MORPHOLOGIC PATTERNS OF DIVERSIFICATION: EXAMPLES FROM TRILOBITES

by MIKE FOOTE

ABSTRACT. The morphologic diversification of the Trilobita is investigated using a Fourier description of the cranidia of Cambrian and Ordovician trilobites from North America. Morphologic diversity increases from the Early Cambrian to the Middle Ordovician, but does not correlate well with patterns of generic or familial diversity. Suprageneric taxa of trilobites are shown objectively to represent morphotypes. Morphologic dispersion among suprageneric taxa and the distinctness of these taxa both increase from the Cambrian to the Ordovician. This result agrees with patterns based on hypostomal morphology (Whittington 1988*a*, 1988*b*), and therefore is not an artifact of using cranidial morphology. These patterns are caused by the origination of new higher taxa, not evolution within established higher taxa. Higher taxa tend to retain the same morphology once established, rather than diverging gradually. In this respect, higher taxa may be said to have sudden origins. The origination of higher taxa may be linked to the opening of new adaptive zones, particularly in the Early Ordovician, following widespread extinctions of trilobites.

THE fossil record clearly indicates that evolutionary change is not evenly distributed over time, but is concentrated in episodes of evolutionary radiation. For the Metazoa at least, the early Phanerozoic represents the most important of these episodes. Yet, despite its significance, a limited number of approaches has been used to study this great diversification, most notably the analysis of taxonomic data (e.g. Valentine 1969; Erwin *et al.* 1987). Often implicit in the analysis of diversification by 'taxon counting' is the assumption either that morphologic diversity can be measured by taxonomic diversity, or that the number of taxa reflects the number of objectively discernible morphotypes. Valentine (1969), for example, used the assumption that the separation among groups at a higher taxonomic level usually represents a larger morphological divergence than that among groups at a lower level in order to draw conclusions about community evolution from temporal patterns in the appearance of groups at various taxonomic levels.

Although we know that taxonomic data and morphologic data often correlate, taxonomic and morphologic approaches are not simply redundant. If taxa are consistently defined, then taxonomic data can tell us about the number of biological units at a given time. But if we want to know the nature of these units, how they originate, and how they evolve once established, morphologic data are clearly necessary. Since form represents the raw data of palaeobiology, it is important to document significant events in the history of life from the standpoint of morphology.

Because the events of the early Phanerozoic diversification are concentrated in the Cambrian and Ordovician, documenting patterns of morphologic evolution associated with this radiation requires a well preserved fossil group that is diverse and abundant during these two periods. Trilobites are clearly the group of choice. Although all skeletonized metazoan phyla were present by the Ordovician, some 75% of known Cambrian species were trilobites, while trilobites account for 23% of described Ordovician species (Raup 1976). It is the availability of trilobites, rather than any intrinsic property such as complexity, that makes them useful for a case study in diversification.

This study has two principal objectives: (1) to document patterns of morphologic diversification in the Trilobita during the Cambrian and Ordovician; and (2) to investigate morphologic dispersion within and among suprageneric taxa of trilobites in order to determine the taxonomic level(s) at which morphologic diversification is concentrated. Although this paper focuses on trilobites, it is important to keep in mind that trilobites provide only a case study. It is hoped that the results may yield generalizations regarding morphologic radiation when compared to information from other

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groups of organisms and other times in the history of life. Finally, while it is interesting and important to test hypotheses regarding the mechanisms and processes of evolution, it is necessary first to document patterns in the rough. Therefore, although ecological and evolutionary processes will be discussed, the following analysis is largely exploratory.

MATERIAL AND METHODS

Morphometric foundations

The consideration of large scale patterns of morphologic evolution requires the establishment of a morphospace, i.e., a multidimensional lattice of morphologic variables in which biological forms can be consistently and objectively represented. This involves (1) the selection of an aspect of form (some part or parts of an organism), and (2) the means to describe that aspect of form. The choice of the part of the organism can be justified *a priori* (e.g. on ecological grounds), or *a posteriori* if patterns of evolution based on a subset of morphology seem concordant with patterns based on a more extensive set of features.

For trilobites, the cranidium is appropriate for studying large scale evolutionary patterns. First, it is well preserved and recognizable through time and across nearly all taxonomic lines. Second, it has ecological significance in reflecting the size and orientation of sensory structures such as eyes, the style of moulting, and the attachment of feeding appendages. Finally, as shown below, patterns of cranidial evolution are concordant with subjective assessments based on gross morphology and hypostomal morphology.

For nearly all Cambrian and Ordovician trilobites the cranidium, or 'central dorsal portion of cephalon bounded laterally by facial sutures' (Harrington *et al.* 1959, p. O119), is easy to define and identify. In the case of marginal sutures (e.g. Harpina, Trinucleacea), the lateral bounds of the cranidium can be identified with the lateral margin of the cephalon. In some cases (e.g. some Phacopina) the facial suture is not functional, but can nevertheless be identified. The only difficulty is with olenellids and some agnostids, which lack a facial suture. For purposes of this study the cranidium in such cases is operationally defined as if the cephalon were bounded by a marginal suture. This solution is purely operational, and the 'cranidium' so defined obviously does not have the same biologic significance as the true cranidium. However, it seems that for these few exceptions it would be unwise to discard an otherwise very useful morphologic system. It should be noted that in the material studied here, the number of specimens without a definable cranidium is less than 2% of the total sample size. Therefore it is unlikely *a priori* that this limitation would present a serious bias.

The question of morphologic evolution involves the consideration of descent with modification. Therefore, one would ideally hope to recognize a set of homologous points or features that could be defined consistently among all taxa at all times. This is difficult for the cranidium, since the suture is a continuous feature with few discrete landmarks. (Of course, the cranidial midline or axis itself is an homologous feature, but it alone enables little morphologic description.) Considering other parts of the trilobite, homologous points may be identified within certain groups, for example fringe pits in trinucleids (Hughes 1970) and tubercles in encrinurids (Temple and Tripp 1979). However, such features cannot be meaningfully recognized on all trilobites.

Given this limitation, it is necessary to consider shape *per se*. This has previously been done by considering sets of linear measures (e.g. Ashton and Rowell 1975; Rowell *et al.* 1982), but the utility of this approach generally depends on restricting the analysis to a relatively small group of trilobites. In this study, shape was quantified by a Fourier description of the closed curve that represents the projected outline of the cranidium. (This method is discussed in detail elsewhere (Foote 1989*b*), and only cursory treatment will be given here.) The glabella is an important biological feature, since it reflects cephalic segmentation, as well as a feature of much utility in taxonomy. However, because it is often difficult to identify consistently, especially in many of the

taxa with effaced forms, such as the Asaphacea and Scutelluina, its morphology was not considered in this study. The cranidium provides only a limited assessment of morphology, but it is necessary to sacrifice detail for the sake of a large-scale analysis such as that presented here (see also Raup 1966, 1967). For work at finer scales, the cranidial outline would clearly be inadequate.

Following the guidelines of Shaw (1957, p. 194), the cranidium is placed in a standard orientation. The cranidium is oriented with the palpebral lobe horizontal, or, if this is not possible, with the axial furrows horizontal. With very convex forms, the chord to the palpebral lobe or axial furrow is used to orient the specimen (Shaw 1957, p. 194). This standard orientation allows comparison among many diverse forms, and thus has an advantage over using presumed 'life positions', which vary from group to group, and in many cases are not known. The error associated with orienting and measuring specimens has been shown to be small (Foote 1989*b*).

The projected outlines of cranidia were drawn with a microscope and camera lucida. These drawings were digitized electronically and shape analysis was performed on the stored images. As described previously (Foote 1989*b*), 12 Fourier coefficients contain approximately 99% of the shape information contained in the cranidial outline. These 12 coefficients were used as morphometric variables, forming the basis of a 12-dimensional morphospace. In order to allow equal weighting of the variables, the data were standardized as $x' = (x-\bar{x})/s$, where x is the original variate, $\bar{x}$ is its mean, s is its standard deviation, and x' is the standardized variate. (Standardization was used rather than a method such as the percent-range or percent-maximum transformation, since these last two techniques rely on single, observed values [minimum and/or maximum]. In general, such single values are expected to be more heavily influenced by sampling than statistics of the entire population [the mean and standard deviation], which are more reliably determined.) In order to allow comparisons among stratigraphic intervals, all data were standardized at once, rather than one interval at a time.

The definition of the outline is straightforward except when there are spines. These spines are of two types: (1) those that actually form part of the cranidial margin (e.g. genal spines), and (2) those that are not part of the margin but project out over it (e.g. occipital spines). Because spines of the first type actually define the outline of the cranidium, these were included. Spines of the second type were excluded, i.e., the cranidial outline was drawn as if the projecting spine were not present.

Scope

This study is limited to the Cambrian and Ordovician. Although the Cambrian and Ordovician do not contain the major part of the total diversity of most skeletonized marine animals, the majority of trilobite abundance and diversity is concentrated in these two periods. Thus, the analysis documents most of the evolutionary history of the trilobites.

To keep the study tractable, sampling is limited to North America. Because the analysis presented here is at a coarse taxonomic level (the evolutionary history of superfamilies, suborders and orders), biogeographic changes alone would seem unlikely, *a priori*, to cause the observed patterns. It is shown below that patterns documented with North American trilobites are concordant with those subjectively determined using more extensive distributions of trilobites. Therefore, with respect to the questions addressed here, the evolution of trilobites in North America is representative of the evolution of the global trilobite fauna. Furthermore, but perhaps less significantly, provinciality appears not to change from the Cambrian to the Ordovician (Valentine *et al.* 1978; Sepkoski 1988).

Preservation

Trilobites are frequently sheared, compressed, or crushed. For character recognition, identification, and systematics, this may not present severe problems. However, morphometric analysis requires either undistorted material or material that is consistently distorted. Consistent distortion is nearly impossible to obtain, so one must use undistorted material. For this reason, sampling was limited almost exclusively to carbonates. Fossils in carbonates are generally not appreciably distorted, even though the rocks themselves may be compacted (Shinn *et al.* 1977). Some well preserved cranidia are used from non-carbonate rocks (e.g. some chert nodules), but the vast majority of specimens are

from carbonates. (This lithologic restriction implies that the material represents an environmentally biased sample. However, the coarse scale of the analysis, as well as the fact that the patterns documented here are consistent with other work involving a broader range of environments (see below), suggest that this bias is unlikely to be the cause of the observed patterns.)

Sampling

Historically there has been one group of systematists that worked primarily on Cambrian trilobites and another group on post-Cambrian forms (Whittington 1954; Fortey, pers. comm.). Thus, Cambrian and Ordovician genus concepts are unlikely to be comparable, and sampling simply from a list of genera might impart a bias. One possible solution to this problem is to sample strictly randomly. This introduces an unknown amount of error or bias reflecting collecting methods. The magnitude of this bias should decrease as the size of collections and the number of collectors increases. Therefore, material for this study was drawn from large museum collections, both stratigraphic and systematic (at the United States National Museum, the Museum of Comparative Zoology (Harvard University), and the Yale Peabody Museum). While museum collections are not strictly random subsets of all available fossils, they probably represent a more random sampling than would a list of genera or species.

Specimens were chosen randomly from museum collections by looking through every drawer known to contain trilobites and selecting every specimen that was sufficiently well preserved to allow morphometric description. The number of usable specimens in the combined collections of the three museums is in the hundreds to thousands.

Random sampling presents problems of its own. Groups of species tend to show right-skewed abundance-frequency distributions. That is, there are many species with a low abundance and a few species with a high abundance (e.g. Koch 1987). It is therefore likely that completely random sampling would force patterns to be dominated by a few abundant species. In order to circumvent this problem, sampling was arbitrarily limited to a maximum of three specimens per species per time horizon per locality. (To avoid cumbersome working, I will hereafter use the phrase 'per population' without implying the same meaning for 'population' that a neontologist uses.) In this way, some degree of intra-populational variability is quantified, but the overdominance of very abundant species is avoided. (Because data from many time planes are stratigraphically lumped to increase sample sizes (see below), it is possible for more than three specimens from a species to occur within the data of a single stratigraphic interval.) Each datum in this study represents a single cranidium selected as described above. Total sample size is 560, representing over 250 genera and over 400 species. A list of genera and species used in this study, and the Fourier coefficients for all specimens, were given by Foote (1989*a*).

Clearly some taxonomic bias remains with this method of sampling, since it implicitly assumes that species represent some real and consistent unit. If a 'true' species is finely split into many nominal species then more sampling is permitted from this species than from a species which is not oversplit in this way. Since it is possible (see above) that Cambrian species are more finely split than Ordovician species, one would expect the morphologic differences among related Cambrian species to be systematically less than among related Ordovician species. However, the data do not indicate this bias. It is shown below that the morphologic difference among specimens within higher taxa does not systematically increase through time. Thus, although the analysis cannot be said to be completely free of taxonomic bias, whatever bias may be inherent at the species level does not appear to have a great effect.

Stratigraphic division

The traditional stratigraphic division of the Cambrian into Lower Cambrian, Middle Cambrian, and Upper Cambrian (e.g. Lochman-Balk and Wilson 1958; Robison 1964) is adopted here (Table 1). A recent, comprehensive correlation of Ordovician formations of the United States (Ross *et al.* 1982) divides the Ordovician into the Ibexian, Whiterockian, Mohawkian, and Cincinnatian Series. Because of the large hiatus in the Whiterockian, sample size for this series is very low. It would be

TABLE 1. Stratigraphic division and sample sizes. Ages and durations in parentheses based on Sloan (in press). Others based on Sepkoski (1979) and Ross *et al.* (1982). Ages in millions of years before present, rounded to nearest million years. Durations in millions of years.

Interval	Age at base	Duration	Sample size
Silurian	435 (438)		
Ordovician 3	465 (454)	30 (16)	73
Ordovician 2	485 (477)	20 (23)	127
Ordovician 1	504 (504)	19 (27)	116
Upper Cambrian	518 (527)	14 (23)	125
Middle Cambrian	540 (554)	22 (27)	86
Lower Cambrian (trilobite-bearing)	562 (577)	22 (23)	33

useful to have a subdivision of the Ordovician that involved roughly comparable intervals of time and comparable sample sizes. I have therefore divided the Ordovician into three informal intervals, Ordovician 1, Ordovician 2, and Ordovician 3 (Table 1). (It is shown below that using the conventional division into Ibexian, Whiterockian, Mohawkian, and Cincinnatian Series does not alter the evolutionary patterns documented here.) Ordovician 1 is defined as that the interval from the base of the Ordovician approximately to Ross's Zone N, near the middle of the Whiterockian (*c.* middle of the Llanvirnian). (The placement of the boundary between Ordovician 1 and Ordovician 2 is somewhat arbitrary, since it lies within an interval that is barren with respect to data collected here. This barren interval reflects the major unconformity between the Sauk and Tippecanoe sequences (Sloss 1963). All the trilobites studied are either clearly from the lower part of the Whiterockian or the upper part, but not from the middle.) The top of Ordovician 2 coincides with the Blackriverian/Rocklandian boundary (*c.* middle of the Caradocian), and the top of Ordovician 3 coincides with the Ordovician/Silurian boundary.

The ages given in Table 1 are not known with certainty, and reflect the time scale given by Sepkoski (1979) for the Cambrian, and Ross *et al.* (1982) for the Ordovician. The apparently long duration of Ordovician 3 may appear to present problems, but it should be noted that most of the data for Ordovician 3 (63 out of 73 specimens) are pre-Cincinnatian and so lie within roughly the first half of Ordovician 3. An alternative chronology (dates in parentheses in Table 1) of the Cambrian and Ordovician (Sloan in press) yields interval durations that are rather different (and less variable) than those based on Sepkoski (1979) and Ross *et al.* (1982). (For the dates presented here, the Whiterockian is arbitrarily divided in half.) Because this study does not use absolute ages (e.g. to calculate evolutionary rates), the finer details of dating are of minor importance.

Classification of specimens into suprageneric taxa

The genealogies of trilobites are generally not sufficiently well known that all suprageneric taxa represent natural groupings (e.g. Bergström 1973; Fortey and Chatterton 1988). No claim is made here that every taxon used is a clade. However, it is reasonable to assume for the sake of discussion that higher taxa are rough approximations to monophyletic groups. Eldredge (1977, p. 320) expressed the opinion that 'many, if not most' superfamilies as defined in Harrington (1959) 'seem reasonably homogeneous', i.e. 'more or less monophyletic'. This seems more reasonable for some taxa (e.g. Trinucleacea) than others (e.g. Ptychopariacea) (Fortey and Chatterton 1988).

For the purposes of analysing variability within and among higher taxa of trilobites, the level of the superfamily is used. This taxonomic level generally allows reasonably large sample sizes, and in many cases superfamilies appear to represent morphotypes. The classification used is primarily that of the *Treatise*. Although this classification is by no means perfect, it is often presented as the closest thing to a consensus (e.g. Clarkson 1986). Modifications to the *Treatise* classification were based on later work by Fortey and Owens (1975) (Proetida), Lane and Thomas (1983) (Scutelluina),

and Fortey and Chatterton (1988) (Asaphina). The families Lecanopygidae and Plethopeltidae were included in the Proetida. These forms had not been sufficiently studied by Fortey and Owens (1975) to determine their affinities, but they are linked with other proetids in the *Treatise*. Genera named after the publication of the *Treatise* were generally classified according to the author's taxonomic assignment. Where suprageneric classification is not given but an author expresses belief in a certain relationship, that relationship was used for suprageneric assignment.

In cases where no superfamilies are defined (e.g. Redlichiina), suborders are treated as if consisting of a single superfamily; thus, these suborders are treated as taxa of rank equivalent to that of superfamilies. Similarly, where no suborders are defined (e.g. Odontopleurida), the order is treated as if consisting of a single superfamily. Of the 560 specimens used, 303 (54·1 %) are assigned to established superfamilies, 99 (17·7 %) are assigned to suborders treated here as superfamilies, and 158 (28·2 %) are assigned to orders treated here as superfamilies. Sample sizes for the higher taxa range from 1–50 and are given in Foote (1989*a*). The known stratigraphic range for the higher taxa correlates well with the stratigraphic range represented in this study (Foote 1989*a*).

The higher taxa are analysed as groups irrespective of their position in the taxonomic hierarchy. For example, if the Proetida were best considered a suborder of the Ptychopariida, or the Remopleuridacea a superfamily within the Ptychopariina rather than within the Asaphina, this would have absolutely no bearing on the analysis. In addition, reassignment of specimens to different families, genera or species would leave the analysis unaffected as long as they remained within the same suprafamilial taxon. An analysis (not presented here) using the suborder, rather than the superfamily, as the fundamental higher taxonomic unit yielded results in agreement with those presented here.

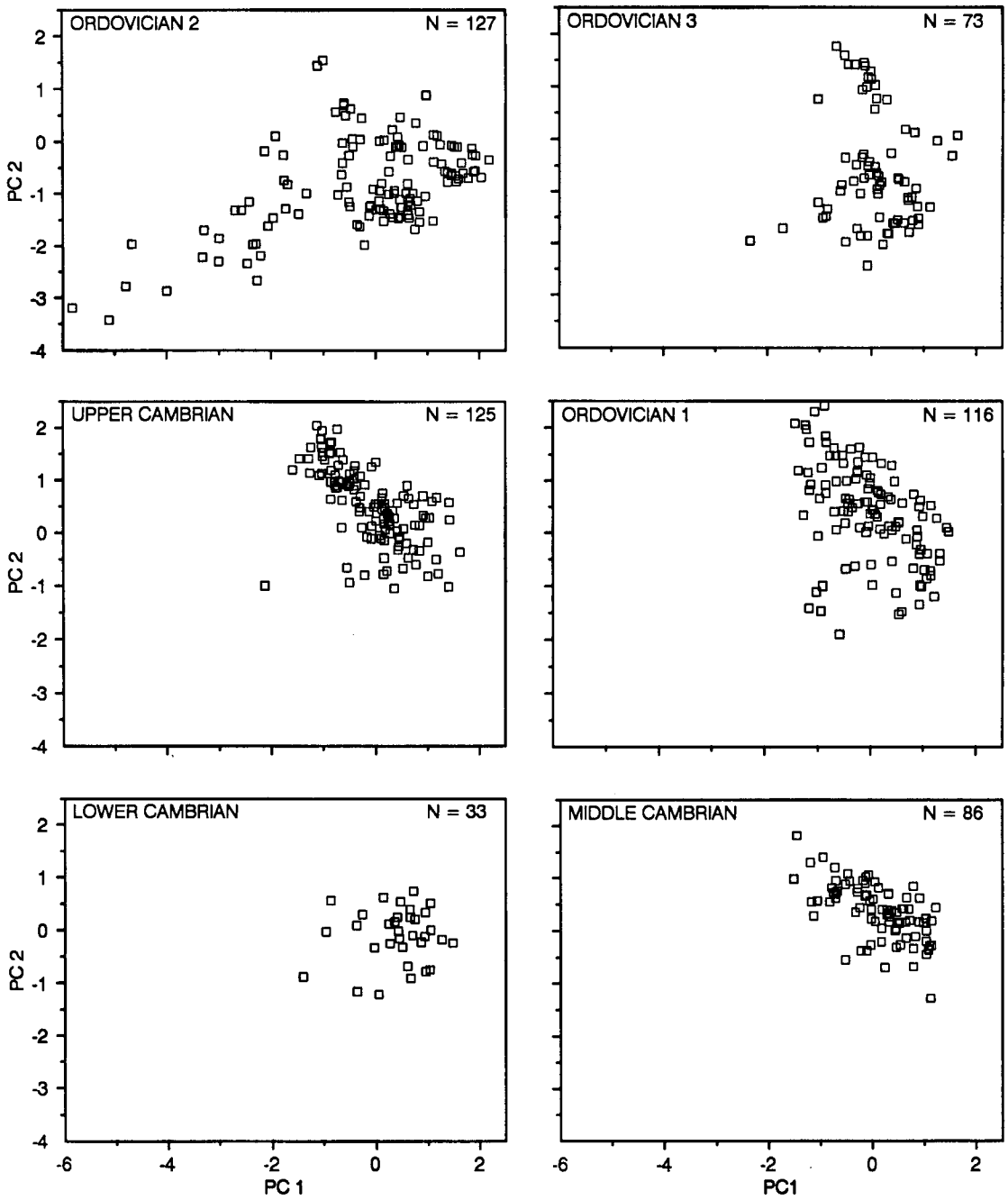
DATA ANALYSIS

Diversification within the Trilobita as a whole

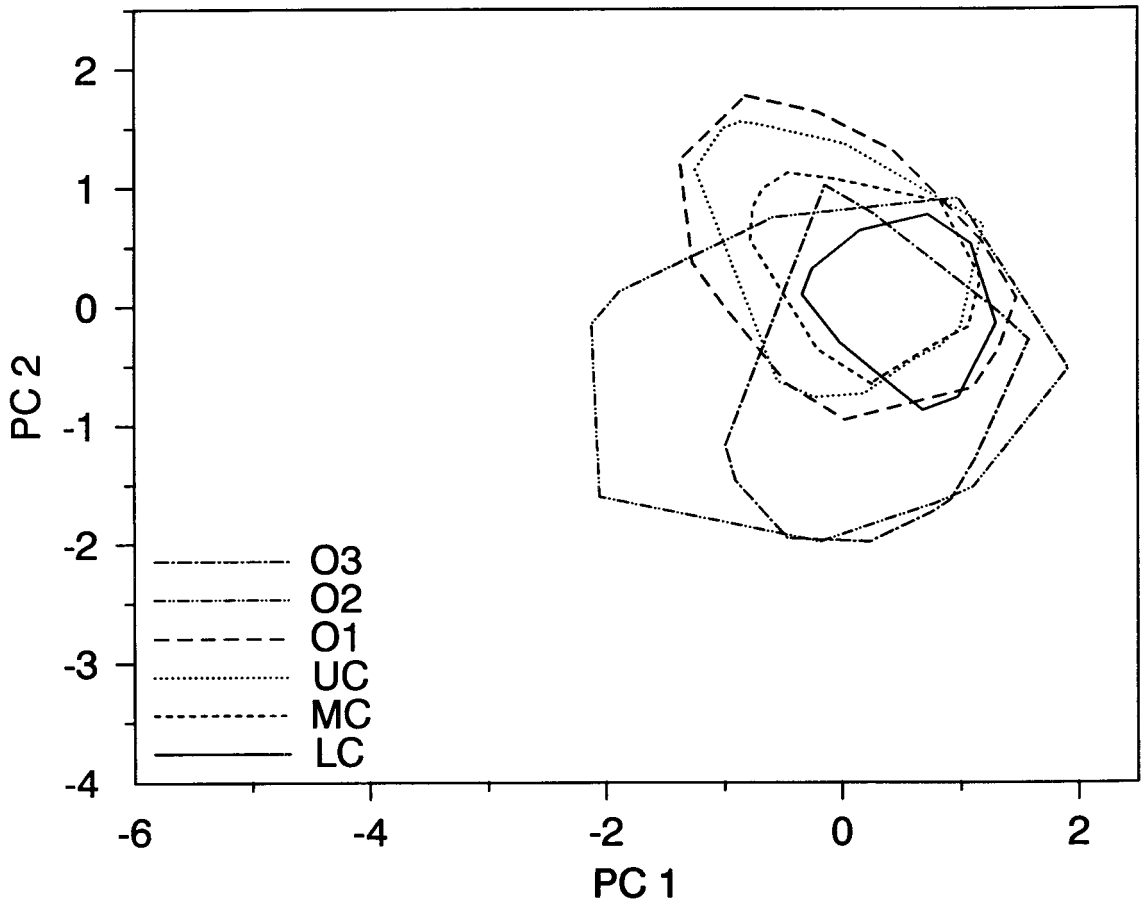
Before looking at the evolution of higher taxa of trilobites, it is useful to determine the patterns of morphologic diversity for the trilobites as a whole. Text-figure 1 shows all data plotted in a two-dimensional principal-component space, based on the correlation matrix of the original 12-dimensional morphospace of Fourier coefficients. (These two principal components summarize approximately 63 % of the variability among specimens contained in the 12-dimensional morphospace.) The principal components are used for graphical purposes only; later calculations are based on the complete, twelve-dimensional Fourier space. Inspection of Text-figure 1 reveals a clear increase in morphologic dispersion or variability through time.

Just a few morphologically extreme specimens could strongly affect one's visual impression of this pattern. It is therefore useful to remove the influence of extreme specimens. For each stratigraphic interval the morphologic centroid is determined. An envelope is then constructed which contains the 80 % of the data lying closest to the centroid (in the principal-component space) (Text-fig. 2). Thus, the most extreme 20 % of the data are excluded. Note that the figure 80 % is an arbitrary one, and this is not meant to be a robust statistical method for the removal of outliers. The point is to remove the effects of extreme forms without the assumption or belief that they 'don't belong'. It is clear from Text-figure 2 that the apparent increase in overall dispersion is not the result of a few extreme specimens.

That morphologic variability depicted in this way tends to increase is in agreement with what one would expect from a subjective assessment of the diversity of trilobite form. Comparing the diversity among post-Cambrian phacopids, asaphids, trinucleids, proetids, and odontopleurids to the diversity among Cambrian corynexochids, redlichiids and ptyhoparioids, the picture presented in Text-figures 1 and 2 should come as no surprise. Nevertheless, the quantitative documentation of this pattern is important and useful for at least two reasons. First, it allows a degree of confidence that is greater than that permitted by a subjective impression, no matter how keen. Second, it allows more detailed evolutionary questions to be addressed, such as the taxonomic level at which the diversification is concentrated (see below).



TEXT-FIG. 1. Trilobite cranidia plotted in principal-component space. Standardized scores for the first (PC 1) and second (PC 2) principal components are shown. Each point represents a single specimen. Sample sizes given by *N*.

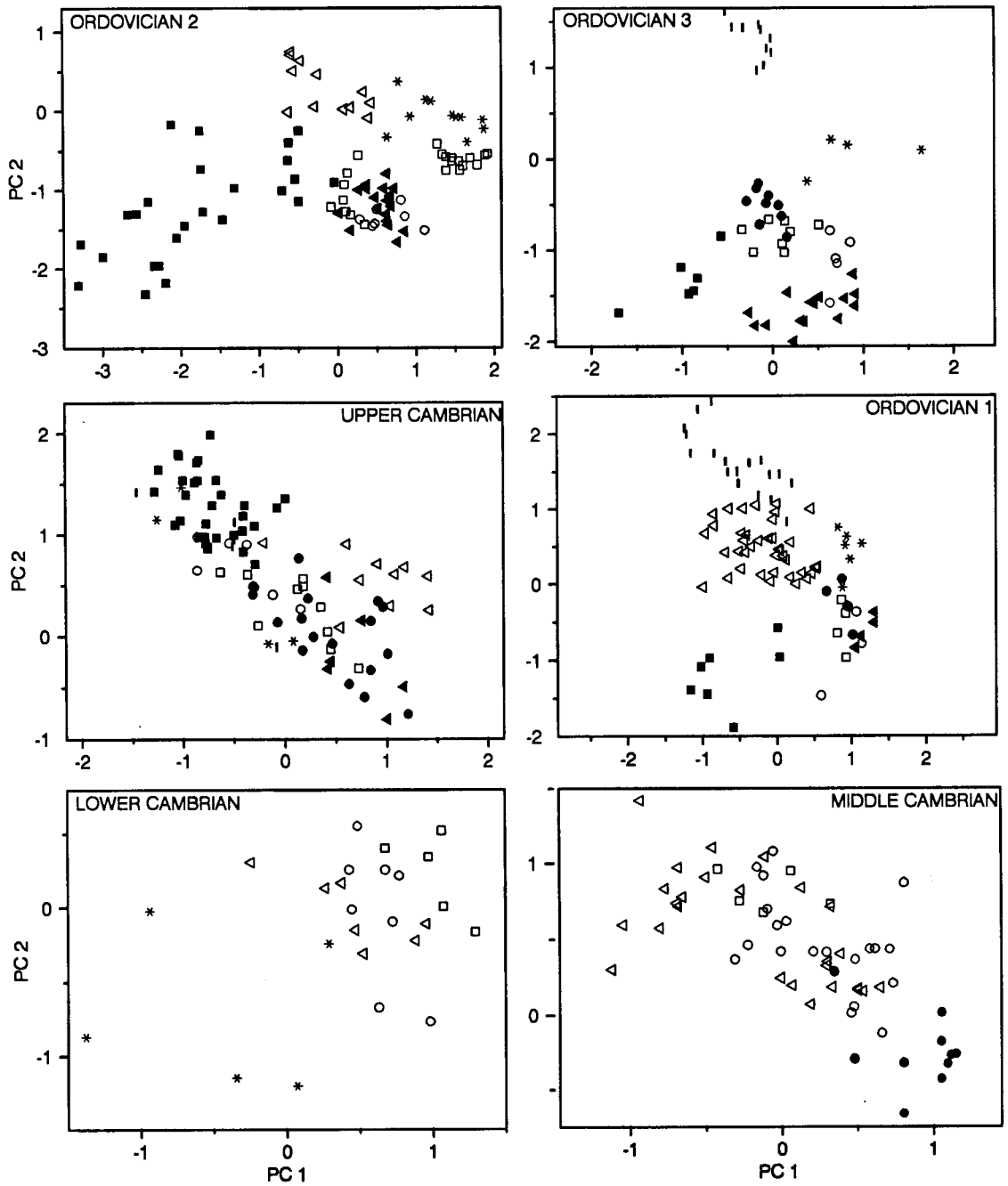


TEXT-FIG. 2. Envelopes surrounding the 80% of the specimens lying closest to the centroid for each respective stratigraphic interval. Axes as in Text-figure 1. Abbreviations: LC, Lower Cambrian; MC, Middle Cambrian; UC, Upper Cambrian; O1, Ordovician 1; O2, Ordovician 2; O3, Ordovician 3.

Even disregarding our knowledge of the fossil record of trilobites, such an increase in variability may be expected. As Stanley (1973) and Gould (1988) have argued, if a clade or lineage begins its history with a certain morphology, it is the null expectation that morphologic variance will increase as new and different forms evolve. It is intriguing that morphologic variability continues to increase into Ordovician 2, even though generic and familial diversity are greatest in the Middle to Upper Cambrian and decline through the Ordovician (Sepkoski 1982, 1984, and unpublished generic data). Even under conditions of decreasing taxonomic diversity, an increase in morphologic dispersion may be the null expectation if we consider morphologic evolution as a 'diffusive process'. The total range of morphospace occupied could tend to increase even if the number of biologic units occupying that morphospace decreased.

Preliminary analysis of higher taxa

The morphometric methods established above allow further questions to be addressed concerning the morphologic evolution of the trilobites. How does the gross pattern of diversification correlate with patterns among higher taxa? Does diversification proceed at many scales, and is the increase



TEXT-FIG. 3. Scatterplots of the 80% of the specimens for each group lying closest to the group centroid. Only groups with five or more specimens are shown. Axes as in Text-figure 1. Key: Lower Cambrian: △, Corynexochida; □, Eodiscina; ✱, Olenellina; ○, Ptychopariacea; Middle Cambrian: △, Corynexochida; □, Marjumiacea; ○, Ptychopariacea; ●, Solenopleuracea; Upper Cambrian: ■, Anomocaracea; ▮, Illaenuracea; ▲, Komaspidacea; □, Marjumiacea; ✱, Raymondinacea; △, Proetida; ○, Ptychopariacea; ●, Solenopleuracea; Ordovician 1: ▮, Asaphacea; ■, Cheirurina; □, Conocoryphacea; ✱, Cyclopygacea; ▲, Komaspidacea; ●, Olenacea; △, Proetida; ○, Scutelluina; Ordovician 2: ■, Cheirurina; □, Odontopleurida; △, Proetida; ✱, Remopleuridacea; ○, Scutelluina; ▲, Trinucleacea; Ordovician 3: ▮, Asaphacea; other symbols as for Ordovician 2.

in dispersion evident within higher taxa as well? Do higher taxa represent morphotypes, as was implicitly assumed above?

The dispersion within and among higher taxa is depicted graphically in Text-figure 3. Here, only the 80% of the specimens lying closest to the morphologic centroid (in principal-component space) for each group are presented. As above, the purpose of this culling procedure is to remove the visual effect of extreme specimens. To keep the graphs simple, only groups with sample sizes of at least five are plotted. Two patterns are evident here:

1. There is no obvious tendency for within-group dispersion to increase through time. (Note that the scatterplots for different intervals are drawn at different scales.) At all times there are groups encompassing a large range of morphology, as well as morphologically more restricted taxa. This is true even though some of the higher taxa are at the level of the order.

2. The separation among groups clearly increases through time. This pattern is most striking when the Cambrian as a whole is compared to the Ordovician as a whole, but the trend is also evident within the Ordovician. Cambrian trilobites are difficult to partition into suprageneric groups that correspond to well-defined morphotypes, while at least some Ordovician taxa correspond to morphologically well defined units. This is in accord with previous observations (e.g. Rasetti 1954, 1961; Palmer 1958; Whittington 1966). It is likely that if more dimensions (i.e. morphologic variables) were added to this analysis, the Cambrian groups would become easier to discriminate. However, the fact that discrimination has historically been relatively difficult suggests that the difference between the Cambrian and the Ordovician is real.

Dispersion within groups shows no obvious trend, while dispersion among groups increases. This suggests that the overall morphologic diversification among the trilobites is tied to patterns at higher taxonomic levels. This is not meant to imply that there are superfamily-level evolutionary processes that differ fundamentally from evolutionary mechanisms within populations.

Quantitative analysis of higher taxa

The patterns depicted in two dimensions appear striking, but should be quantified in the 12-dimensional space. I emphasize that *all subsequent analyses in this paper are based on the complete, 12-dimensional Fourier space, not the principal-component space.* This quantification requires the use of multivariate measures of dispersion. There has been much discussion about how to measure morphologic dissimilarity (e.g. Van Valen 1974; Ashton and Rowell 1975; Atchley *et al.* 1982; Cherry *et al.* 1982). In principle, variances (e.g. Pearson 1926) and covariances (e.g. Atchley *et al.* 1982) should be taken into account when describing morphologic distances among groups. In practice, however, it has been found that simple distance measures that do not consider variances and covariances are more reliably estimated (Atchley *et al.* 1982; Cherry *et al.* 1982). Atchley *et al.* (1982) point out that simple distance measures may be more precise (i.e. more reliably estimated) but may be further from the morphologic 'truth'. For purposes of this study, it is more important that distance measures be reliable so that they can be compared among taxa and among times. Therefore, simple Euclidean distance is used here as a measure of morphologic dissimilarity. If there are p variables, then the Euclidean distance between two specimens is given by

$$d_{12} = \left[\sum_{j=1}^{p} (X_{j1} - X_{j2})^2 \right]^{\frac{1}{2}} \quad (1)$$

where X_{j1} and X_{j2} are the values of variable j on specimens 1 and 2.

Three dispersion indices were defined for the 12-dimensional Fourier space. W is the weighted mean of all within-group distances, and gives a measure of the morphologic variability within higher taxa. (Methods of weighting are discussed below.) A is the weighted mean of the distances among group centroids, and provides a measure of the morphologic variability among higher taxa. (The group centroid is an imaginary point representing the average morphology of the group, i.e., the arithmetic average for each of the variables measured on all specimens within a group.) Intuitively, it seems that the less dispersion there is within taxa and the greater the distance among taxa, the

better defined or more distinct those taxa are. Therefore, discreteness, D, is defined as A/W. D is qualitatively similar to Mahalanobis' generalized distance, D^2 (Davis 1986, p. 486). D differs from Mahalanobis' D^2 in that it does not take into account variable correlations (which may not be reliably estimated for small sample sizes (Atchley *et al.* 1982; Cherry *et al.* 1982)), and does not assume a homogeneous variance–covariance structure.

In computing W, the number of pairwise comparisons increases with the square of the group sample size rather than with the sample size itself. This implies that large groups contribute disproportionately to the average distance. A method of weighting was used to correct for this. Within-group distances were weighted so that each group contributes to W according to its sample size rather than the number of comparisons made within that group. This method of weighting is explained below.

If: G is the number of groups; n_i is the number of specimens in group i ($i = 1, \ldots, G$); G' is the number of groups with $n_i > 1$ (i.e. the number of groups in which comparisons can be made); c_i is the number of pairwise comparisons in group i (equal to $n_i(n_i-1)/2$; N is the total number specimens; N' is the total number of specimens in groups with $n_i > 1$ (i.e. the total number of specimens in groups in which comparisons can be made); d_{ijk} is the Euclidean distance between specimens j and k in group i; and $\bar{d}_i$ is the mean of all pairwise distances within group i, (equal to $\sum_{j=1}^{n_i}\sum_{k=j+1}^{n_i} d_{ijk}/c_i$); then W is defined as follows:

$$W = \frac{1}{N'}\sum_{i=1}^{G} \bar{d}_i n_i \tag{2}$$

where the sum is only over those groups where $n_i > 1$.

If A were computed without weighting, then a group with a large sample size, i.e. a group whose centroid is very reliably determined, and a group with a small sample size, i.e. a group whose centroid is less reliably determined, would make the same contribution to the average distance among groups (and therefore to the determination of discreteness, D). A method of weighting was used so that each group contributes to A in proportion to its sample size. Thus, groups whose position in morphospace is better determined have greater weight. This is explained below.

If: N, G, and n_i are defined as above; $\bar{n}$ is the average group sample size (equal to N/G); M is the number of comparisons among groups (equal to $G(G-1)/2$); and d_{ij} is the distance between the centroids of groups *i and j*; then

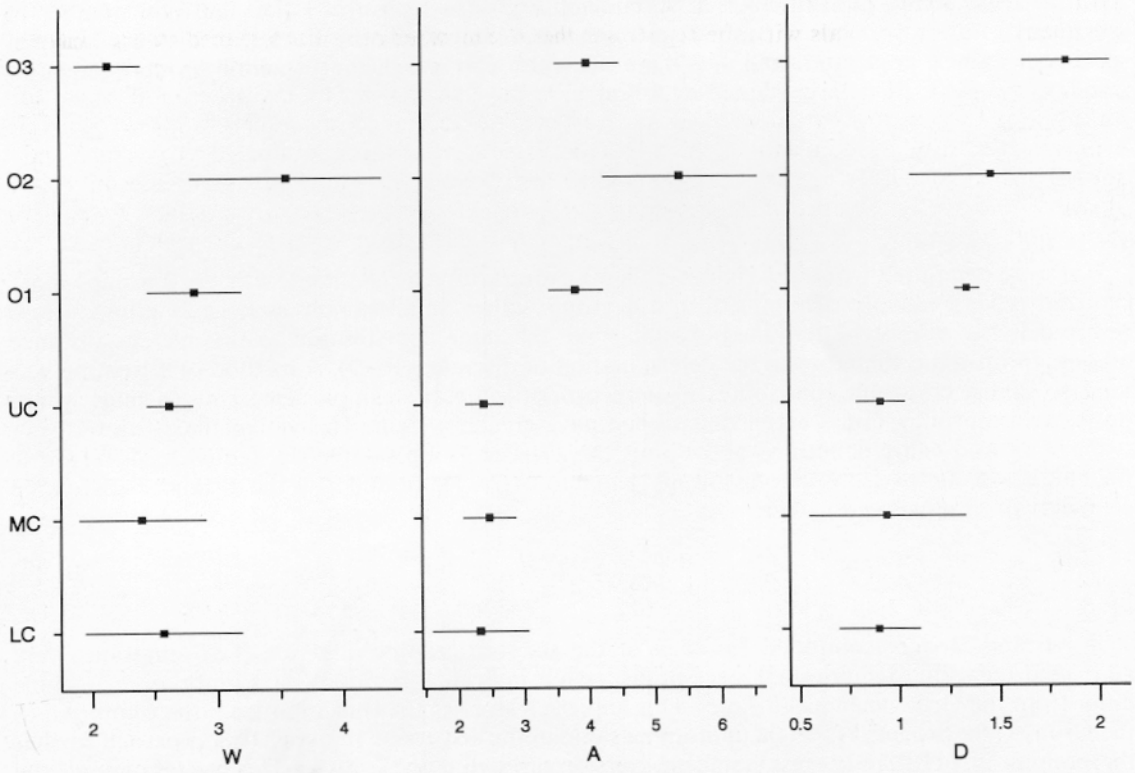
$$A = \frac{1}{2\bar{n}M}\sum_{i=1}^{G}\sum_{j=i+1}^{G} d_{ij}(n_i+n_j). \tag{3}$$

W, A, and D were computed for each of the six stratigraphic intervals. Two questions were addressed regarding temporal changes in dispersion indices. First, does the Cambrian as a whole differ from the Ordovician as a whole? This approach stresses the transition from the Cambrian to the Ordovician. Second, is there a monotonic trend in the dispersion indices? This approach stresses the continuity of the patterns. Some means of comparing these dispersion indices among the intervals is needed. This involves the estimation of how well constrained the indices are, i.e. the estimation of the standard error.

Jackknifing (Sokal and Rohlf 1981, p. 795) was used to obtain unbiased estimates of W, A, and D and to determine the variability associated with these estimates. By this method one group is omitted and W, A and D are recomputed. (Because W is not defined for a group with a sample size of one, it is recomputed only if the group omitted has a sample size greater than one.) If G_i is the number of groups in the ith interval, then a pseudovalue, Y_j, is calculated as $Y_j = G_i(X)-(G_i-1)(X_j')$, where X is the original value (i.e. W, A, or D), and X_j' is the value calculated when the jth group is omitted. (When calculating pseudovalues corresponding to W, G_i' is substituted for G_i.) Each group is left out in turn, and the mean of all the Y_j provides an unbiased estimate of X. The standard error of the Y_j provides an unbiased estimate of the standard error of X.

TABLE 2. Dispersion indices and their standard errors. In this and all subsequent tables, G is the number of higher taxa relevant to the calculation of A and D, G' is the number of higher taxa relevant to the calculation of W, and SE stands for 'standard error'. Abbreviations: LCAM, Lower Cambrian; MCAM, Middle Cambrian; UCAM, Upper Cambrian; ORD1, Ordovician 1; ORD2, Ordovician 2; ORD3, Ordovician 3.

Interval	G	G'	W	SE	A	SE	D	SE
LCAM	6	4	2·57	0·62	2·33	0·72	0·90	0·20
MCAM	9	6	2·40	0·50	2·47	0·39	0·94	0·39
UCAM	14	10	2·62	0·18	2·39	0·28	0·91	0·12
ORD1	10	10	2·82	0·37	3·80	0·41	1·34	0·06
ORD2	10	9	3·55	0·76	5·39	1·16	1·46	0·40
ORD3	8	8	2·14	0·26	3·98	0·49	1·84	0·22



TEXT-FIG. 4. Unbiased estimates of within- and among-group dispersion plotted against stratigraphic position. Error bars give one standard error on either side of dispersion index. Abbreviations as in Text-figure 2.

The unbiased estimates of W, A, and D are given with their standard errors in Table 2 and are shown in Text-figure 4. A method of comparing values through time is needed. One could use parametric statistical approaches, for example, making multiple comparisons among the values, or using the standard errors for analysis of variance. Using the standard errors estimated with jackknifing is analogous to treating each pseudovalue as if it were a single observation. Non-parametric statistical approaches are developed below, but this same approach is used: each pseudovalue is treated as a single datum.

To test for differences between the Cambrian and the Ordovician, the Kruskal–Wallis statistic, H (a non-parametric analogue to analysis of variance), was computed (Sokal and Rohlf 1981, p. 430). This method treats each observation (pseudovalue) as a ranked variate. For example, there are 57 observations (pseudovalues) computed for the analysis of A. In a ranking from lowest to highest, the six observations for the Lower Cambrian have ranks of 30, 2, 1, 14, 47, and 41, corresponding to the pseudovalues calculated when the groups Eodiscina, Corynexochida, Ptychopariacea, Solenopleuracea, Olenellina, and Redlichiina, respectively, are omitted. In the statistical testing of H, the distribution of ranks among categories (i.e. stratigraphic intervals) is compared to the distribution expected for a random partitioning of ranks. H is distributed approximately as χ^2 for a random partitioning (Sokal and Rohlf 1981, p. 432).

To test for monotonic changes in the dispersion indices, Kendall's rank correlation coefficient, τ, was computed (Sokal and Rohlf 1981, p. 602). The observations are ranked as above, and each stratigraphic interval is ranked from lowest to highest. Statistical tables were constructed by randomization. For example, in the testing of A there are six intervals with 6, 9, 14, 10, 10, and 8 groups, respectively. Thus the total number of observations is 57. The ranks 1 to 57 are randomly assigned to the six intervals with the constraint that the number of ranks assigned to each interval be equal to the actual number of observations in that interval. τ is then computed for the randomized ranks. This procedure is repeated 1000 times to construct a distribution of values of τ that would be expected by chance (Table 3). If an observed value of τ exceeds, say, 95% of the values obtained by randomization, this observed value is considered significant at $p = 0{\cdot}05$ and a monotonic trend is inferred. For the data studied here and for the culled data sets discussed below, distributions of τ were constructed and compared to the normal approximation (Burr 1960; Sokal and Rohlf 1981, p. 606; Rohlf and Sokal 1981, p. 77) (Table 3). Inspection of the results reveals that the distributions constructed by randomization are generally conservative for statistical testing, i.e., the null hypothesis of lack of monotonicity is less likely to be rejected.

TABLE 3. Critical values of τ, the rank correlation coefficient, generated by randomization. 'Tables' refers to other tables in the text to which these values are relevant. 'Indices' refers to dispersion indices in the relevant tables for which these values are used. Subscripts for τ refer to the significance levels generated by randomization. P-values give the corresponding significance level obtained using the normal approximation.

Tables	Indices	$\tau_{0{\cdot}05}$	P	$\tau_{0{\cdot}01}$	P	$\tau_{0{\cdot}001}$	P
4	*W*	0·215	0·033	0·272	0·0072	0·347	0·0006
4, 11	*A, D*	0·190	0·037	0·247	0·0068	0·285	0·00014
9	*W, A, D*	0·397	0·021	0·506	0·0034	0·599	0·0006
11	*W*	0·235	0·038	0·286	0·0062	0·323	0·002

As would be expected from the two-dimensional representations of higher taxa (Text-fig. 3), there is no significant change in within-group dispersion through time (Table 4). This result holds whether the Cambrian as a whole is compared to the Ordovician as a whole, or whether all six intervals are compared sequentially for monotonic changes. Thus, the obvious increase in total morphological dispersion among all trilobites does not result from the increase in the diversity of forms within an existing suprageneric taxon.

Also in agreement with the view presented in Text-figure 3, there is a significant increase in among-group dispersion (Table 4). The Cambrian as a whole differs from the Ordovician as a whole, and the changes among the six intervals indicate a monotonic trend. The total increase in dispersion among all trilobites is therefore linked to evolutionary patterns at taxonomic levels above that of the genus. This increase in among-group dispersion may result from either (1) the first appearance of new higher taxa that are morphologically well removed from their ancestors, or (2) the morphological divergence of established higher taxa, or some combination of these two. These

TABLE 4. Kruskal–Wallis statistics and Kendall rank correlation coefficients. In this and all subsequent tables, * indicates statistically significant at $P < 0{\cdot}05$, ** means significant at $P < 0{\cdot}01$, and *** means significant at $P < 0{\cdot}001$. All statistical tests in this study are two-sided.

Index	H	τ
W	0·600	0·029
A	14·676***	0·325***
D	14·191***	0·349***

alternatives are discussed below. Finally, given the significant increase in among-group dispersion and the lack of pattern in within-group dispersion, the morphologic discreteness of higher taxa increases through time (Table 4). This is in accord with previous observations that post-Cambrian trilobites are easier to classify into suprageneric taxa than are Cambrian forms (e.g. Whittington 1966).

Reality of morphotypes

In addition to investigating temporal changes in dispersion among taxa, it is important to determine whether, for a single stratigraphic interval, the taxa have some reality as morphotypes. One way to test this is to determine whether the discreteness value observed for a single stratigraphic interval differs significantly from discreteness values that would be expected for a random arrangement of specimens into groups. For each interval there are G groups with sample sizes n_i, $i = 1, \ldots, G$. Groups were artificially constructed so that the specimens were randomly divided among the G groups with the corresponding sample sizes. The discreteness, D, was then calculated for this random arrangement. One hundred unique randomizations were constructed for each stratigraphic interval, yielding a distribution of values of D that would be expected by chance. Comparison between observed values of D and the distributions of randomized values for each interval indicates that, with the possible exception of the Lower Cambrian, the arrangement of specimens into higher taxa is morphologically non-random (Table 5). Higher taxa of trilobites are thus shown to represent morphotypes, at least with respect to the shape of the cranidium.

TABLE 5. Number of randomized discreteness values greater than observed. Based on 100 randomizations.

Interval	N
Lower Cambrian	6
Middle Cambrian	0
Upper Cambrian	0
Ordovician 1	0
Ordovician 2	0
Ordovician 3	0

Analysis of persistent taxa

To determine whether new higher taxa are morphologically displaced from their ancestors, or established higher taxa move away from each other in morphospace, all higher taxa that appear in but a single interval were first removed from the data set, leaving all taxa that persist for two or more intervals. These remaining taxa were then arranged into sets of coexisting, persistent taxa to form smaller sets of data. Five such data sets were constructed and analysed as above (Tables 6–10). The rank correlation coefficient was computed only if the number of stratigraphic intervals was greater than two.

TABLE 6. Dispersion indices for Eodiscina, Corynexochida, Ptychopariacea and Solenopleuracea in Lower Cambrian and Middle Cambrian.

	Lower Cambrian	Middle Cambrian	*H*
G	4	4	
G′	3	4	
W (SE)	2·06 (0·28)	2·48 (0·55)	0·50
A (SE)	1·42 (0·62)	2·12 (0·66)	0·33
D (SE)	0·66 (0·34)	0·88 (0·32)	0·08

TABLE 7. Dispersion indices for Asaphiscacea, Crepicephalacea, Marjumiacea, Norwoodiacea, Ptychopariacea and Solenopleuracea in Middle Cambrian and Upper Cambrian.

	Middle Cambrian	Upper Cambrian	*H*
G	6	6	
G′	4	5	
W (SE)	1·89 (0·06)	2·62 (0·25)	4·86*
A (SE)	2·21 (0·59)	1·98 (0·41)	0·41
D (SE)	0·79 (0·36)	0·76 (0·17)	2·56

TABLE 8. Dispersion indices for Proetida, Komaspidacea, and Olenacea in Upper Cambrian and Ordovician 1.

	Upper Cambrian	Ordovician 1	*H*
G	3	3	
G′	2	3	
W (SE)	2·88 (0·39)	2·81 (0·52)	0·33
A (SE)	1·72 (0·08)	4·48 (1·56)	3·86*
D (SE)	0·56 (0·14)	1·75 (0·48)	3·86*

TABLE 9. Dispersion indices for Scutelluina, Cheirurina, Proetida, Asaphacea, Remopleuridacea and Trinucleacea in Ordovician 1, Ordovician 2, and Ordovician 3. *G′* is equal to *G* for all intervals. *H* measures the overall heterogeneity among the three intervals.

	ORD1	ORD2	ORD3	*H*	τ
G	6	6	6		
W (SE)	2·90 (0·63)	3·57 (1·13)	2·30 (0·32)	1·91	−0·27
A (SE)	3·90 (0·64)	4·81 (1·10)	4·46 (0·51)	0·22	0·21
D (SE)	1·33 (0·11)	1·26 (0·28)	1·92 (0·24)	3·94	0·428*

TABLE 10. Dispersion indices for Scutelluina, Odontopleurida, Cheirurina, Proetida, Asaphacea, Remopleuridacea and Trinucleacea in Ordovician 2 and Ordovician 3. *G′* is equal to *G* for both intervals.

	Ordovician 2	Ordovician 3	*H*
G	7	7	
W (SE)	3·48 (0·81)	2·30 (0·26)	1·80
A (SE)	4·38 (1·07)	4·13 (0·54)	0·20
D (SE)	1·25 (0·15)	1·78 (0·24)	2·55

If established higher taxa diverged morphologically, one would expect an increase in among-group dispersion within the subsets of persistent taxa. This is generally not the case. The only exception is the transition from the Upper Cambrian to Ordovician 1. Here a significant increase in among-group dispersion is marked by changes in taxonomic composition within the higher taxa. Komaspidacea in the Upper Cambrian is dominated by the Elviniidae, and in the Lower Ordovician by the Komaspididae. Perhaps more importantly, the Upper Cambrian Proetida are dominated by plethopeltids, and the Lower Ordovician Proetida by hystricurids. That higher taxa tend to occupy a relatively fixed place in morphospace is also evident from inspection of Text-figure 3.

Discussion

Since persistent higher taxa do not diverge appreciably, the significant increase in among-group dispersion is tied to the origin of new higher taxa. This might be seen as an inevitable consequence of the practice of classification. When forms show significant morphological divergence, they are perforce assigned to new higher taxa, leaving a paraphyletic residue. The phylogenetic relationships among higher taxa of trilobites are not sufficiently well known to state with certainty which groups are paraphyletic. However, the following discussion of higher taxa used in this study suggests that, at the least, we can be confident that paraphyly is more prevalent among Cambrian taxa than among post-Cambrian taxa.

Either Redlichiina or Olenellina would appear to be paraphyletic. If opisthoparian sutures are primitive, then Redlichiina may be seen as the paraphyletic ancestor of Olenellina (Eldredge 1977). If, on the other hand, lack of dorsal sutures is the primitive condition, then Olenellina may be the paraphyletic ancestor of Redlichiina (Fortey and Whittington 1989). Eodiscoids are probably derived relative to polymeroid trilobites, and primitive relative to agnostoids (Eldredge 1977; Fortey and Whittington 1989). This suggests that Eodiscina is the paraphyletic ancestor to holophyletic Agnostina. Lane and Thomas (1983), in expressing their belief in the relationship between Corynexochida and Scutelluina, left open the question of whether the corynexochids are a paraphyletic ancestor of Scutelluina, or a holophyletic sister group.

Paraphyly appears to be quite common among the ptychoparioid superfamilies. Robison (1987, p. 231) believes that 'many or most families [of trilobites] arose independently from an unspecialized stock (ptychoparian) ...' As Eldredge (1977) points out, most similarities among trilobite groups represent symplesiomorphies, and many of the diagnoses of ptychoparioid superfamilies in the Treatise (Harrington *et al.* 1959) read like descriptions of a generalized trilobite. Of the superfamilies considered here, Asaphiscacea, Crepicephalacea, Komaspidacea, Leiostegiacea, Marjumiacea, Ptychopariacea, and Solenopleuracea seem to fit the description of a generalized ptychoparioid trilobite. On the other hand, a few ptychoparioid superfamilies are characterized by features that *may* be seen as valid synapomorphies. Conocoryphaceans lack eyes, norwoodiaceans are characterized by proparian or gonatoparian sutures, olenaceans have free cheeks that are fused or separated by a median suture, and raymondinaceans are characterized by cedariiform sutures (Harrington *et al.* 1959).

Phylogenetic analysis of the Asaphina (Fortey and Chatterton 1988) suggests that paraphyly is much less common in this predominantly post-Cambrian suborder. While Fortey and Chatterton believe the Asaphacea and Anomocaracea to be paraphyletic, Cyclopygacea, Dikelocephalacea, Remopleuridacea, and Trinucleaca appear to be holophyletic (Fortey and Chatterton 1988). Although not supported completely by formal phylogenetic analysis, it would seem that other post-Cambrian taxa are quite homogeneous and well derived, so that they are likely to be holophyletic. These include Harpina, Lichida, Odontopleurida, Phacopina, Proetida, and Scutelluina.

While the greater prevalence of paraphyletic taxa in the Cambrian no doubt contributes to patterns of within- and among-group dispersion, one observation suggests that this bias is not alone responsible. If taxonomic practice forced among-group dispersion to increase in the way outlined above, it could be argued that the increase should be rather regular. Instead, there is a large jump from the Upper Cambrian to Ordovician 1, and even within the Ordovician the increase can be seen. But within the Cambrian there is virtually no change in among-group dispersion. There is

something about the distribution of forms in the Ordovician that *allows* systematists to define groups in such a way that newer groups are morphologically far removed and distinct relative to older taxa. If the separation of younger taxa were merely the result of this taxonomic artifact, then one would expect to see the pattern within the Cambrian, *if the distribution of Cambrian forms allowed this taxonomic practice to be exercised.*

Taxonomic artifact of another sort must also be considered. As discussed above and elsewhere (e.g. Whittington 1954; Foote 1988), it is possible that Cambrian and post-Cambrian genus concepts are not wholly compatible. The sampling methods employed here were designed to circumvent this bias. However, if taxonomic concepts were disparate at higher levels as well, this difference could, in part, cause the patterns seen here. The results shown above could conceivably tell more about changes in taxonomic practice than in the occupation of morphospace. However, changes in taxonomic practice are not independent of changes in the distribution of forms. It seems reasonable to suppose that if genera in the Cambrian showed a distribution of forms that would allow them to be arranged into discrete suprageneric taxa, then they would have been. Simply put, the results of this quantitative analysis are in agreement with what students of trilobites have long known regarding the distinctness of higher taxa (e.g. Rasetti 1954, 1961; Whittington 1954, 1966; Palmer 1958).

The pattern of increasing taxonomic separation is clearly linked to the overall morphological diversification of the trilobites. It is conceivable that Cambrian forms are difficult to arrange into discrete suprageneric groups because the total amount of morphospace occupied is so small. It is also possible that taxonomic separation is high in the Ordovician because of the influence of a few extreme groups. Ordovician taxa in the inner regions of morphospace might be similar in distinctness to Cambrian taxa. If so, the increase in average separation could be caused by the large among-group distances associated with the morphologically peripheral taxa. However, the observed pattern is not the result of these two factors, as shown by the following analysis.

The morphologic centroid (in the complete, 12-dimensional space) was calculated for each stratigraphic interval. A morphologic distance was chosen that defines a hypersphere centred on the Middle Cambrian centroid, and within which 90% of the Middle Cambrian data happen to fall. (This choice is somewhat arbitrary, but is justifiable. A much smaller volume would exclude too much of the Ordovician data. For example, the volume containing 80% of the Middle Cambrian data includes only 14% of the data of Ordovician 2, and therefore makes statistical analysis dubious. On the other hand, a much larger volume would include too much data, and therefore make the analysis nearly identical with that presented above.) The same volume is placed in turn in each of the six stratigraphic intervals, centred on the morphologic centroid for that interval. This constant volume contains 79% of the Lower Cambrian data, 90% for the Middle Cambrian, 77% for the Upper Cambrian, 59% for Ordovician 1, 44% for Ordovician 2, and 58% for Ordovician 3.

Analyses of the data within the constant volume indicates the same pattern as the unculled data. There is no significant change in within-group dispersion, but among-group dispersion and discreteness increase significantly. This implies that the pattern is not caused by extreme taxa, and can be detected at a smaller scale. With respect to taxonomic practice, we can conclude that Cambrian forms are difficult to classify into discrete higher taxa not because the total amount of morphospace occupied is smaller, but because the Ordovician morphospace is occupied in a more discontinuous manner.

BIASES IN DATA COLLECTION AND STRATIGRAPHIC CLASSIFICATION

Several analyses are presented below to correct for various potential biases in data collection and stratigraphic classification. These analyses involve subsets of data that are culled from the original data set. Space limitations preclude detailed presentation of results, but all further analyses yield patterns in general agreement with those presented above. More detailed treatment can be found in Foote (1989*a*).

General statement regarding data standardization

As explained above, all data were standardized to allow for equal weighting of the variables. Because the standardized variates depend on the calculated mean and standard deviation of the original variates, they will differ somewhat depending on whether the data are standardized before or after culling. The following general guideline is used to decide when to perform the standardization. If the purpose of culling is to correct for a bias that is expected to 'distort' the morphospace, then standardization is done after culling. (For example, oversampling of a particular group or time period would bias the mean and standard deviation, so standardization would be done after the oversampled data were removed.) Otherwise, data would be standardized before culling.

Differences in sample size

It is conceivable that changes in sample size could contribute to the pattern in group separation. For example, an increase in sample size would increase the chance of sampling morphologically extreme forms, and this could tend to increase the apparent dispersion among groups. This seems unlikely *a priori*. The Upper Cambrian, Ordovician 1, and Ordovician 2 have roughly the same sample sizes, but the pattern of increasing among-group dispersion is still evident if these intervals are compared (Table 2). Nevertheless, the effects of this potential bias should be treated explicitly.

To do so, the data were culled in two ways: (1) The Lower Cambrian was omitted because of its very small sample size, and from each of the remaining five intervals 73 specimens (corresponding to the smallest of the sample sizes, that for Ordovician 3) were chosen at random. (2) The Lower Cambrian was retained, and 33 specimens (corresponding to the Lower Cambrian sample size) were randomly chosen from each interval. In both cases the data were standardized after culling and were subjected to the same analysis outlined above. The results of this analysis are in agreement with those presented above, indicating that differences in sample size are not the cause of the observed patterns.

Sampling procedure

Perhaps more significant than sample size itself is the way in which specimens were chosen. The sampling procedure described above allowed up to three specimens per population to be sampled. Systematic changes in abundance could bias the pattern of within-group variability. There are more species in the Ordovician that are represented well enough in museum collections to reach this 'saturation point' of three specimens per population. This partly reflects the diverse silicified faunas from the Ibexian of Utah (Ross 1951) and the Whiterockian and Mohawkian of Virginia (Whittington 1941, 1956, 1959; Whittington and Evitt 1953). In general, replicates of the same species reduce the amount of within-group dispersion, since replication results in more within-species comparisons, i.e. more small distances. If this bias were strong enough it would artificially

TABLE 11. Dispersion indices for data set allowing maximum of one specimen per population. Abbreviations for stratigraphic intervals as in Table 2.

	G	*G'*	*W* (SE)	*A* (SE)	*D* (SE)
LCAM	6	4	3·01 (0·72)	2·42 (0·75)	0·80 (0·17)
MCAM	9	6	2·42 (0·51)	2·48 (0·41)	0·94 (0·36)
UCAM	14	10	2·69 (0·19)	2·37 (0·27)	0·88 (0·11)
ORD1	10	9	3·06 (0·42)	3·87 (0·45)	1·26 (0·08)
ORD2	10	8	3·81 (0·82)	5·68 (1·2)	1·42 (0·43)
ORD3	8	7	2·27 (0·31)	4·12 (0·51)	1·79 (0·26)
H			0·98	17·49***	13·13***
τ			0·051	0·352**	0·353**

increase the apparent discreteness of the Ordovician groups. To eliminate this bias the data were culled so that a maximum of a single specimen per population was retained. The data were standardized after culling, and analysed as above.

As would be expected, within-group dispersion for all stratigraphic intervals is higher when the replicates are removed (Table 11). Although this effect appears to be greater in the Ordovician, it does not significantly alter the patterns observed. Of course, this does not address the issue of what would have happened had a different limit been imposed, say six replicates rather than three. But the small difference between one and three replicates suggests that the effect would probably have been small. It is likely that unlimited (i.e. completely random) sampling would have a greater effect, but such a method of sampling is difficult to justify, as explained above.

Extreme data

There are two types of extreme data that could potentially affect the evolutionary patterns observed: (1) specimens that are extreme relative to the majority of specimens within a stratigraphic interval, and (2) specimens within a group that lie at the morphological periphery of that group. A few extreme data of the first kind in the Ordovician could conceivably cause the observed increase in among-group distance, but this appears not to be the case here. This potential bias was implicitly tested above when the data were culled to exclude all specimens lying outside a certain constant volume in morphospace. The same patterns are seen near the centre of morphospace as throughout the entire morphospace.

Extreme specimens within a group may increase mean within-group distance. To determine whether such specimens have a strong effect, the data were culled as follows. The morphological centroids were determined for each group. The 80% of the specimens in each group falling closest to the group centroid were retained, and the remaining 20% of the data discarded. This procedure is not intended to define outliers statistically but rather to determine the effects of the morphologically least ordinary specimens within a group. It is not claimed that the specimens defined in this way as 'extreme' do not 'belong' in the data set, i.e., there is no 'distortion' of morphospace by these specimens. Therefore, the data were standardized before culling. The results indicate that none of the dispersion indices change as a result of culling in such a way as to alter the basic evolutionary pattern.

Small groups

There are several higher taxa that at certain times are represented by only a few specimens. Dispersion statistics for smaller groups are generally less reliable (Atchley *et al.* 1982). One way that small sample size is accounted for here is by using dispersion indices that do not rely on the estimation of the covariance structure of the variables. In addition, small groups are given less weight in the calculation of dispersion indices. Finally, as the analyses of culled data presented above indicate, the patterns observed are relatively robust in the face of changes in sample size. Nevertheless, it is worth testing explicitly for the effects that small group sizes might have on the determination of within- and among-group measures of dispersion.

To do so, the data were culled to remove all groups with less than an arbitrary minimum of five specimens. Because this culling procedure is intended to test whether small groups represent an unbiased subset of all groups rather than whether small groups 'distort' morphospace, the data were standardized before culling. Within- and among-group dispersion indices for the culled data are very similar to those for the unculled data. Furthermore, the pattern of secular changes in the dispersion indices is unaltered, suggesting that small groups do not bias the results. There is nothing intrinsically different about small groups relative to large groups with respect to morphologic dispersion.

Stratigraphic division of the Ordovician

Different aspects of sampling strategy and sample size appear to have but minor effects on the dispersion indices calculated here. It is possible, however, that the way in which the data are lumped

has some influence. To test for this, an alternative method for subdividing the Ordovician was used, namely, the four-fold North American standard of Ibexian, Whiterockian, Mohawkian, and Cincinnatian series (Ross *et al.* 1982). Both the unculled data and the data culled to correct for sample size yield results in agreement with those obtained using the three-fold division of the Ordovician.

DISCUSSION

The analyses presented above indicate that the observed patterns of within- and among-group dispersion are unlikely to result from biases inherent in the methods of data collection and analysis. It should be noted that the different data sets that are analysed are not independent. Thus, the various results do not provide independent verification of the patterns.

How a morphospace is defined is one determinant of the patterns detected in that morphospace. This study has drawn conclusions about trilobite evolution based on the evolution of the trilobite cranidium. It might reasonably be asked what patterns would have emerged if a different aspect of trilobite form had been considered. Two facts suggest that the patterns would have been concordant with those documented here. First, the result that higher taxa in the Ordovician are more distinct than those in the Cambrian is in agreement with previous observations based on gross morphology (e.g. Whittington 1954, 1966). Many aspects of trilobite morphology have contributed to their classification (Harrington 1959). That patterns based on the cranidium agree with the general impressions of trilobite workers serves as an *a posteriori* justification for the choice of the cranidium in defining the trilobite morphospace. Second, Whittington (1988*a*, 1988*b*) has found that the hypostomes of post-Cambrian trilobites map well onto suprageneric groups, while Cambrian taxa are more difficult to characterize by their hypostomes. This provides independent documentation of the same pattern shown in this study, but with a completely different morphological system.

Interpretations of the results of this study are reliable only insofar as the taxa employed have biological reality. The classification of trilobites is certainly not at its acme. Future changes in classification will clearly affect the fine details and perhaps even the major features of the patterns presented. This study is not intended as the last word on the evolution of higher taxa of trilobites. But the approaches presented here are valid for the investigation of patterns in the occupation of trilobite morphospace.

Two potential biases in the analysis need to be considered, but cannot be dealt with by simple culling of the data. These are (1) variation in the duration of stratigraphic intervals, and (2) inaccuracies and inconsistencies in the definition of higher taxa.

Because of time-averaging, a greater variety of form is likely to be lumped within a stratigraphic interval in proportion to the amount of time represented by that interval. As more time is lumped into a single interval, the distinctness of higher taxa should decrease as time-averaging causes them to be represented by a more variable array of forms. Thus, a systematic decrease in the duration of intervals higher in the stratigraphic column could artificially induce an increase in discreteness. It appears, however, that this bias is not at work here. The dates for the boundaries of stratigraphic intervals cannot be taken too literally, but neither the conventional time scale nor that based on Sloan's work suggests a systematic shortening of interval lengths (Table 1). While there can be no doubt that the duration of an interval must affect the dispersion indices, secular changes in these indices are not the result of variations in interval length.

If there were changes in taxonomic turnover rates, then stratigraphic lumping could conceivably cause the patterns. Given intervals of equal duration, more variability would accumulate within a taxon (because of time-averaging) if turnover were more rapid. The rate of generic turnover in trilobites decreased from the Cambrian to the Ordovician (Foote 1988; Sloan in press), but Cambrian taxa apparently did not accumulate more morphologic variability within a stratigraphic interval. Within-group dispersion in the Cambrian is not significantly higher than in the Ordovician.

If there were inconsistencies in the concepts of higher taxa such as superfamilies, then these could conceivably bias the results of any analysis that relied on higher taxa as defined. It is argued above and elsewhere (e.g. Whittington 1954) that the apparent differences between Cambrian and

Ordovician taxa are unlikely to arise from different taxonomic practice alone. Nevertheless, it would be desirable to have greater compatibility among taxonomic concepts. One approach would be progressively to improve the taxonomy of trilobites. As higher categories are defined more consistently, different taxa at different times can be compared more meaningfully. And as higher taxa more closely approximate natural groups, evolutionary interpretations of patterns at the higher taxonomic level will be more reliable. Yet, there will always be room for improvement. Furthermore, the very existence of a taxonomy imposes structure on the analysis.

The finding that trilobite taxa become more distinct through time implies that the gaps in morphospace become more pronounced, and the clusters in morphospace tighter. As discussed above, each specimen is represented by a single point in morphospace. If the apparent pattern is not simply the result of taxonomic practice, then changes in the occupation of morphospace should be detected as changes in the degree of clustering of these points. Several methods exist in ecology (e.g. Clark and Evans 1954), physical cosmology (Peebles 1980), and other fields to quantify the intensity of clustering of points. Results based on a modification of one of these methods indicate that morphological clusters do become tighter from the Cambrian to the Ordovician. Therefore, the patterns documented here are not solely the result of taxonomic artifact (Foote 1989*a*).

Massive extinctions are potentially important in causing the patterns documented here. It is commonly argued that extinctions can foster subsequent radiations by clearing out large areas of ecospace (e.g. Valentine 1969; Colbert 1980, p. 443). While such radiations proceed by the multiplication of species, the scale and tempo of radiations into relatively empty ecospace result in patterns detected at higher taxonomic levels (Valentine 1969). The largest single increase in the separation among higher taxa of trilobites occurs in the transition from the Upper Cambrian to the Lower Ordovician. (Although the difference in among-group dispersion, A, between Ordovician 1 and Ordovician 2 is numerically slightly larger, the standard error associated with A in Ordovician 2 is so large as to make this transition less striking [Table 2].) The Upper Cambrian and Tremadocian both are well known as times of rapid turnover in the trilobites (e.g. Stubblefield 1960; Fortey 1983; Palmer 1984). Because of the importance of international correlation, much attention has been paid to the Cambro–Ordovician boundary itself (e.g. Bassett and Dean 1982). However, increased resolution (Sepkoski 1979, p. 223) and more detailed palaeontological investigation have shown that many Cambrian trilobite families endure into the Ordovician (e.g. Fortey 1983; Westrop and Ludvigsen 1987). Considering the coarse scale of analysis used here, the exact temporal distribution of the extinctions is not of the utmost importance. The extinctions were apparently sufficiently significant to effect the evacuation of ecospace, and play a role in the post-Cambrian radiation of higher taxa of trilobites (e.g. Stubblefield 1960).

The analyses presented above show that morphotypes become better defined and morphologic gaps become more pronounced through time. Within-group dispersion does not change significantly from the Cambrian to the Ordovician. The latter statement is somewhat misleading, however. Overall dispersion and the dispersion among higher taxa do increase substantially. Therefore, dispersion within groups decreases as a proportion of the total amount of morphospace occupied. There is a morphologic radiation, but diversification at lower levels does not keep up with diversification at higher levels.

Occupation of different adaptive zones by related groups of organisms is often marked by morphological differences among those groups (e.g. Van Valen 1971). The large divergence among trilobite morphotypes may indicate the colonization of new adaptive zones. Valentine (1969) saw the Palaeozoic radiation as taking place primarily by the subdivision of niches, while the Mesozoic and Cenozoic radiations involved the opening of new adaptive zones. The data here appear consistent with a slightly modified view of the Palaeozoic radiation (at least for trilobites). If morphotypes in some rough way can be said to approximate adaptive zones, then the morphologic radiation of trilobites in the middle and upper Cambrian, as Valentine (1969) said, may not proceed by the opening of new adaptive zones. But the Ordovician radiation of new morphotypes may indicate a change in the mode of diversification, involving the opening of new adaptive zones.

Higher taxa of trilobites represent discernible morphotypes, as shown by the non-random

arrangement of specimens into higher taxa. However, these morphotypes need not represent adaptive zones. Raup and Gould (1974) showed that stochastic simulations of morphologic evolution result in clades that are morphologically distinct. Coherent morphotypes are to be expected from genealogical processes and may say nothing about adaptive themes. Similarly, an increase in the total range of morphospace occupied may be a null expectation (Raup and Gould 1974; Gould 1988).

How does the morphologic radiation of the trilobites compare to that in other groups? Campbell and Marshall (1987) analysed the diversification of the Echinodermata in terms of the origination of new characters. They concluded that the echinoderm classes do not converge morphologically toward their origin, but are distinct at their earliest occurrence. Smith (1988) has disputed this claim, arguing that it rests largely on taxonomic practice. Runnegar (1987) has expressed the opinion that early molluscan taxa are recognizable only in hindsight because they subsequently diversified. Yochelson (1979), however, believes that molluscan classes originated abruptly as morphologically distinct units. That different workers reach opposite conclusions working with the same material suggests that new approaches to the problem may be needed. In contrast to Campbell and Marshall's view of the Echinodermata and Yochelson's view of the Mollusca, the evidence from orders of mammals suggests that their Cenozoic radiation has largely involved continued morphological divergence (Simpson 1953, p. 226; Van Valen 1971).

As Campbell and Marshall (1987) imply, the issue underlying whether origins are 'sudden' is not just about differences in rates. It is also important whether morphologic divergence continues throughout the history of a group, or is concentrated in one or a few episodes. It cannot be argued that trilobite taxa are recognizable *merely* in hindsight, after they diverge and diversify. Quantitative, morphological evidence presented here demonstrates that higher taxa of trilobites, from the point in the stratigraphic record where they are recognizable as higher taxa, do not continue to diverge. In this respect, the origin of higher taxa of trilobites may justifiably be regarded as 'sudden'.

SUMMARY AND CONCLUSIONS

1. A Fourier description of the trilobite cranidium allows the quantitative documentation of morphologic diversification in the Cambrian and Ordovician.

2. Morphologic variability in the trilobites as a whole increased from the Early Cambrian to the Middle Ordovician, with a decline in the Late Ordovician.

3. Diversity of form and generic diversity do not correlate strongly. Previous work indicates that the latter showed a maximum in the Middle to Upper Cambrian, while results presented here show that the former was highest in the Middle Ordovician.

4. Morphologic dispersion within higher taxa of trilobites did not change significantly through time, although it did decrease in proportion to the total amount of morphospace occupied. This result is sensitive to the way higher taxa are defined.

5. Morphologic dispersion among higher taxa increased significantly from the Cambrian to the Ordovician, as did the morphologic distinctness of higher taxa. This pattern resulted from the origination of new higher taxa, not the divergence of established higher taxa. Patterns involving higher taxa are sensitive to the way that higher taxa are defined, but are not caused solely by taxonomic practice.

6. These patterns are observed even in confined regions in morphospace and therefore do not result solely from the contribution of extreme taxa.

7. The patterns do not result from any likely bias in data collection or treatment.

8. The cause for this increase in morphologic discontinuity is not clear. Possible explanations include (*a*) the expectation of a stochastic process and (*b*) radiation into new adaptive zones. The latter process was facilitated by extinctions in the Late Cambrian and Early Ordovician.

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REFERENCES

ASHTON, J. H. and ROWELL, A. J. 1975. Environmental stability and species proliferation in Late Cambrian trilobite faunas: a test of the niche-variation hypothesis. *Paleobiology*, **1**, 161–174.

ATCHLEY, W. R., NORDHEIM, E. V., GUNSETT, F. C. and CRUMP, P. L. 1982. Geometric and probabilistic aspects of statistical distance functions. *Systematic Zoology*, **31**, 445–460.

BASSETT, M. G. and DEAN, W. T. (eds). 1982. *The Cambrian–Ordovician boundary: sections, fossil distributions, and correlations*. National Museum of Wales, Cardiff, Geological Series No. 3, 227 pp.

BERGSTRÖM, J. 1973. Organization, life and systematics of trilobites. *Fossils and Strata*, **2**, 1–69.

BURR, E. J. 1960. The distribution of Kendall's score *S* for a pair of tied rankings. *Biometrika*, **47**, 151–171.

CAMPBELL, K. S. W. and MARSHALL, C. R. 1987. Rates of evolution among Palaeozoic echinoderms. 61–100. *In* CAMPBELL, K. S. W. and DAY, M. F. (eds). *Rates of evolution*. Allen and Unwin, London, 314 pp.

CHERRY, L. M., CASE, S. M., KUNKEL, J. G., WYLES, J. S. and WILSON, A. C. 1982. Body shape metrics and organismal evolution. *Evolution*, **36**, 914–933.

CLARK, P. J. and EVANS, F. C. 1954. Distance to nearest neighbour as a measure of spatial relationships in populations. *Ecology*, **35**, 445–453.

CLARKSON, E. N. K. 1986. *Invertebrate palaeontology and evolution*. (2nd ed.). Allen and Unwin, London, 382 pp.

COLBERT, E. H. 1980. *Evolution of the vertebrates*. (3rd ed.). John Wiley and Sons, New York, 510 pp.

DAVIS, J. C. 1986. *Statistics and data analysis in geology*. (2nd ed.). W. H. Freeman and Company, San Francisco, 646 pp.

ELDREDGE, N. 1977. Trilobites and evolutionary patterns. 305–332. *In* HALLAM, A. (ed.). *Patterns of evolution as illustrated by the fossil record*. Elsevier, Amsterdam, 591 pp.

ERWIN, D. H., VALENTINE, J. W. and SEPKOSKI, J. J. JR. 1987. A comparative study of diversification events; the early Paleozoic versus the Mesozoic. *Evolution*, **41**, 177–186.

FOOTE, M. 1988. Survivorship analysis of Cambrian and Ordovician trilobites. *Paleobiology*, **14**, 258–271.

—— 1989*a*. Morphologic evolution of Cambrian and Ordovician trilobites. Unpublished Ph.D. thesis, University of Chicago.

—— 1989*b*. Perimeter-based Fourier analysis: a new morphometric method applied to the trilobite cranidium. *Journal of Paleontology*, **63**, 880–885.

FORTEY, R. A. 1983. Cambrian–Ordovician boundary trilobites from western Newfoundland and their phylogenetic significance. *Special Papers in Palaeontology*, **30**, 179–211.

—— and CHATTERTON, B. D. E. 1988. Classification of the trilobite suborder Asaphina. *Palaeontology*, **31**, 165–222.

—— and OWENS, R. M. 1975. Proetida – a new order of trilobites. *Fossils and Strata*, **4**, 227–239.

—— and WHITTINGTON, H. B. 1989. The Trilobita as a natural group. *Historical Biology*, **2**, 125–138.

GOULD, S. J. 1988. Trends as changes in variance: a new slant on progress and directionality in evolution. *Journal of Paleontology*, **62**, 319–329.

HARRINGTON, H. J. 1959. Classification. O145–O170. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part O. Arthropoda 1*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 560 pp.

—— MOORE, R. C. and STUBBLEFIELD, C. J. 1959. Morphological terms applied to Trilobita. O117–O126. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part O. Arthropoda 1*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 560 pp.

—— HENNINGSMOEN, G., HOWELL, B. F., JAANUSSON, V., LOCHMAN-BALK, C., MOORE, R. C., POULSEN, C., RASETTI, F., RICHTER, E., RICHTER, R., SCHMIDT, H., SDZUY, K., STRUVE, W., TRIPP, R., WELLER, J. M. and WHITTINGTON, H. B. 1959. Systematic descriptions. O170–O540. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology.*

Part O. Arthropoda 1. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 560 pp.

HUGHES, C. P. 1970. Statistical analysis and presentation of trinucleid (Trilobita) fringe data. *Palaeontology*, **13**, 1–9.

KOCH, C. 1987. Prediction of sample size effects on the measured temporal and geographic distribution patterns of species. *Paleobiology*, **13**, 100–107.

LANE, P. D. and THOMAS, A. T. 1983. A review of the trilobite suborder Scutelluina. *Special Papers in Palaeontology*, **30**, 141–160.

LOCHMAN-BALK, C. and WILSON, J. L. 1958. Cambrian biostratigraphy in North America. *Journal of Paleontology*, **32**, 312–350.

PALMER, A. R. 1958. Morphology and ontogeny of a Lower Cambrian ptychoparioid trilobite from Nevada. *Journal of Paleontology*, **32**, 154–170

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

PEARSON, K. 1926. On the coefficient of racial likeness. *Biometrika*, **18**, 103–117.

PEEBLES, P. J. E. 1980. *The large-scale structure of the Universe.* Princeton University Press, Princeton, New Jersey, 422 pp.

RASETTI, F. 1954. Phylogeny of the Cambrian trilobite family Catillicephalidae and the ontogeny of *Welleraspis*. *Journal of Paleontology*, **28**, 599–612.

—— 1961. Dresbachian and Franconian trilobites of the Conococheague and Frederick limestones of the central Appalachians. *Journal of Paleontology*, **35**, 104–124.

RAUP, D. M. 1966. Geometric analysis of shell coiling: general problems. *Journal of Paleontology*, **40**, 1178–1190.

—— 1967. Geometric analysis of shell coiling: coiling in ammonoids. *Journal of Paleontology*, **41**, 43–65.

—— 1976. Species diversity in the Phanerozoic: a tabulation. *Paleobiology*, **2**, 279–288.

—— and GOULD, S. J. 1974. Stochastic simulation and evolution of morphology – towards a nomothetic paleontology. *Systematic Zoology*, **23**, 305–322.

ROBISON, R. A. 1964. Middle–Upper Cambrian boundary in North America. *Bulletin of the Geological Society of America*, **75**, 987–994.

—— 1987. Superclass Trilobitomorpha. 221–241. *In* BOARDMAN, R. S., CHEETHAM, A. H. and ROWELL, A. J. (eds). *Fossil invertebrates.* Blackwell Scientific Publications, Palo Alto, California, 713 pp.

ROHLF, F. J. and SOKAL, R. R. 1981. *Statistical tables.* (2nd ed.). W. H. Freeman and Company, San Francisco, 219 pp.

ROSS, R. J. JR. 1951. Stratigraphy of the Garden City Formation in Northeastern Utah, and its trilobite faunas. *Peabody Museum of Natural History Bulletin*, **6**, 1–161.

—— ADLER, F. J., AMSDEN, T. W., BERGSTROM, D., BERGSTROM, S. M., CARTER, C., CHURKIN, M., CRESSMAN, E. A., DERBY, J. R., DUTRO, J. T. JR, ETHINGTON, R. L., FINNEY, S. C., FISHER, D. W., FISHER, J. H., HARRIS, A. G., HINTZE, L. F., KETNER, K. B., KOLATA, D. L., LANDING, E., NEUMAN, R. B., SWEET, W. C., POJETA, J. JR, POTTER, A. W., RADER, E. K., REPETSKI, J. E., SHAVER, R. H., THOMPSON, T. L. and WEBERS, G. F. 1982. *The Ordovician System in the United States.* International Union of Geological Sciences, Publication No. 12, 73 pp.

ROWELL, A. J., ROBISON, R. A. and STRICKLAND, K. 1982. Aspects of Cambrian agnostoid phylogeny and chronocorrelation. *Journal of Paleontology*, **56**, 161–182.

RUNNEGAR, B. 1987. Rates and modes of evolution in the Mollusca. 39–60. *In* CAMPBELL, K. S. W. and DAY, M. F. (eds). *Rates of evolution.* Allen and Unwin, London, 314 pp.

SEPKOSKI, J. J. JR. 1979. A kinetic model of Phanerozoic taxonomic diversity II. Early Phanerozoic families and multiple equilibria. *Paleobiology*, **5**, 222–251.

—— 1982. A compendium of fossil marine families. *Milwaukee Public Museum Contributions in Biology and Geology*, **51**, 125 pp.

—— 1984. A kinetic model of Phanerozoic taxonomic diversity III. Post-Paleozoic families and mass extinctions. *Paleobiology*, **10**, 246–267.

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

SHAW, A. B. 1957. Quantitative trilobite studies II. Measurement of the dorsal shell of non-agnostidean trilobites. *Journal of Paleontology*, **31**, 193–207.

SHINN, E. A., HALLEY, R. B., HUDSON, J. H. and LIDZ, B. H. 1977. Limestone compaction: an enigma. *Geology*, **5**, 21–25.

SIMPSON, G. G. 1953. *The major features of evolution.* Columbia University Press, New York, 434 pp.

SLOAN, R. E. in press. A chronology of North American Ordovician trilobite genera. *Proceedings of the Fifth International Symposium on the Ordovician System*, Geological Survey of Canada.

SLOSS, L. L. 1963. Sequences in the cratonic interior of North America. *Bulletin of the Geological Society of America*, **74**, 93–114.
SMITH, A. B. 1988. Patterns of diversification and extinction in early Palaeozoic echinoderms. *Palaeontology*, **31**, 799–828.
SOKAL, R. R. and ROHLF, F. J. 1981. *Biometry*. (2nd ed.). W. H. Freeman and Company, San Francisco, 859 pp.
STANLEY, S. M. 1973. An explanation for Cope's rule. *Evolution*, **27**, 1–26.
STUBBLEFIELD, C. J. 1960. Evolution in trilobites. *Quarterly Journal of the Geological Society of London*, **115**, 145–162.
TEMPLE, J. T. and TRIPP, R. P. 1979. An investigation of the Encrinurinae (Trilobita) by numerical taxonomic methods. *Transactions of the Royal Society of Edinburgh*, **70**, 223–250.
VALENTINE, J. W. 1969. Patterns of taxonomic and ecological structure of the shelf benthos during Phanerozoic time. *Palaeontology*, **12**, 684–709.
—— FOIN, T. C. and PEART, D. 1978. A provincial model of Phanerozoic marine diversity. *Paleobiology*, **4**, 55–66.
VAN VALEN, L. 1971. Adaptive zones and the orders of mammals. *Evolution*, **25**, 420–428.
—— 1974. Multivariate structural statistics in natural history. *Journal of Theoretical Biology*, **45**, 235–247.
WESTROP, S. R. and LUDVIGSEN, R. 1987. Biogeographic control of trilobite mass extinction at an Upper Cambrian "biomere" boundary. *Paleobiology*, **13**, 84–99.
WHITTINGTON, H. B. 1941. Silicified Trenton trilobites. *Journal of Paleontology*, **15**, 492–522.
—— 1954. Status of invertebrate paleontology, 1953 VI. Arthropoda: Trilobita. *Bulletin of the Museum of Comparative Zoology, Harvard University*, **112**, 193–200.
—— 1956. Silicified Middle Ordovician trilobites: the Odontopleuridae. *Bulletin of the Museum of Comparative Zoology, Harvard University*, **114**, 155–288.
—— 1959. Silicified Middle Ordovician trilobites: Remopleurididae, Trinucleidae, Raphiophoridae, Endymioniidae. *Bulletin of the Museum of Comparative Zoology, Harvard University*, **121**, 369–496.
—— 1966. Phylogeny and distribution of Ordovician trilobites. *Journal of Paleontology*, **40**, 696–737.
—— 1981. Paedomorphosis and cryptogenesis in trilobites. *Geological Magazine*, **118**, 591–602.
—— 1988*a*. Hypostomes and ventral cephalic sutures in Cambrian trilobites. *Palaeontology*, **31**, 577–609.
—— 1988*b*. Hypostomes of post-Cambrian trilobites. *Memoirs of the New Mexico Bureau of Mines and Mineral Resources*, **44**, 321–339.
—— and W. R. EVITT. 1953. Silicified Middle Ordovician trilobites. *Memoirs of the Geological Society of America*, **59**, 1–137.
YOCHELSON, E. L. 1979. Early radiation of Mollusca and mollusc-like groups. 323–358. *In* HOUSE, M. R. (ed.). *The origin of major invertebrate groups*. Academic Press, London, 515 pp.

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