasion the majority of trilobites within biomeres had endemic origins, i.e., evolved during the deposition of the biomere within Laurentia.

Hypotheses

The questions to be addressed center on the stratigraphic distribution of ptychopariid trilobite morphologies, both for the entire Laurentian assemblage and for regions within Laurentia. Thus, hypotheses to be statistically tested include: (1) Do North American trilobites show a morphological expansion within the Marjumiid biomere? (2) Do trilobite assemblages from different regions of North America also show a morphological expan-
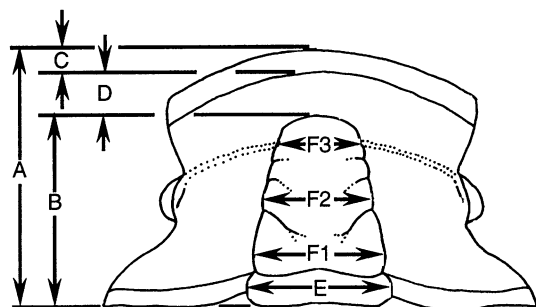
sion within the Marjumiid biomere? and (3) Do trilobite assemblages from these different regions have similar morphological expansions? In addition, the initial trilobite assemblages from different regions are statistically compared to determine if they have "similar" morphologies.

Methods

Data

The data consist of measurements of eight cranidial characters (Fig. 2) on 1118 trilobite specimens from the Marjumiid biomere of North America: 303 specimens from the Appalachians, 63 specimens from Texas, and 752 specimens from the Great Basin. Two hundred seventy-one species and subspecies within 79 genera were measured. These specimens were either studied earlier by Palmer (1954), Robison (1964, 1971), Derby (1965), Rasetti (1965), Oldroyd (1973), Randolph (1973), White (1973), Eby (1981), Kopaska-Merkel (1983), or Vorwald (1983); collected for later study by D. Strickland or R. Robison; or collected for this study (Sundberg 1990, 1994).

The selected features (Fig. 2) characterize glabellar and cranidial shapes. Cranidial width was also measured, but was not used due to the few specimens with the entire posterior area of the fixigena prepared or preserved. Characters were measured with a micrometer attached to a binocular microscope or with vernier calipers. No attempt was made to correct for compaction differences between

TABLE 1. The number of trilobite specimens measured for each major taxonomic group.

Taxa	Specimen count	Percent
Solenopleuracea	130	11.6
Norwoodiacea	103	9.2
Leiostegiacea	1	<0.1
Asaphiscacea	70	6.2
Raymondinacea	107	9.6
Marjumiacea	298	26.7
Ptychopariacea	309	27.6
Unknown Affinity	100	8.9
TOTAL	1118	99.8

specimens preserved in limestone or shale. Evidence indicates preservational differences may have had little influence on overall morphologies (e.g., Labandeira and Hughes 1994).

Ptychopariid trilobites in the Marjumiid biomere are assigned to eight major groups (superfamilies) using nomenclature from the *Treatise on Invertebrate Paleontology* (Harrington et al. 1959): Asaphiscacea, Raymondinacea, Marjumiacea, Ptychopariacea, Norwoodiacea, Solenopleuracea, Leiostegiacea, and miscellaneous taxa of unknown affinity (Table 1, Appendix). Some of the supergeneric taxa listed in the Appendix may represent new taxonomic groups that are not closely related to the other taxa presently included in the *Treatise* superfamilies (e.g., Ptychopariacea, see Sundberg 1990, 1994). No detailed study of the phylogeny of the groups was undertaken; revision of these groups is outside the scope of this paper.

Species range charts of the Marjumiid biomere (not illustrated) were constructed using data from Palmer (1954), Robison (1964), Rasetti (1965), Derby (1965), Randolph (1973), White (1973), Eby (1981), Vorwald (1983), Sundberg (1989, 1990, 1994), and unpublished locality descriptions. Correlations of biozones among regions are based on common trilobite taxa and the biomere boundaries. Construction and correlation of the range charts are discussed by Sundberg (1990).

Palmer (1954) recognized trilobite assemblages from the *Bolaspidella* to *Crepicephalus* biozones in the Texas section. This biostratigraphic framework is used here; however, the presence of *Kormagnostus seclusus* (Walcott) in the upper portion of the reported *Bolaspidella*

Biozone may indicate that this portion of the biozone represents the lower *Cedaria* Biozone.

Species ranges are expanded to encompass half-biozone intervals to compensate for imperfect stratigraphic control (see Sundberg 1990 for taxa ranges). For example, a species occurring in the lower quarter of the *Bolaspidella* Biozone would have its range extended to encompass the entire lower half of the biozone. These extensions probably over-estimate species ranges.

Raw Data Conversion

This study concentrates on changes in the *range* of trilobite morphologies within the biomere and not on changes in body size. Thus, morphological characters are represented either by relative sizes (individual characters or principal component scores for species) or by hypervolumes of a trilobite assemblage (see below).

Relative sizes were obtained by dividing each character by the square root of the sum of squared characters for each specimen (Eldredge 1972):

$$M_x = \frac{m_x}{\left[\sum_{n=1}^{r} m_r^2\right]^{0.5}} \qquad (1)$$

where M_x = size corrected character x, m_x = uncorrected character x, and m_r = uncorrected characters 1 through r. This method is similar to dividing one character by another to determine a relative size (e.g., glabellar length divided by cranidial length), but is not reliant on an individual character that could have also changed during the biomere.

A hypervolume is used to measure the range of morphological diversity of a trilobite group. A hypervolume is analogous to a three-dimensional volume but is produced by multiplying the ranges of more than three characters together to produce a multidimensional volume:

$$\prod_{M=1}^{r} (M_{max} - M_{min}), \qquad (2)$$

where M is the corrected morphological character, r is the number of characters being studied, M_{max} is the maximum value of character
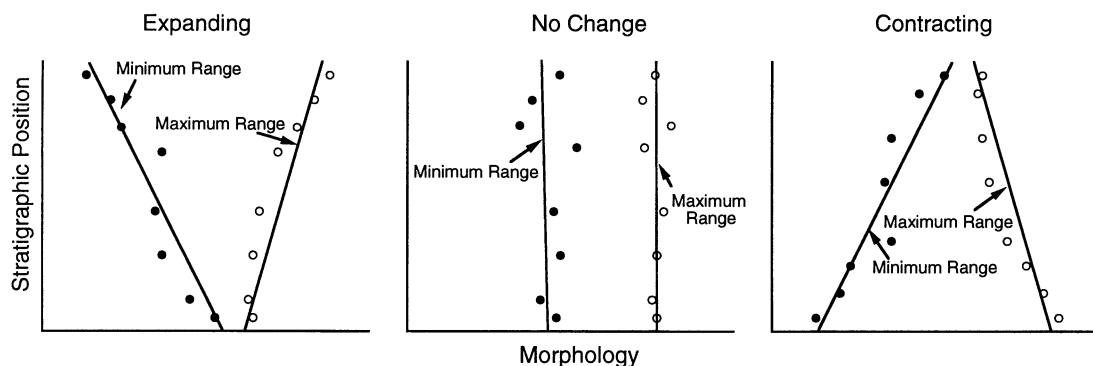
FIGURE 3. Examples of spindle diagram shapes depicted by autoregression lines for the maximum and minimum character ranges vs. stratigraphic position.

M, and M_{min} is the minimal value of character M. Hypervolumes are calculated for each biostratigraphic level and represent the amount of hyperspace that contains all specimens.

Van Valen (1974) discussed the potential problem of hypervolumes generated by variance or eigenvalues. Hypervolumes in this study are based on morphological range. Ranges can have the same problem as variances where an unusually small value for a single morphology would strongly influence the total amount of hypervolume. However, analysis of range illustrates no unusually small values. The smallest values per morphology varied from 0.2 to 2.0 with an average of 0.86, $s = 0.33$.

Size-corrected characters are plotted against an extended stratigraphic range of the species (e.g., Fig. 5). These plots, called spindle diagrams, illustrate the changes in morphological ranges within the Marjumiid biomere. The first and second scores from a principal component analysis are used for the illustrated spindle diagrams, rather than the multitude of individual diagrams for each of the eight characters.

Hypervolumes are plotted against their respective biostratigraphic level and also illustrate changes in morphological range within the biomere (e.g., Fig. 4).

Analysis of Trends in Morphological Range

If morphology expanded during the deposition of the Marjumiid biomere, then the range between maximum and minimum limits of trilobite morphology also should have

expanded. The minimum limit of morphology should have become smaller and the maximum limit should have become larger. Thus, we can show that morphological diversification occurred by analyzing the trends of these extreme morphologies throughout the biomere. These trends are represented as two linear regressions, the minimum limits versus stratigraphic position and the maximum limits versus stratigraphic position. Autoregressions are used because these extremes are not strictly independent. In evolution, the morphology of one species is strongly dependent on its ancestor; thus, there is a high potential of extreme morphologies giving rise to other extreme morphologies. Autoregression equations will make statistical testing more conservative. A partial F-test is used to determine if the autoregression equations for the maximum and minimum limits are significantly different.

If the two autoregression equations are significantly different, then t-tests of the slope and intercept parameters will determine if the two limits show expansion, contraction, or covariance. If the two limits covary (Fig. 3), then they should not have significantly different slopes. Spindle diagrams with either contracting or expanding morphologic ranges should show significantly different slopes (Fig. 3). Whether the morphology is expanding or contracting will depend on the relative difference between the slopes of the two autoregression equations.

The t-test of the stratigraphic distribution of hypervolumes provides an additional method

of testing the morphological expansion of trilobites. The hypervolume values from the lower portion of the biomere are compared to those in the upper portion. Hypervolumes were calculated only for the midlevel of each half biozone because taxon ranges were extended to span half biozones (n = 8). The lower portion of the biomere consists of the lower *Ehmaniella* to upper *Bolaspidella* biozones. The upper portion consists of the lower *Cedaria* to upper *Crepicephalus* biozones. In Texas, where only part of the biomere is represented, the hypervolumes from the upper *Bolaspidella* to upper *Cedaria* biozones are compared to the hypervolumes from the lower and upper *Crepicephalus* Biozone (n = 5).

A trilobite group has increased its morphological range during the deposition of the biomere if: (1) most characters show statistically different slopes for the maximum and minimum limits or (2) hypervolumes in the upper half of the biomere are significantly larger than hypervolumes in the lower half. The first criterion requires significant differences between the minimum and maximum equations, significant differences between slope estimates, and slope directions that would produce an expanding morphological range. If a character has significant partial F-tests but non-significant t-tests for the slopes and intercepts, then it is judged to have a possible change in range if the t estimate is higher for the slope than for the intercept.

Analysis of Regional Similarities

Trilobite assemblages are considered similar if they have a high proportion of morphological overlap and the same overall morphological trend. The amount of morphological overlap is based on the amount of hypervolume the two assemblages have in common. This overlap is reported as a percentage relative to the taxonomic assemblage with the smallest total hypervolume. This smaller group contains the maximum hypervolume that two groups can have in common. In addition, the overlap percentage is an average value for each morphology because the actual amount of overlap can be misleading. For example, 12% actual overlap of hypervolumes for two groups appears small. However, if all

eight characters have the same amount of overlap, then the actual amount of overlap per character is 77% (0.77^8 = 0.12 or 12%).

For regional assemblages to have similar diversification patterns, they must also have similar morphological trends. Thus, the autoregression equations for each of the regional assemblages are compared using a partial F-test. Each autoregression equation is based on the average morphology vs. the stratigraphic midrange of each component species. Average morphology is represented by the first three scores of a principal component analysis of all characters (approximately 84% of the variation).

The overlap between regional assemblages is considered different if the partial F-tests for the principal component scores are significant ($p \leq 0.05$). However, the acceptance of the null hypothesis that the autoregression equations are not different does not demonstrate that the two equations are the same. Acceptance could result from the high variance of the data, a potential problem with this data set. For this reason, autoregression equations are considered only *similar* if the F scores have probabilities between 0.05 and 0.95 and *very similar* if above 0.95.

Results

The principal component analyses and the specific results from individual t-tests and partial F-tests are presented by Sundberg (1990). Tables 2, 3, and 5 presented here summarize these statistical tests.

North American Patterns

Ptychopariid trilobites expand in morphological range within the Marjumiid biomere (Figs. 4, 5). Six to seven of the eight characters show expansion using 0.05 or 0.10 significance levels (Table 2). Hypervolumes in the upper portion of the biomere are significantly larger than in the lower portion ($0.05 > p > 0.02$, Table 3). Expansion of the cranidial characters has an average increase of 182% of the original character range. Individual characters increased 41 to 481% (table 4). Most characters at least doubled in their range within the biomere.

This expansion in morphological range is

TABLE 2. Number of characters in each taxon or group of taxa that showed an increase, decrease, or no change in morphological range. Based on partial F-test and t-tests of the maximum and minimum limits of the spindle diagrams. ? = possible change in range (see text). NS = partial F-test not significant.

Taxa/region(s)	Significance level	De-crease	No change	In-crease	NS
Ptychopariida					
All regions	(0.05)	0	1	6	1
	(0.10)	0	0	7	1
Appalachians	(0.05)	0	3	5	0
	(0.10)	0	2	6	0
Great Basin	(0.05)	0	4	0	4
	(0.10)	0	4	4	0
Texas	(0.05)	0	0	5	3
	(0.10)	0	0	6	2
Asaphiscacea, Raymondinacea, and Marjumiacea					
All regions	(0.05)	0	0	5	3
	(0.10)	0	0	8	0
Appalachians	(0.05)	0	0	3(1?)	4
	(0.10)	0	0	4(1?)	3
Great Basin	(0.05)	0	0	5	3
	(0.10)	0	0	7	1
Texas	(0.05)	0	0	5	3
	(0.10)	0	0	6	2

TABLE 3. Autoregression and t-test results for changes in hypervolumes. + = $p < 0.1$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. Slope estimate is for the autoregression analyses on hypervolumes, and t-test is for the upper vs. lower biomere hypervolumes.

Taxa/region(s)	df	t-test	slope
Ptychopariida			
All regions	6	2.79*	*
Appalachians	6	1.94+	*
Great Basin	6	2.60*	+
Texas	3	4.01*	*
Asaphiscacea, Raymondinacea, and Marjumiacea			
All regions	5	6.32**	+
Appalachians	4	2.69*	+
Great Basin	5	7.23***	+
Texas	3	5.92**	+

not the result of the number of specimens measured. Hypervolumes, the most sensitive metric to the number of observations, have a very weak negative correlation to the number of specimens used ($r^2 = 0.0002$, T = 2.46, $p = 0.05$, Fig. 4). There is a moderate to weak positive correlation of hypervolumes with the number of species ($r^2 = 0.489$, T = 4.406, $p < 0.01$) and genera ($r^2 = 0.216$, T = 3.29, $p = 0.03$), demonstrating a link between taxonomic and morphological diversity.

The Superfamilies Asaphiscacea, Raymondinacea, and Marjumiacea, when analyzed together, also show a morphological diversification within the biomere (Figs. 5, 6). Five to all eight characters show expansion using 0.05 or 0.10 significance levels (Table 2). Hypervolumes in the upper portion of the biomere are significantly larger than in the lower portion ($p < 0.01$, Table 3). The expansion of the cranidial characters has an average increase of 454% of the original character range. Individual characters increased 189 to 1691% (Table 4).

Regional Patterns

The initial trilobites of the biomere have similar morphologies. Assemblages from the lower *Ehmaniella* Biozone of the Great Basin
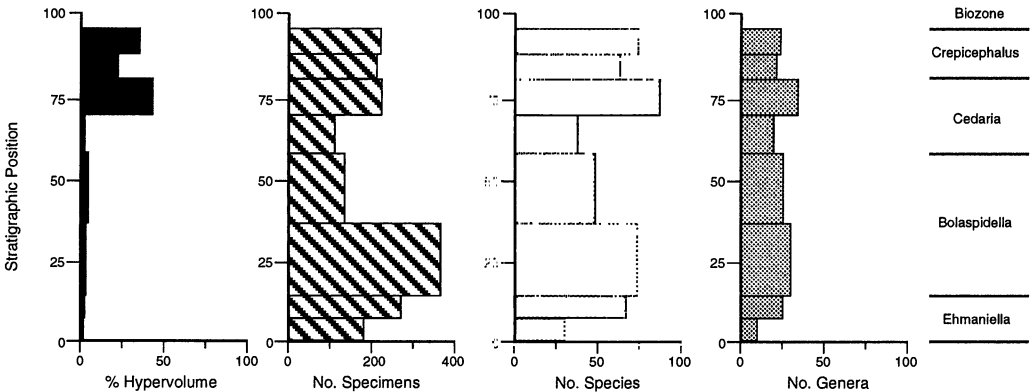

FIGURE 4. Stratigraphic distribution of hypervolumes, number of specimens, species, and genera for all ptychopariids in the Marjumiid biomere. Values were calculated from the middle level of each half-biozone interval and are shown as ranging throughout the half biozone. Hypervolume present in each half biozone is expressed as a percentage of the total hypervolume for the entire spindle diagram.
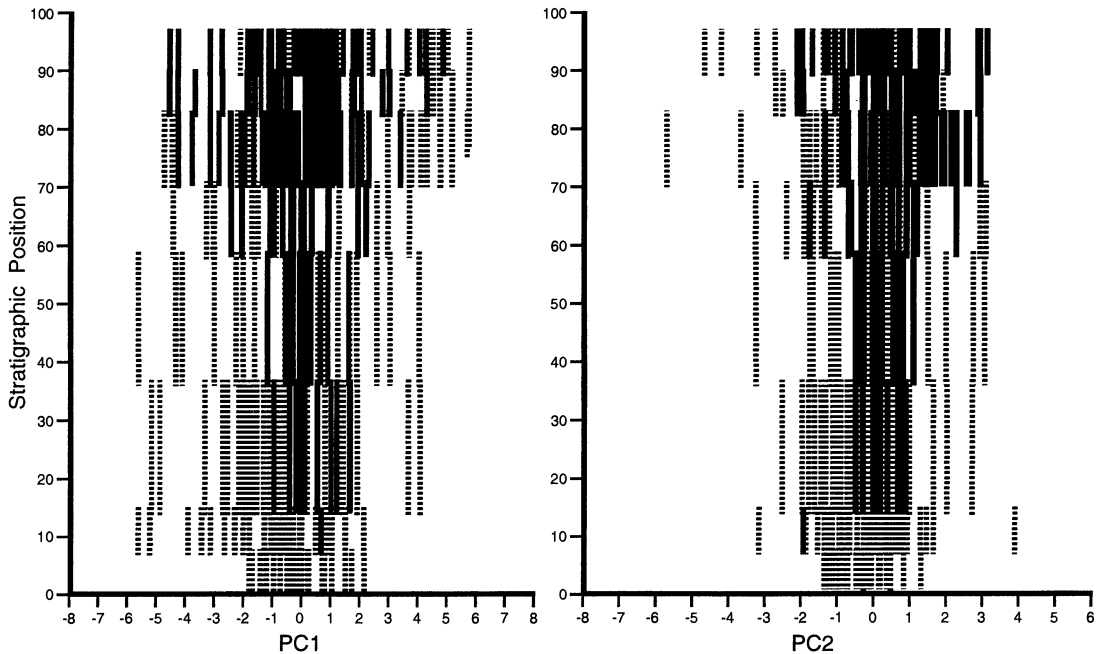
FIGURE 5.   Stratigraphic distribution of ptychopariid morphologies (principal components 1 and 2) from all three geographic regions studied. Each line represents an average species morphology (represented as scores on principal components) plotted against its stratigraphic range. Solid lines = Asaphiscacea, Raymondinacea, and Marjumiacea; striped lines = other ptychopariids.

and Appalachia occur within the same region of morphospace (Fig. 7). The amounts of variation within each region, however, are significantly different (MANOVA $p = 0.0003$).

Each of the regional data sets for all ptychopariids and the combined set of Asaphiscacea, Raymondinacea, and Marjumiacea shows an expansion in morphological range within the Marjumiid biomere (Figs. 5, 6, 8–11). The diversifications are based on the number of characters showing expansion (Table 2) and/ or the t-test of the hypervolumes (Table 3).

The similarity among regions is illustrated by their similar top-heavy plot of hypervolumes (Fig. 8), degree of overlap, and autoregression analyses (Table 5). In all instances, the amount of overlap between assemblages is greater than 80%. Autoregression analyses show only one significant difference in the distribution of phenotypes, which occurred in

TABLE 4.   Percent change in range of different cranidial characters for taxa and taxonomic groups in the Marjumiid biomere. Percent change is based on the lowermost morphological range (Lr) and uppermost morphological range (Ur) using $[(Ur - Lr)/Lr]100$. • = nonsignificant results from partial F-test using 0.10 significance level; — = no significant increase or decrease in morphological range. See Figure 2 for morphologies.

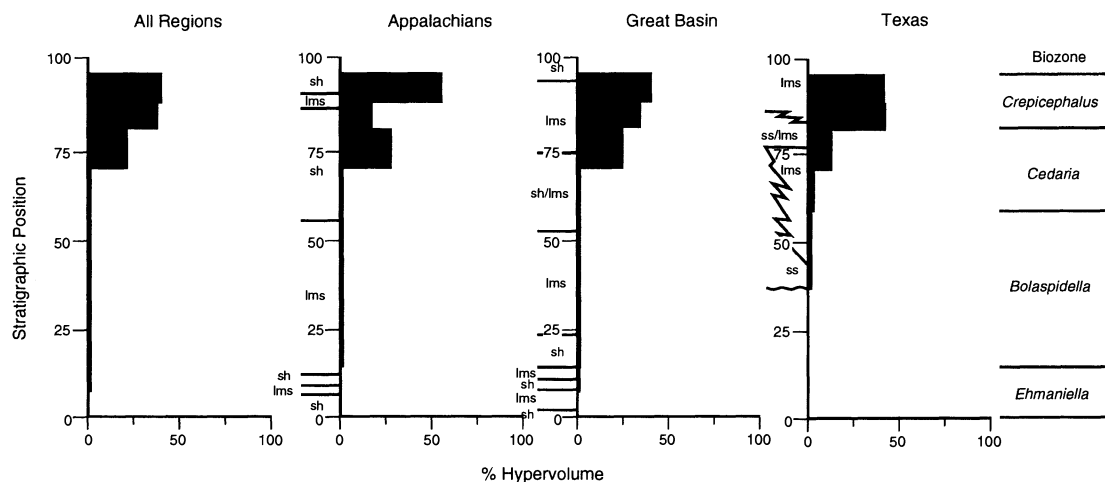| Character Taxa/region	A	B	C	D	E	F1	F2	F3
All Ptychopariida								
All regions	81	171	481	•	261	110	41	131
Appalachian	120	227	1000	—	200	142	—	269
Great Basin	60	64	—	—	74	53	92	98
Texas	66	204	213	•	120	57	•	258
Asaphiscacea, Raymondinacea, and Marjumiacea								
All regions	203	274	1691	340	327	336	273	189
Appalachian	69	146	•	91	240	•	•	58
Great Basin	203	142	762	340	72	220	•	185
Texas	217	•	256	54	345	317	•	421

FIGURE 6. Stratigraphic distribution of hypervolumes for the subset composed of Asaphiscacea, Raymondinacea, and Marjumiacea. The dominate lithology shown on the Y axis (lms = limestone, sh = shale, ss = sandstone).

principal component 3 when comparing the Appalachian and Great Basin data sets. In turn, only principal component 2 for the Appalachian and Texas assemblages and principal component 3 for all regions illustrate a high degree of similarity for the combined set of Asaphiscacea, Raymondinacea, and Marjumiacea ($p > 0.95$; Table 5).

The amount of character expansion for the ptychopariid assemblages varies among
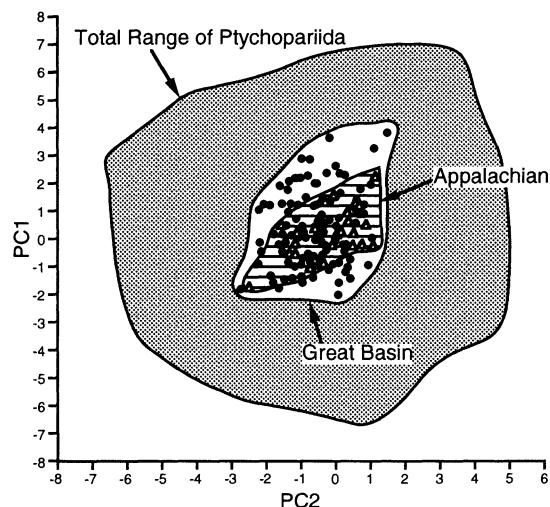

FIGURE 7. Morphologic distribution (principal components 1 and 2) of ptychopariid specimens in the lower *Ehmaniella* Biozone. ● = Great Basin specimens, △ = Appalachian specimens. The outer line is the total range of all ptychopariid specimens from the Marjumiid biomere measured for this study.

regions (Table 4). The Appalachian data set shows the largest amount of expansion with an average increase of 326%. The Appalachian values are generally higher than the amount of expansion for all regions combined. This results from a morphologically less diverse assemblage in the bottom of the biomere in Appalachia. The Texas data set has a relatively low amount of expansion with an average increase of 153%. This results from the absence of the basal portion of the biomere in that region. The Great Basin data set also has a relatively low amount of expansion with an average increase of 74%. This low amount results from a relatively lower morphological diversity in the top of the biomere.

The combined morphospace of Asaphiscacea, Raymondinacea, and Marjumiacea also shows variation in the amount of expansion among regions (Table 4). The Great Basin data set shows the greatest amount of expansion with an average increase of 275% because there is only a single known species of *Modocia* in the upper *Ehmaniella* Biozone. The Appalachian data set shows the least amount of expansion with an average increase of 121%.

Discussion

This sampling of ptychopariid trilobites from Laurentia illustrates a morphological diversification within the Marjumiid biomere. The regional data sets illustrate that this mor-
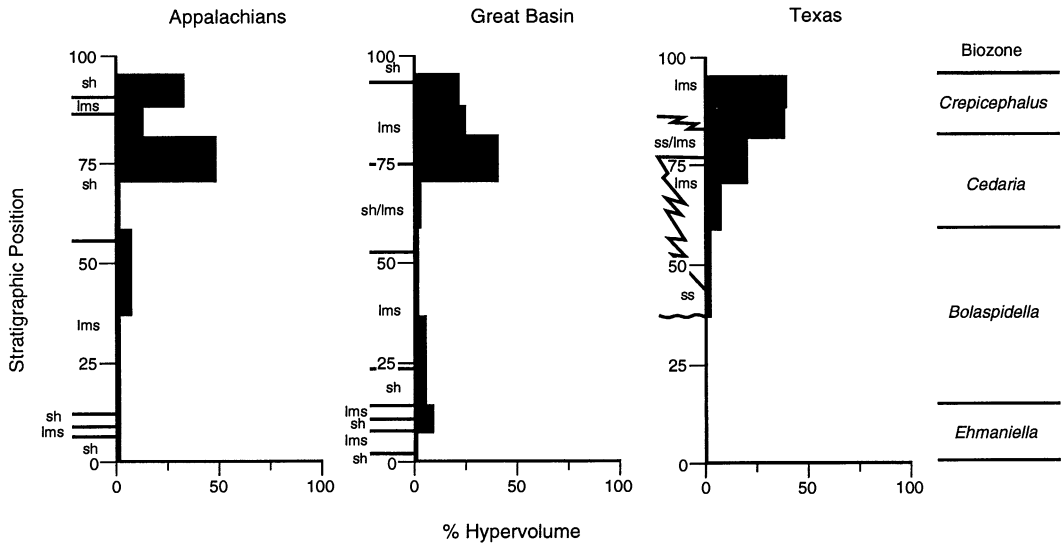
FIGURE 8. Stratigraphic distribution of hypervolumes for all ptychopariids in the Marjumiid biomere. The dominate lithology shown on the Y axis (lms = limestone, sh = shale, ss = sandstone).

phological diversification also occurs in the assemblages from local regions. In addition, the diversification is similar among regions, although not identical. The subset of the characteristic taxa from the biomere, Asaphiscacea, Raymondinacea, and Marjumiacea, also

illustrates a diversification and similarity to the overall pattern of Laurentia.

The occurrence of a morphological diversification is an expected result if biomere boundaries are extinction events. The extinction of most shallow-water taxa from the pre-
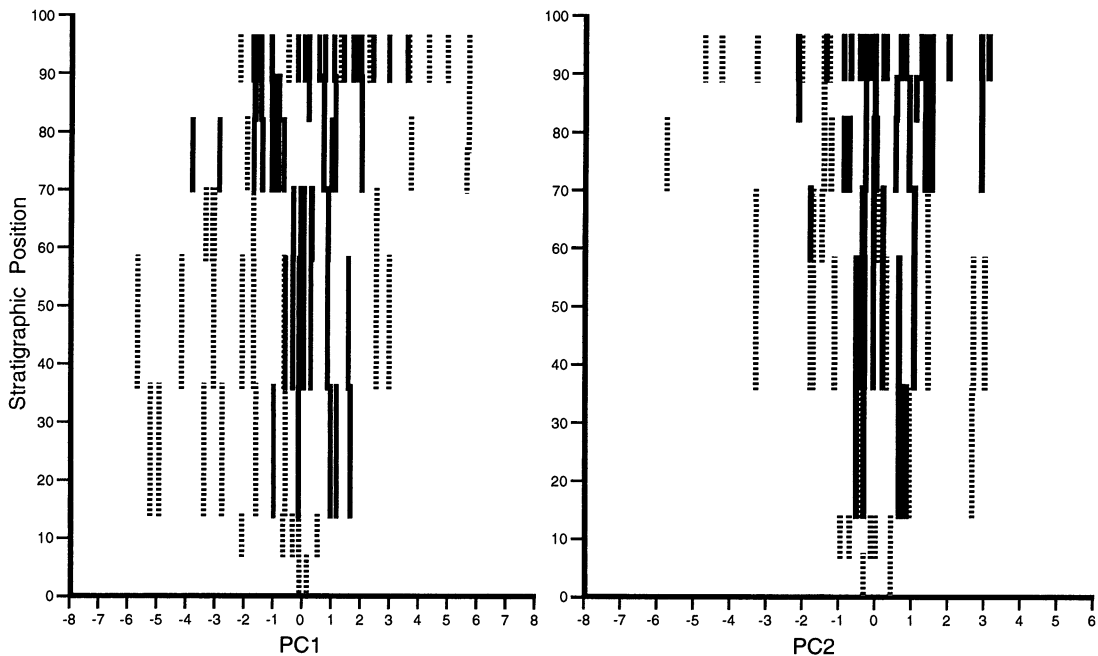

FIGURE 9. Stratigraphic distribution of ptychopariid morphologies (principal components 1 and 2) from the Appalachian data set. Solid lines = Asaphiscacea, Raymondinacea, and Marjumiacea; striped lines = other ptychopariids.
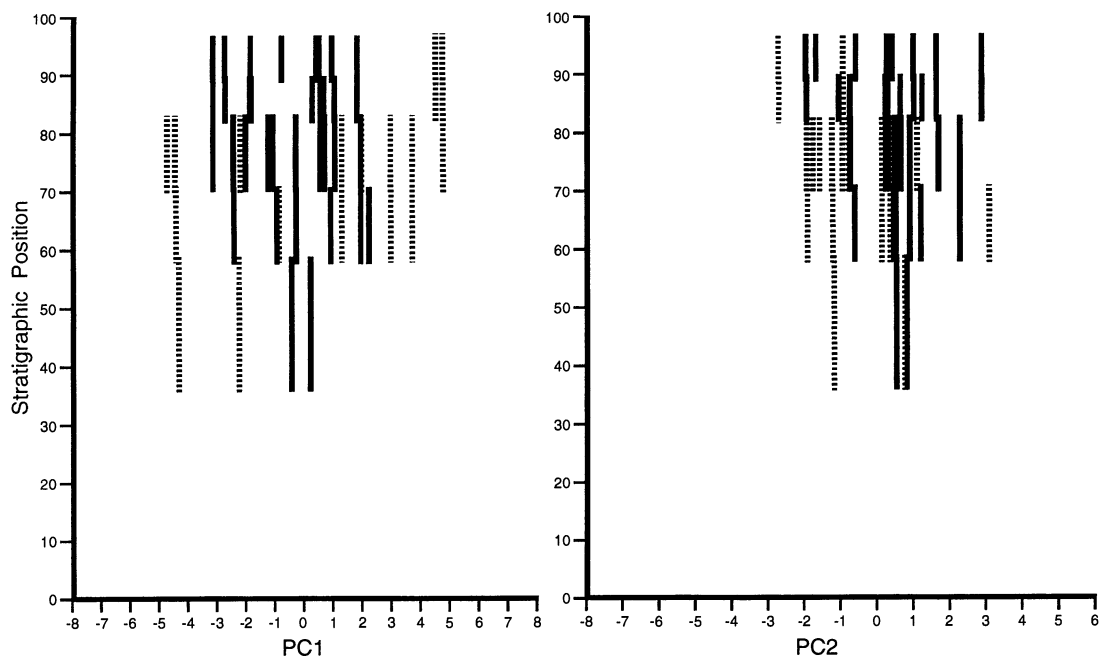
FIGURE 10.   Stratigraphic distribution of ptychopariid morphologies (principal components 1 and 2) from the Texas data set. Solid lines = Asaphiscacea, Raymondinacea, and Marjumiacea; striped lines = other ptychopariids.
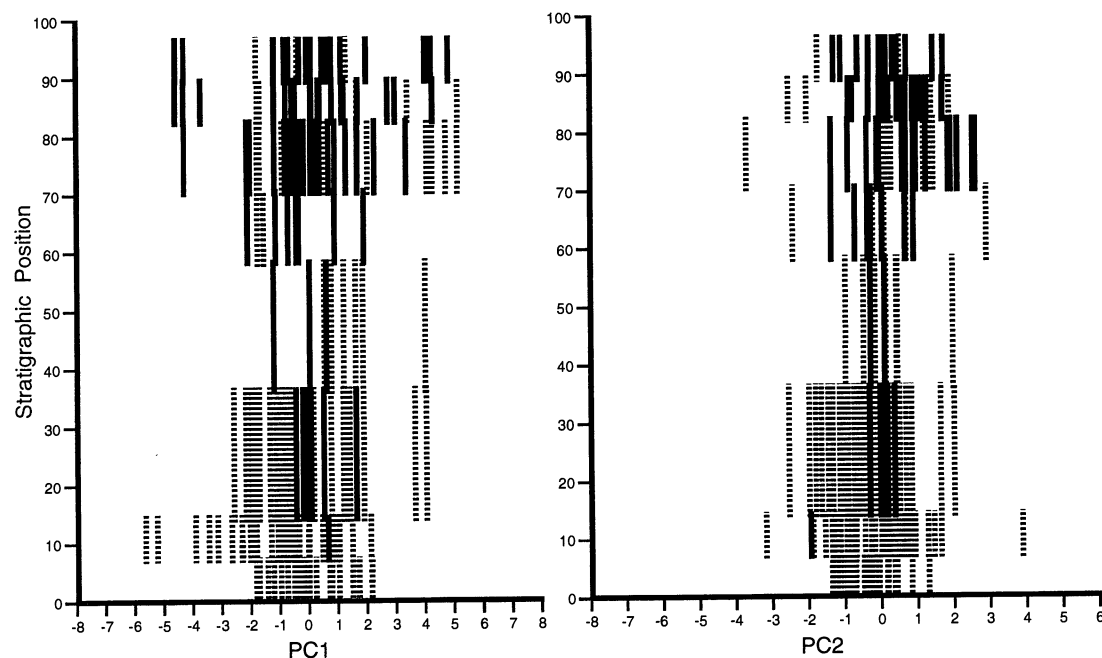

FIGURE 11.   Stratigraphic distribution of ptychopariid morphologies (principal components 1 and 2) from the Great Basin data set. Solid lines = Asaphiscacea, Raymondinacea, and Marjumiacea; striped lines = other ptychopariids.

TABLE 5. Average amount of overlap and degree of similarity between trilobite groups from different geographic regions. PC = principal component, S = not significantly different ($p \geq 0.05$) with high overlap (>70%), s = very similar ($p \geq 0.95$) with high overlap, — = comparison of all three regions, overlap not determined, * = $p \leq 0.05$, ● = $p \geq 0.95$. The Appalachian or Great Basin data sets were truncated at the bottom of the upper *Bolaspidella* Biozone to coincide with the lower range of the Texas material.

Taxa Region 1 vs. Region 2	% Overlap	PC1	PC2	PC3	Similarity
Ptychopariida					
All regions ($F_{4,283}$)	—	1.92	1.88	2.12	s
Appalachians vs. Great Basin ($F_{2,248}$)	88	2.14	1.93	4.35*	s
Appalachians vs. Texas ($F_{2,104}$)	96	0.14	0.57	0.31	s
Asaphiscacea, Raymondinacea, and Marjumiacea					
All regions ($F_{4,133}$)	—	1.18	0.58	0.14●	s
Appalachians vs. Great Basin ($F_{2,108}$)	84	0.99	0.32	0.56	s
Appalachians vs. Texas ($F_{2,62}$)	93	0.10	0.02●	0.29	S
Great Basin vs. Texas ($F_{2,71}$)	93	0.37	0.97	0.43	s

vious biomere would empty several ecological niches. If ecological and morphological diversities are correlated, then the reoccupation of these niches would increase the morphological diversity of the assemblage.

Similarity among regions and their overall similarity to the Laurentian pattern should also be an expected result. The shallower areas of Laurentia contain only one biotic province in the Cambrian (Palmer 1979). If biomeres represent adaptive radiations, then an increase in diversity would result from an increase both within and between communities (alpha and beta diversity of Sepkoski 1988) and not from an increase in provinciality (gamma diversity). These diversity changes should be reflected on a local scale. Thus, when the biomere began with limited taxonomic and morphologic content, the fossil assemblages in smaller regions would be constrained in morphology regardless of the paleocommunity that may be represented. As time progressed, the increased taxonomic diversity or morphological range would be incorporated into the existing paleocommunities and/or in assemblages moving into the previously unoccupied environments. This increased packing of taxa or morphologies into the ecosystem should be reflected in different paleocommunities and environments preserved in the stratigraphic sections of smaller regions. This is similar to the introduction of new taxa seen within the Ptychaspid biomere (Westrop 1990) and from the Cambrian to the

Ordovician (Bambach 1983, 1985; Sepkoski 1988).

The reasons for this diversification, however, are not clear. Are the observed patterns the result of either endemic origins, migration, environmental control, or a combination of two or more factors? Palmer (1965) and Stitt (1975) have suggested that trilobites within biomeres have endemic origins. Hardy (1985), Westrop and Ludvigsen (1987), and Westrop (1988) have suggested that patterns of species diversity (and potentially morphological diversity) within the younger Ptychaspid biomere are influenced by the migration of new taxa or environmental controls (for an opposing view see Loch et al. 1993). In addition, some taxa have been reported from other continents (e.g., see Öpik 1967), which also points to the potential of migration influencing the morphological diversity of Laurentia. The potential influence of endemic origins, migrations, and environments on the diversification is discussed below.

Endemic Origins

Palmer (1965) proposed that species within a biomere were derived from a slowly evolving basic stock of deeper-water origins. This stock invaded the depopulated shallow-shelf environments after the extinction event. Under this scenario, these new immigrants would begin to invade unoccupied ecospace as they spread across the shallow-water environment. As they adapted to different life

habits, new species would arise. Stitt (1975) has supported this general view of biomere evolution.

The migration of a basic stock would result in a low morphological diversity in the bottom of the biomere and subsequent speciation would increase the morphological range in the biomere. Data presented here are compatible with the endemic origin of taxa within the Marjumiid biomere. Trilobites in the biomere began with a limited range of morphology and later diversified.

These data, however, do not directly test the endemic origin of taxa within the Marjumiid biomere. The endemic origin of some Laurentian trilobites undoubtedly occurred given the number of similar species and genera found in close stratigraphic proximity. These endemic species probably contributed to the morphological diversification. The endemic origin of the major groups of trilobites, however, is more questionable. How much of a role migration played in the introduction of new forms into Laurentia has not been fully documented.

Migration

The migration of taxa could have had a significant effect on the stratigraphic distribution of morphologies within the Marjumiid biomere. This migration can be divided into three separate aspects: (1) shallow-water taxa migrating within Laurentia; (2) deeper-water taxa migrating into shallow-water environments; and (3) taxa migrating from other continents to Laurentia.

Local Migrations.—Migration within Laurentia had a significant effect on the regional patterns of morphological diversification within the Marjumiid biomere. Genera are widespread in the cratonic deposits of North America and, no doubt, they migrated among regions. The similarity of the stratigraphic distribution of morphologies among regions is probably the result of the relatively rapid migration of new morphologies into the different regions. Rapid migration is supported by the appearance of new genera within the same biozone in all three regions studied. Although biozones are based on the first appearance of taxa, this conclusion is justified

because not all taxa are used to define the biozones. Pelagic(?) agnostid trilobites are also used for correlations.

Deeper Water to Shallower Water Migrations.—The migration of deeper-water taxa that possessed different morphologies would have increased the morphologic diversity of the shallow-water assemblages. However, these deeper water forms apparently do not possess different morphologies. The deep-water faunas of the *Ehmaniella* Biozone (Rasetti 1951; Campbell 1971; Fritz 1971) contain ptychopariid assemblages similar to their contemporary shallow-water assemblages. This indicates that both deep- and shallow-water faunas began with very similar morphologies and with limited taxonomic and morphologic diversity.

Subsequent evolution of these deeper-water forms could have produced distinct morphologies. The later migration or lack of migration of these new forms into shallower-water environments would have influenced the observed morphological diversity. In either situation, the observed morphological diversity would not contain the range of morphologies present at a particular time within Laurentia. Again, deep-water faunas from the *Bolaspidella* and *Cedaria* biozones (Robison 1964, 1988; Hood and Robison 1988) suggest that this did not happen. The *in situ* deeper-water assemblages do not contain any distinctly new morphologies that are not present in shallower-water assemblages.

Intercontinental Migrations.—It is more difficult to establish the influence of intercontinental migrations on the morphological diversification of trilobites in Laurentia. Several species and genera of agnostids, eodiscoids, and corynexochids are widely distributed throughout the Middle Cambrian world (Palmer 1979). In contrast, ptychopariids are typically endemic (Palmer 1979). Only a few ptychopariid genera are known to occur both within and outside Laurentia during the Marjumiid biomere (Öpik 1967; Robison 1988).

Whereas most ptychopariid genera and species of Laurentia are endemic, their families and superfamilies are presently recognized worldwide. The occurrence of the suprageneric taxa on different continents would suggest an exchange of taxa (and morphologies) dur-

ing the Middle Cambrian. At present, it cannot be shown if the genera within these wide-ranging taxa are closely related or have been lumped together as the result of their similar general morphologies (e.g., Harrington et al. 1959). Suprageneric classification of Cambrian ptychopariid trilobites has not yet reached a consensus.

Environmental Constraints

The influences of environmental controls on Cambrian trilobite assemblages are well documented, for example, by Robison (1976), Taylor (1977), Ludvigsen and Westrop (1983a,b), Sundberg (1991), and Westrop (1992). The morphological range of a trilobite assemblage is probably influenced by the environment in which the assemblage lived. Thus, environmental constraints could influence the observed morphological diversification.

The potential influence of local environmental controls on the overall pattern of morphological diversification was greatly reduced by combining trilobites from the Appalachians, Great Basin, and Texas. The Marjumiid biomere in these regions was deposited in different paleogeographic settings (Fig. 12). If biofacies can be crudely correlated to lithofacies, then the regions also contain several different biofacies. The Appalachian materials were derived from sediments deposited in a siliciclastic intracratonic basin and the adjacent portion of the carbonate bank (Markello and Read 1981, 1982; Srinivasan and Walker 1993). The Texas materials were derived from coarse- to fine-grained, siliciclastic sediments deposited in a nearshore setting and the cratonward portion of a carbonate bank (Cornish 1975; King and Chafetz 1983). The Great Basin materials from the lowermost portion of the biomere were derived from siliciclastic and carbonate sediments deposited in an intracratonic basin and the adjacent portion of a carbonate bank (Kopaska-Merkel 1988; Sundberg 1991). The materials from the remaining portion of the biomere were derived from the open-ocean side of the carbonate bank and siliciclastic and carbonate open-shelf or embayment settings (Lohmann 1976; Brady and Koepnick 1979; Rees 1986; Sundberg 1991).

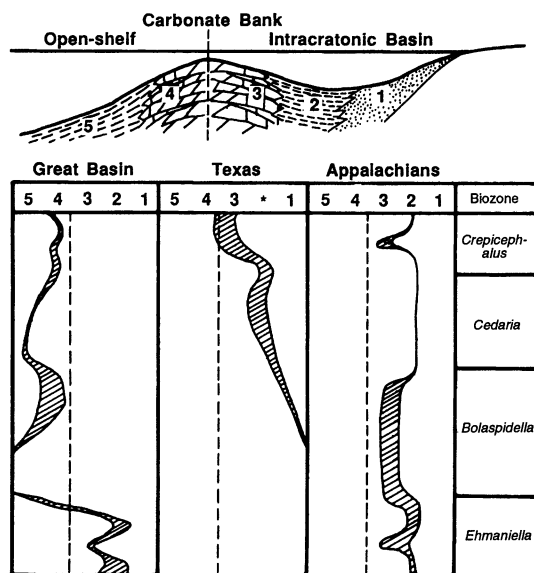This diversity in depositional environments

FIGURE 12. Paleogeographic setting of deposits sampled for specimens in the Marjumiid biomere in the Appalachians, the Great Basin, and Texas. The numbers refer to general depositional settings: 1 = nearshore siliciclastics, 2 = intracratonic-basin shales and limestones, 3 = carbonate bank on intracratonic-basin side, 4 = carbonate bank on the open-ocean side, and 5 = deeper-shelf, open-ocean siliciclastics and carbonates. Hatchered portion under each region represents the environmental range of deposits sampled for this study. *Facies 2 not present in Texas section.

could have strongly influenced the regional diversification patterns. Nonetheless, the regional assemblages have similar diversification patterns despite their differences in the depositional environments (Figs. 6, 8). These patterns are also similar to the overall Laurentian pattern (Figs. 4, 6). This similarity among patterns suggests that the diversification of ptychopariids in Laurentia is the overall controlling influence on the regional patterns. However, individual regions do not show identical patterns, which points to the potential influence of local environmental condition on the regional morphological patterns.

Larger-scale changes in Laurentian paleogeography may have also played a role in the generation of the morphological diversification of trilobites. A general eustatic sea-level rise occurred during the deposition of the Marjumiid biomere (Bond et al. 1989; Osleger 1991). This flooding of the continent would make territory progressively more available for colonization by trilobites. Based on general

species/area relationships (see Sepkoski 1976; Flessa and Sepkoski 1978), one would expect an increase in the taxonomic diversity and, potentially, morphological diversity.

Conclusions

The results from the morphometric analyses of the Ptychopariida from the Marjumiid biomere indicate that these trilobites underwent a morphological diversification during the deposition of the biomere and that this diversification was similar among geographic regions. Analysis of a subset of the Asaphiscacea, Raymondinacea, and Marjumiacea again indicates a morphological diversification during the biomere, and that this diversification was also similar in different regions. These results suggest that the proposed adaptive radiations of the Cambrian biomeres are, at least for the Marjumiid biomere, represented by a morphological diversification. The similar morphological diversification patterns among regions suggest that assemblages from smaller regions reflect the larger-scale macroevolutionary patterns of the Cambrian biomeres.

At this time, there are no clear causes for the diversification of trilobite morphologies in the Marjumiid biomere. Possible mechanisms influencing the overall morphological diversification pattern include endemic evolution, migration of shallow-water taxa within Laurentia, and potentially increased habitat area resulting from a general rise in sea level. Local depositional environments probably did not influence the overall Laurentian pattern but most likely modified the patterns for the regional assemblages. At this time, the role of intercontinental migration cannot be ascertained.

Literature Cited

Bambach, R. K. 1983. Ecospace utilization and guilds in marine communities through the Phanerozoic. Pp. 719–746 *in* M. J. S. Tevesz and P. L. McCall, eds. Biotic interactions in Recent and fossil benthic communities. Plenum, New York.
———. 1985. Classes and adaptive variety: the ecology of diversification in marine faunas through the Phanerozoic. Pp. 191–253 *in* J. W. Valentine, ed. Phanerozoic diversity patterns: profiles in macroevolution. Princeton University Press and Pacific Division, American Association for the Advancement of Science, Princeton, N.J.
Bond, G. C., M. A. Komina, M. S. Steckler, and J. P. Grotzinger. 1989. Role of thermal subsidence, flexure, and eustasy in the evolution of early Paleozoic passive-margin carbonate platforms. *In* P. D. Crevello, J. L. Wilson, J. F. Sarg, and J. F. Read, eds. Controls on carbonate platform and basin development. Society of Economic Paleontologists and Mineralogists Special Publication 44:39–61.
Brady, M. J., and R. B. Koepnick. 1979. A Middle Cambrian platform-to-basin transition, House Range, west central Utah. Brigham Young University, Geological Studies 26:1–7.
Campbell, L. D. 1971. Occurrence of "*Ogygopsis* Shale" fauna in southeastern Pennsylvania. Journal of Paleontology 45:437–440.
Cornish, F. G. 1975. Tidal flat facies in the Hickory Sandstone, Upper Cambrian of central Texas. Geological Society of America Abstracts with Programs 7:154.
Derby, J. R. 1965. Paleontology and stratigraphy of the Nolichucky Formation in southwest Virginia and northeast Tennessee. Ph.D. dissertation. Virginia Polytechnic Institute and State University, Blacksburg.
Eby, R. G. 1981. Early Late Cambrian trilobite faunas of the Big Horse Limestone and correlative units in central Utah and Nevada. Ph.D. dissertation. State University of New York, Stony Brook.
Eldredge, N. 1972. Systematics and evolution of *Phacops rana* (Green, 1882) and *Phacops iowensis* Delo, 1935 (Trilobita) from the Middle Devonian of North America. Bulletin of the American Museum of Natural History 147:45–114.
Flessa, K. W., and J. J. Sepkoski, Jr. 1978. On the relationship between Phanerozoic diversity and changes in habitable area. Paleobiology 4:359–366.
Foote, M. 1993. Discordance and concordance between morphological and taxonomic diversity. Paleobiology 19:185–204.
Fritz, W. H. 1971. Geological setting of the Burgess Shale. Proceedings of the North American Paleontological Convention 2:1155–1170.
Hardy, M. C. 1985. Testing for adaptive radiation: the Ptychaspid (Trilobita) biomere of the Late Cambrian. Pp. 379–397 *in* J. W. Valentine, ed. Phanerozoic diversity patterns: profiles in macroevolution. Princeton University Press, Princeton, N.J.
Harrington, H. J., G. Henningsmoen, B. F. Howell, V. Jaanusson, C. Lochman-Balk, R. C. Moore, Chr. Poulsen, F. Rasetti, E. Richter, R. Richter, H. Schmidt, K. Sdzuy, W. Struve, Leif Størmer, C. J. Stubblefield, R. Tripp, J. M. Weller, and H. B.

Whittington, eds. 1959. Trilobita. Pp. 038–0540 *in* Arthropoda 1, Part O of R. C. Moore, ed. Treatise on invertebrate paleontology. Geological Society of America and University of Kansas Press, Lawrence, Kans.

Hood, K. C., and R. A. Robison. 1988. Trilobites and lithofacies relationships in the Holm Dal Formation (late Middle Cambrian), central North Greenland. Meddelelser om Grønland Geoscience 20:105–112.

King, D. T., Jr., and H. S. Chafetz. 1983. Tidal-flat to shallow-shelf deposits in the Cap Mountain Limestone Member of the Riley Formation, Upper Cambrian of central Texas. Journal of Sedimentary Petrology 53:261–273.

Kopaska-Merkel, D. C. 1983. Paleontology and depositional environments of the Whirlwind Formation (Middle Cambrian), west-central Utah. Ph.D. Dissertation. University of Kansas, Lawrence.

———. 1988. Depositional environments and stratigraphy of a Cambrian mixed carbonate/terrigenous platform deposit: west-central Utah, USA. Carbonates and Evaporates 2:133–147.

Labandeira, C. C., and N. C. Hughes. 1994. Biometry of the Late Cambrian trilobite genus *Dikelocephalus* and its implications for trilobite systematics. Journal of Paleontology 68:492–517.

Loch, J. D., J. H. Stitt, and J. R. Derby. 1993. Cambrian–Ordovician boundary interval extinctions: implications of revised trilobite and brachiopod data from Mount Wilson, Alberta, Canada. Journal of Paleontology 67:497–517.

Lohmann, K. C. 1976. Lower Dresbachian (Upper Cambrian) platform to deep-shelf transition in eastern Nevada and western Utah: an evaluation through lithologic cycle correlation. *In* R. A. Robison and A. J. Rowell, eds. Paleontology and depositional environments: Cambrian of western North America. Brigham Young University Geology Studies 23:139–152.

Ludvigsen, R., and S. R. Westrop. 1983a. Franconian trilobites of New York State. New York State Museum Memoir 23.

———. 1983b. Trilobite biofacies of the Cambrian–Ordovician boundary interval in northern North America. Alcheringa 7:301–319.

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

———. 1982. Upper Cambrian intrashelf basin, Nolichucky Formation, southwest Virginia Appalachians. American Association of Petroleum Geologists Bulletin 66:860–878.

Oldroyd, J. D. 1973. Biostratigraphy of the Cambrian *Glossopleura* Zone, west-central Utah. M.S. thesis. University of Utah, Salt Lake City.

Öpik, A. A. 1967. The Mindyallan fauna of north-western Queensland. Bureau of Minerals Resources of Australia, Bulletin 74.

Osleger, D. 1991. Cyclostratigraphy of Late Cambrian carbonate sequences: an interbasinal comparison of the Cordilleran and Appalachian passive margins. Pp. 801–828 *in* J. D. Cooper and C. Stevens, eds. Paleozoic paleogeography of the western United States–II. Pacific Section, Society of Economic Paleontologists and Mineralogists, Los Angeles.

Palmer, A. R. 1954. The faunas of the Riley Formation in central Texas. Journal of Paleontology 28:709–786.

———. 1965. Biomere—a new kind of biostratigraphic unit. Journal of Paleontology 39:149–153.

———. 1979. Cambrian. Pp. A119–A135 *in* R. A. Robison and C. Teichert, eds. Treatise on invertebrate paleontology, Part A, Introduction. Geological Society of America and University of Kansas, Boulder, Colo. and Lawrence, Kans.

———. 1984. The biomere problem: evolution of an idea. Journal of Paleontology 58:599–611.

Randolph, R. L. 1973. Paleontology of the Swasey Limestone,

Drum Mountains, west-central Utah. M.S. thesis. University of Utah, Salt Lake City.

Rasetti, F. 1951. Middle Cambrian stratigraphy and faunas of the Canadian Rocky Mountains. Smithsonian Miscellaneous Collections 116:1–277.

———. 1965. Upper Cambrian trilobite faunas of northeastern Tennessee. Smithsonian Miscellaneous Collections 148:1–127.

Rees, M. N. 1986. A fault-controlled trough through a carbonate platform: the Middle Cambrian House Range embayment. Geological Society of America Bulletin 97:1054–1069.

Robison, R. A. 1964. Late Middle Cambrian faunas from western Utah. Journal of Paleontology 38:510–566.

———. 1971. Additional Middle Cambrian trilobites from the Wheeler Shale of Utah. Journal of Paleontology 45:796–804.

———. 1976. Middle Cambrian trilobite biostratigraphy of the Great Basin. *In* R. A. Robison and A. J. Rowell, eds. Paleontology and depositional environments: Cambrian of western North America. Brigham Young University Geology Studies 23:39–50.

———. 1988. Trilobites of the Holm Dal Formation (late Middle Cambrian) central North Greenland. Meddelelser om Grønland Geoscience 20:23–103.

Sepkoski, J. J., Jr. 1976. Species diversity in the Phanerozoic: species-area effects. Paleobiology 2:298–303.

———. 1988. Alpha, beta, or gamma: where does all the diversity go? Paleobiology 14:221–234.

Srinivasan, K., and K. R. Walker. 1993. Sequence stratigraphy of an intrashelf basin carbonate ramp to rimmed platform transition: Maryville Limestone (Middle Cambrian), southern Appalachians. Geological Society of America Bulletin 105:883–896.

Stitt, J. H. 1975. Adaptive radiation, trilobite paleoecology, and extinction, Ptychaspid biomere, Late Cambrian of Oklahoma. Fossils and Strata 4:381–390.

Sundberg, F. A. 1989. Biostratigraphy of the lower Conasauga Group, a preliminary report. Appalachian Basin Industrial Associates Spring Program, 1989, 15:166–176.

———. 1990. Morphological diversification of the ptychopariid trilobites in the Marjumiid Biomere (Middle to Upper Cambrian). Ph.D. dissertation, Virginia Polytechnic Institute and State University, Blacksburg.

———. 1991. Paleogeography of western Utah and eastern Nevada during the *Ehmaniella* Biochron (Middle Cambrian). Pp. 387–399 *in* J. D. Cooper and C. H. Stevens, eds. Paleozoic Paleogeography of the Western United States–II. Pacific Section Society of Economic Paleontologists and Mineralogists, Los Angeles.

———. 1994. Corynexochida and Ptychopariida (Trilobita, Arthropoda) of the *Ehmaniella* Biozone (Middle Cambrian), Utah and Nevada. Los Angeles County Museum of Natural History, Contributions in Science 446.

Taylor, M. E. 1977. Upper Cambrian of western North America: trilobite biofacies, environmental significance, and biostratigraphic implications. Pp. 397–425 *in* E. G. Kauffman and J. E. Hazel, eds. Concepts and methods of biostratigraphy. Dowden, Hutchinson and Ross, Stroudsburg, Penn.

Van Valen, L. 1974. Multivariate structural statistics in natural history. Journal of Theoretical Biology 45:235–247.

Vorwald, G. R. 1983. Paleontology and paleoecology of the upper Wheeler Formation (late Middle Cambrian), Drum Mountains, west-central Utah. M.S. thesis. University of Kansas, Lawrence.

Westrop, S. R. 1988. Trilobite diversity patterns in an Upper Cambrian stage. Paleobiology 14:401–409.

———. 1990. Mass extinction in the Cambrian trilobite faunas of North America. *In* D. G. Mikulic, ed. Arthropod paleobiology. Short Courses in Paleontology 3:99–115.

———. 1992. Upper Cambrian (Marjuman-Steptoean) trilo-

bites from the Port au Port Group, western Newfoundland. Journal of Paleontology 66:228–255.

Westrop, S. R., and R. Ludvigsen. 1987. Biogeographic control of trilobite mass extinction at an Upper Cambrian "biomere" boundary. Paleobiology 13:84–99.

White, W. W., III. 1973. Paleontology and depositional environments of the Cambrian Wheeler Formation, Drum Mountains, west-central Utah. M.S. thesis. University of Utah, Salt Lake City.

Appendix

Taxonomic groupings of genera in the Marjumiid biomere database. The numbers in parentheses are the number of species/subspecies in three different data sets for each taxonomic level: Appalachian, Great Basin, Texas. * = New genera, which are listed by number (e.g., New Genus 1). These taxa have been informally named in theses and dissertations and are presented in Sundberg 1990: table 2.

Order	Superfamily	Family	Genus
Ptychopariida (84,166,35)	Solenopleuracea (9,21,3)	Solenopleuridae (0,7,0)	*Solenopleura*? (0,1,0)
			Solenopleurella (0,1,0)
			Spencella (0,5,0)
		Lonchocephalidae (4,9,0)	*Agelagma* (1,1,0)
			Amiaspis (2,0,0)
			Glaphyraspis (0,2,0)
			Terranovella (1,1,0)
			Trymataspis (0,3,0)
			Unidentified (0,1,0)
			Welleraspis (0,1,0)
		Kingstoniidae (2,5,2)	*Ankoura* (1,0,1)
			Brachyaspidion (0,2,0)
			Kingstonia (1,3,1)
		Catillicephalidae (3,0,1)	*Madarocephalus* (1,0,0)
			Pemphigaspis (2,0,1)
	Asaphiscacea (7,13,0)	Asaphiscidae (7,13,0)	New Genus 1* (1,0,0)
			Asaphiscus (2,1,0)
			Blountia (3,10,0)
			Blountiella (0,2,0)
			Maryvillia (1,0,0)
	Raymondinacea (8,15,8)	Cedariidae (3,8,3)	*Bonneterrina* (0,0,1)
			Cedaria (2,6,1)
			Cedarina (1,0,1)
			Carinamala (0,2,0)
		Llanoaspididae (5,7,5)	*Acruolimbus* (0,0,1)
			Genevievella (2,5,1)
			Llanoaspis (3,2,3)
	Norwoodiacea (17,12,4)	Menomoniidae (11,11,2)	*"Acrocephalops"* (3,0,0)
			Bolaspidella (1,6,1)
			Coenaspis (1,0,0)
			Deiracephalus (0,1,1)
			Densonella (1,2,0)
			Holcacephalus (2,1,0)
			Menomonia (3,1,0)
		Norwoodiidae (6,1,2)	*Hardyoides* (0,1,1)
			Norwoodella (5,0,0)
			Norwoodia (1,0,1)
	Marjumiacea (30,32,16)	Crepicephalidae (15,13,10)	*Coosella* (5,7,3)
			Coosia (3,3,2)
			Coosina (2,1,1)
			Crepicephalus (5,2,2)
			Syspacheilus (0,0,2)
		Marjumiidae (11,11,2)	*Bonneterrina* (2,0,0)
			Marjumia (0,2,0)
			Modocia (8,8,2)
			New Genus 2* (0,1,0)
			Talbotina (1,0,0)
		Tricrepicephalidae (4,8,4)	*Meteoraspis* (2,5,2)
			Tricrepicephalus (2,3,2)

Appendix. Continued.

Order	Superfamily	Family	Genus
	Leiostegiacea (1,0,0)	Pagodiidae (1,0,0)	*Ithycephalus* (1,0,0)
	Ptychopariacea (10,43,0)	Ehmaniellidae (10,43,0)	*"Alokistocare"* (1,0,0)
			Altiocculus (0,5,0)
			"Armonia" (2,0,0)
			Blairella (1,0,0)
			Chanciaopsis (0,1,0)
			"Ehmaniella" (6,5,0)
			Elrathia (0,6,0)
			Elrathiella (0,9,0)
			?Glyphaspis (0,1,0)
			Proehmaniella (0,3,0)
			Pseudoalokistocare (0,2,0)
			Pseudomexicella (0,1,0)
			Trachycheilus (0,5,0)
			Tympanuella (0,4,0)
			Utaspis (0,1,0)
	Unknown (2,30,4)	Unknown (2,30,4)	New Genus 3* (0,1,0)
			Bathyocos (0,2,0)
			Brassicicephalus (0,1,1)
			Deltina (0,2,0)
			New Genus 4* (0,2,0)
			Elrathina (0,4,0)
			Hawkinsia (1,0,0)
			Jenkinsonia (0,1,0)
			Loxoparia (1,0,0)
			Semishaerocephalus (0,1,0)
			Unidentified (0,9,3)
			New Genus 5* (0,2,0)
			Yuknessaspis (0,3,0)
			New Genus 6* (0,2,0)