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Mike Foote

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## Discordance and concordance between morphological and taxonomic diversity

Mike Foote

*Abstract.*—Morphological and taxonomic diversity each provide insight into the expansion and contraction of major biological groups, while the nature of the relationship between these two aspects of diversity also has important implications for evolutionary mechanisms. In this paper, I compare morphological and taxonomic diversity within the classes Blastozoa and Trilobozoa, and within the trilobite clades Libristoma, Asaphina, Proetida, Phacopida, and Scutelluina. Blastoid morphology is quantified with homologous landmarks on the theca, and trilobite form is measured with a Fourier description of the cranidium. Morphological diversity is measured as the total variance among forms in morphological space (proportional to the mean squared distance among forms). Blastoid taxonomic diversity is based on published compilation of stratigraphic ranges of genera. The *Zoological Record* was used to determine the number of new species of trilobites described since the publication of the *Treatise*; temporal patterns in species richness are similar to those for generic richness based on the *Treatise*, suggesting a common underlying signal.

Morphological variety and taxonomic richness often increase together during the initial diversification of a clade. This pattern is consistent with diffusion through morphospace, although some form of adaptive radiation cannot be ruled out. Morphological diversity varies little throughout much of the history of Proetida, a pattern that may suggest major constraints on the magnitude and direction of evolution, and that agrees with the perception of Proetida as a morphologically conservative group. Two major patterns are seen during the decline of clades. In Blastozoa, Trilobozoa, Libristoma, and Asaphina, morphological diversity is maintained at substantial levels, and in fact continues to increase, even in the face of striking reductions in taxonomic richness. This pattern suggests continued diffusion through morphospace and taxonomic attrition that is effectively non-selective with respect to morphology. In Phacopida, Scutelluina, and to some extent in Proetida, morphological diversity decreases along with taxonomic diversity. This pattern suggests heterogeneities such as elevated extinction and/or reduced origination in certain regions of morphospace. As found previously for the echinoderm subphylum Blastozoa, all studied clades of trilobites except Proetida show maximal morphological diversity in the Mid-Late Ordovician and maximal taxonomic diversity sometime during the Ordovician, suggesting some degree of common control on diversification patterns in these groups.

Mike Foote. *Museum of Paleontology and Department of Geological Sciences, The University of Michigan, Ann Arbor, Michigan 48109*

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### Introduction

Recently renewed interest in evolutionary patterns of morphological diversity (Stanley 1979; Whittington 1980; Gould 1989, 1991; Fortey and Owens 1990a,b; Foote 1991a,b, 1992a,b) has emphasized the point (Romer 1949) that discordances between morphological and taxonomic diversity demand to be interpreted biologically, not explained away as artifacts of taxonomic practice. For example, some evidence shows that initial morphological diversification in blastozoan echinoderms far exceeded the proliferation of lower-level taxa (Foote 1992b). Such a pattern suggests that morphological transitions were larger earlier in this clade's history, a point

that is relevant to the ecological and evolutionary mechanisms of diversification (Stanley 1979: pp. 132–134; Valentine 1980, 1986; Valentine and Erwin 1987; Foote 1992b). In other taxa, morphological diversity is concentrated later in time than taxonomic diversity (Fortey and Owens 1990a,b; Foote 1991b), a pattern that is consistent with nonselective extinction during the waning of the clade. Not only does morphology provide insight into evolutionary processes when compared to taxonomic diversity, but explicit analysis of form itself allows documentation and interpretation of the evolution, success, and demise of fossil groups.

Emphasis on macroevolutionary patterns

need not imply mechanisms acting on entire clades as unified entities. In addition to being of interest in their own right, macroevolutionary histories suggest testable mechanisms at smaller scales. The data presented here illustrate some general relationships between morphological and taxonomic diversity, each suggesting one or more processes of morphospace filling and emptying. Given the richness of life's history, a clade could conceivably be found to illustrate virtually any imaginable diversity path. An outstanding question concerns the frequency of various kinds of diversity patterns. As a step toward addressing this question, this paper documents evolutionary patterns of morphological and taxonomic diversity in several clades (Blastoidea, Trilobita, and clades within Trilobita), and discusses these patterns and previously documented data in the context of large-scale homo- and heterogeneities in the occupation and evacuation of morphological space.

### Materials and Methods

*Defining Morphological Space and Measuring Morphological Diversity.*—The approach here is to ordinate forms in a multidimensional morphospace and to base morphological differences, and therefore diversity, on the array of points in morphospace (Raup 1966; Cherry et al. 1982). Blastoids are ordinated in a 17-dimensional morphospace based on the Cartesian coordinates of eight homologous landmarks that represent the form of the entire theca as well as that of individual plates (Foote 1991b). A 12-dimensional morphospace for trilobites is based on harmonic coefficients derived from a Fourier description of the cranial outline projected into two dimensions (Foote 1989). Measurement of the cranidium alone has been justified on the grounds that it is ecologically, functionally, and taxonomically informative, and that it yields evolutionary patterns consistent with those based on other aspects of form (Foote 1989, 1991a).

Although assessing morphological variety by measuring form is preferable to using taxonomic proxies, it is not immediately obvious

how to quantify morphological diversity once an ordination in morphospace is obtained. An intuitively appealing diversity metric is the amount (range, area, etc.) of morphospace occupied (e.g., Saunders and Swan 1984; Foote 1991a), but this measure has the practical drawback of being biased by sample size; the larger the sample, the more morphospace occupied (Pearson 1926; Foote 1992a). An alternative metric, also intuitively reasonable, is the average dissimilarity (distance) among points in morphospace. This measure is generally unbiased by sample size, which is particularly important when we are uncertain about the degree of paleontological completeness. Average dissimilarity also extends readily to other measures of distance, such as molecular distance or phenetic distance based on discrete characters, and so is not restricted to taxa that can be easily represented in a continuous morphological space (Briggs et al. 1992; Foote 1992b). Moreover, there tends to be an empirical correlation between average distance and amount of morphospace occupied when sample size is not severely limited (Foote 1992a). For these reasons, morphological diversity is measured here as the total variance (sum of univariate variances of all dimensions in morphospace), which is proportional to the mean squared Euclidean distance among points in morphospace (Van Valen 1974). Although data are portrayed graphically with principal components, diversity measures are all based on the unreduced morphospaces.

*Selection of Clades.*—Extinct, monophyletic taxa are studied in order to allow documentation of complete evolutionary histories, and particularly to allow analysis of both the diversification and decline of clades. (It may bear pointing out that, according to recent phylogenetic studies [authors cited below], the taxa included here are probably strictly monophyletic. Therefore, diversity trajectories are not likely to be governed by the practice of skimming off derived lineages into a new clade and leaving a paraphyletic residue behind.) Taxa are also chosen to be large enough that adequate sample sizes can be obtained for most stratigraphic intervals. The

clades studied are the blastozoan echinoderm class Blastoidea, Trilobita, and the trilobite groups Libristoma (sensu Fortey 1990; Phacopida excluded), Asaphina (sensu Fortey and Chatterton 1988; aphelaspids excluded), Proetida (sensu Fortey and Owens 1975; plethopeltids and lecanopygids excluded), Phacopida, and Scutelluina (sensu Lane and Thomas 1983). Lane and Thomas (1983) and Fortey (1990) present evidence that the affinities of Scutelluina are with Corynexochida, and Fortey (1990) also argues for a relationship with Leiostegiacea. However, the details of these relationships have yet to be worked out. Therefore, rather than including all members of these three higher taxa in a single putative clade, I have used the narrower definition of the clade Scutelluina (Lane and Thomas 1983). Although Asaphina and Proetida are considered to be nested clades within the Libristoma, the relationships among these and other higher taxa of trilobites remain obscure (Fortey 1990). Following Fortey and Whittington (1989) and Fortey (1990), olenelloids and agnostoids are considered trilobites.

*Sampling.*—All morphological data are based on measurement of specimens haphazardly chosen from the range of available, well preserved material in several museum collections. Although the collections, mostly housed in the United States and Great Britain, emphasize North American and European material, the goal was to obtain a record of the global diversity history of various clades; therefore, sampling was not restricted to any particular region or province. Because of the large scale of analysis and the number of independent clades studied, it is unlikely that the gross evolutionary patterns result simply from geographic sampling bias, although this factor probably affects the finer details of evolutionary patterns.

The questions addressed here concern variation among species within a larger clade. Taxonomic treatment seems reasonably stable and uniform for the Blastoidea, at least partly because a small number of collaborators have been able to reach some standards of taxonomic practice. Therefore, each blastoid spe-

cies was represented by the mean morphology of all its measured specimens. Compared to blastoids, trilobites are a larger, more heterogeneous group, and are studied by more workers with a greater variety of approaches. Partly for these reasons, lower-level trilobite taxonomy *seems* less uniform and stable (at least to me). I have therefore used specimens rather than species as the basic sampling unit for trilobites, allowing multiple specimens per species when available, as described previously (Foote 1991a). It should be kept in mind that, for both blastoids and trilobites, evolutionary patterns documented with species and with individuals as sampling units are quite similar (Foote 1990, 1991a, and unpublished analyses). For both trilobites and blastoids, data presented here represent substantial increases in the number of species and specimens compared to previous studies (Foote 1991a,b, 1992a), as well as corrections of misidentifications, errors in classification, and other errors. (For help with corrections I thank R. A. Fortey, A. S. Horowitz, and J. A. Waters.) Further details on sampling can be found elsewhere (Foote 1991a,b).

*Time Scale and Data Distribution.*—In order to allow similar amounts of time-averaging, conventional stratigraphic units were combined to yield intervals of comparable duration (table 1). Intervals were made relatively long to allow reasonably large sample sizes as well as to facilitate correlation of strata on a global scale. Some recent studies suggest a younger date for the base of the Cambrian than the more traditional figure used here (Cooper et al. 1992; Compston et al. 1992; Knoll and Walter 1992). However, there is still much uncertainty regarding the age of the Precambrian–Cambrian boundary (Cowie and Harland 1989), and the younger date of ca. 540 Ma has not yet been universally accepted. Moreover, it is not yet clear how a younger date for the base of the Cambrian would affect the time scale as a whole. I have therefore adopted the more conventional date of 570 Ma for the base of the Cambrian, and have used the time scale of Harland et al. (1990). Because morphological and taxonomic diversity profiles are compared to each other, and

TABLE 1. Time scale and sample sizes. Age at base of interval in millions of years before present (Ma), based on Harland et al. (1990). Duration in millions of years (m.y.), also from Harland et al. (1990). Early Cambrian: Atdabanian and Botomian; Middle and Late Cambrian: post-Botomian; Early Ordovician: Tremadocian and Arenigian; Middle and Late Ordovician: post-Arenigian; Early Devonian: Lochkovian, Pragian, and Emsian; Middle and Late Devonian: post-Emsian. Mid-Late Ordovician interval used for trilobites only; Late Ordovician interval used for blastoids only. Abbreviations in parentheses are used in the figures also.

Stratigraphic interval	Age at base (Ma)	Duration (m.y.)	Sample size						
			Blastoidea	Trilobita	Libristoma	Asaphina	Proetida	Phacopoda	Scutelluina
Early Cambrian (trilobite-bearing) (C1)	560	24	—	43	12	—	—	—	—
Middle and Late Cambrian (C2)	536	26	—	313	245	30	—	—	—
Early Ordovician (O1)	510	34	—	175	137	50	55	16	6
Middle and Late Ordovician (O2)	476	37	—	323	158	115	35	81	36
Late Ordovician (LO)	464	125	1	—	—	—	—	—	—
Silurian (S)	439	30.5	4	117	30	—	28	56	13
Early Devonian (D1)	408.5	22	9	25	14	—	12	8	2
Middle and Late Devonian (D2)	386	23.5	26	59	32	—	31	25	2
Early Carboniferous (EC)	362.5	39.5	60	31	31	—	31	—	—
Late Carboniferous (LC)	323	33	5	12	12	—	12	—	—
Permian (P)	290	45	14	26	26	—	26	—	—

each is based on the same time scale, different time scales do not necessarily affect substantive conclusions regarding the relationship between morphological and taxonomic diversity (see example in Foote 1992b).

Morphological diversity for each stratigraphic interval is measured as the total variance among all species or specimens representing that interval. This approach presents little difficulty for trilobite groups, which tend to be widespread and abundant, but is somewhat problematic for blastoids, which have a spottier record. For the Ordovician, Silurian, Mid-Late Devonian, Early Carboniferous and Permian samples, number of species sampled correlates well with number of genera known from these intervals (Foote 1991b). The Early Devonian and Late Carboniferous, however, are more poorly sampled. To compensate partially for poor sampling, data points were added to these two intervals, corresponding to the average morphology of genera known to be present during these times, but represented by morphological data for other intervals only. Altogether, four points were added to the blastoid data: generic averages for *Hyperblastus* and *Pleuroschisma* to the Early Devonian, and generic averages for *Orbitremites* and *Angioblastus* to the Late Carboniferous. Because taxonomic uncertainties may be greater in some trilobite groups, no such range-through correction was attempted for

trilobites, although there are some stratigraphic intervals where such a correction could profitably be applied. For example, because of a lack of well preserved specimens in the museums visited, within the order Phacopida there are no morphological data representing the suborder Cheirurina for the Early Devonian, even though the suborder is known from this interval. Thus, it may be that the estimate of morphological diversity in Early Devonian Phacopida is too low. On the other hand, it is unlikely that the small sample sizes for Devonian Scutelluina yield severely biased estimates of morphological diversity, since by the Devonian this clade had been reduced to a monotonous assemblage (relative to its morphological variety in the Ordovician) of *Scutellum* and other forms very similar to it. In general, the intervals with low sample size for a taxon represent times of relatively low taxonomic diversity for that taxon.

*Taxonomic Diversity.*—The blastoids are a sufficiently small group that a few workers were able to compile comprehensive data on stratigraphic ranges of all genera (Breimer and Macurda 1972; Horowitz et al. 1985; Waters 1988). Because the great majority of blastoid genera contain one or two species and are short-lived (Waters 1988), generic richness provides a good index for relative levels of species richness, and Waters' compilation of

TABLE 2. Relative numbers of trilobite genera and species over Paleozoic time (number of genera based on Harrington et al. [1959]; number of species based on citations in the *Zoological Record* from 1959 to 1991). Note the overall similarity of the two records of taxonomic diversity. Difference is the difference between percent maximum species diversity and percent maximum generic diversity. Cambrian values are not corrected for turnover rate.

Interval	Genera (% maximum)		Species (% maximum)		Difference
Early Cambrian	169	(27.2)	1349	(39.7)	+12.5
Mid-Late Cambrian	621	(100.0)	3401	(100.0)	0.0
Early Ordovician	262	(42.2)	1253	(36.8)	-5.4
Mid-Late Ordovician	262	(42.2)	1023	(30.1)	-10.1
Silurian	79	(12.7)	688	(20.2)	+7.5
Early Devonian	92	(14.8)	700	(20.6)	+5.8
Mid-Late Devonian	97	(15.6)	360	(10.6)	-5.0
Early Carboniferous	29	(4.7)	260	(7.6)	+2.9
Late Carboniferous	9	(1.5)	86	(2.5)	+1.0
Permian	11	(1.8)	75	(2.2)	+0.4

generic ranges is therefore used here. It is not as immediately clear that generic richness in trilobites provides a good index for species richness. The most recently published compilation of generic ranges (Harrington et al. 1959), is probably out of date, and a more current compilation would be desirable. J. Sepkoski (University of Chicago) is collecting such data, but they are as yet unpublished, as is the revision of the trilobite *Treatise* (Whittington and Fortey in preparation). In order to estimate relative levels of species richness directly, reports of newly described species were compiled from the *Zoological Record*, largely following the methods of Raup (1976), and under the assumption that the number of species described from a stratigraphic interval over a long period of monographic time provides a reasonable index of known species richness for that interval. Data were amassed for the years 1959–1991, i.e., from the publication of the original trilobite *Treatise* to the present day. This approach is not meant to estimate the absolute number of trilobite species that lived at some time in the past, but to provide relative numbers for the various stratigraphic intervals. Neither the set of species measured to assess morphological diversity nor the set of species tabulated to assess taxonomic diversity is a subset of the other.

The number of trilobite genera recognized in the *Treatise* is compared to the number of new species described since the publication of the *Treatise* in table 2. It may interest some

workers, and appall others, to note that over 9000 new species of trilobites have been named in the past three decades. Although the two estimates of taxonomic diversity differ, they tend to fluctuate around each other, rather than showing a systematic difference over geologic time. Since the number of *Treatise* genera and post-*Treatise* species represent largely independent data compilations, the overall similarity between the two data sets suggests that they reflect a common underlying pattern. Valentine (1969) likewise noted the overall similarity between generic and familial diversity curves for trilobites, and Bambach and Sepkoski (1992) have made the general claim that large-scale spatial and temporal diversity patterns at the level of species, genera, and families are well correlated. It is well known that the changing interests of systematists can greatly alter perceived patterns of taxonomic diversity (Williams 1957). However, because the pre- and post-1959 data compilations are in general agreement, diversity patterns at the scale used here do not seem to be dominated by transient changes in the particular groups or stratigraphic intervals that are most intensively studied.

Total species richness provides a good index of standing diversity if interval lengths and taxonomic turnover rates are roughly constant over time. However, several authors have noted differences in longevity between Cambrian and post-Cambrian trilobite taxa (Lochman 1956; Stubblefield 1960; Whittington 1966; Foote 1988; Sloan 1991). Analysis of

generic survivorship suggests that post-Cambrian genera and species endured about three times as long as Cambrian taxa (Foote 1988). To estimate relative levels of standing diversity, therefore, species richness values for the Cambrian were divided by three. Using this correction, trilobites appear to have been most diverse taxonomically in the Early Ordovician rather than the Late Cambrian. The apparent difference in survivorship between Cambrian and post-Cambrian taxa may reflect taxonomic practice rather than a true difference in turnover rates (Foote 1988; Fortey and Owens 1990b: pp. 146–148). The correction used here is agnostic with regard to the reasons for the apparent difference in taxonomic longevity. Whether the large number of Cambrian species results from splitting taxa three times more than they “should” be split, or from more rapid taxonomic evolution in the Cambrian, adjusting the diversity values is necessary and appropriate.

*Analysis of Clade Shape.*—Diversity histories will be treated mainly in terms of their most conspicuous features, and details on clade-shape statistics are given mainly for completeness. Paleontologists have long used large-scale clade shape (sensu Gould et al. 1977) to infer smaller-scale evolutionary mechanisms. For example, Sloss (1950) suggested that symmetrical trajectories of taxonomic diversity are consistent with certain secular patterns in origination rate, extinction rate, and taxonomic longevity. Other major themes in the analysis of clade shape have been the correlation between clade shape and time of clade origin (Müller 1955, 1970, 1974; Gould et al. 1977, 1987; Gilinsky et al. 1989), and comparison of observed clade shapes with those expected for hypothetical clades governed by a simple, stochastic model of evolution (Gould et al. 1977; Kitchell and MacLeod 1988, 1989; Foote 1991b). The purpose of this study is to compare morphological and taxonomic diversity histories, and in this respect at least three general patterns are conceivable. (1) Morphological diversity may be more bottom-heavy (concentrated earlier in time) than taxonomic diversity, a pattern that may suggest relatively large morphological transitions early in a clade’s history (Foote

1992b). (2) Morphological diversity may be more top-heavy (concentrated later in time) than taxonomic diversity, suggesting effectively nonselective attrition of taxa (Foote 1991b). (3) Morphological and taxonomic diversity may show roughly concordant trajectories. The interpretations of these three patterns will be discussed more fully below.

If  $d_i$  and  $t_i$  are the diversity and temporal midpoint of the  $i^{\text{th}}$  stratigraphic interval, then let

$$\begin{aligned}c_0 &= \sum d_i \\c_1 &= \sum d_i t_i \\c_2 &= \sum d_i t_i^2\end{aligned}$$

and

$$c_3 = \sum d_i t_i^3.$$

Then center of gravity (CG) and asymmetry ( $A$ ) are given by

$$CG = c_1/c_0$$

and

$$\begin{aligned}A &= (c_0 c_3 - 3c_1 c_2 + 2c_1^3/c_0) \\ &\div \{c_0^2[(c_2 - c_1^2/c_0)/c_0]^{1.5}\}.\end{aligned}$$

CG is the analog of the mean, where the diversity trajectory is treated as a frequency distribution (Gould et al. 1977), and  $A$  is the standard measure of skewness (Sokal and Rohlf 1981: p. 114) applied to this trajectory (Foote 1992b). Because stratigraphic intervals are not of equal duration, there is often an asymmetry inherent in the time scale (Gould et al. 1987; Foote 1991b, 1992b). For example, if interval lengths increased systematically through time a clade with uniform diversity would appear to be bottom-heavy. It is therefore useful sometimes to assess top- and bottom-heaviness with respect to the clade-shape statistics inherent in the time scale, i.e., the statistics that would characterize a clade with constant diversity (Foote 1991b, 1992b). This point is of secondary importance for the present study, because the main emphasis is to compare morphological and taxonomic diversity to each other, rather than to determine whether either aspect of diversity is top- or bottom-heavy in an absolute sense.

Gould et al. (1977, 1987) and Kitchell and MacLeod (1988) used large samples of clades

to calculate mean clade shape and its standard error. Comparison of morphological and taxonomic diversity for a single clade requires a different approach for estimating uncertainty in clade shape. Standard errors of clade-shape statistics were estimated nonparametrically by a bootstrap resampling procedure (1000 iterations). Given  $N$ , the sample size on which a clade's morphological diversity path was based, bootstrap samples of size  $N$  were drawn with replacement from the total sample for that clade. These specimens (or species) were assigned to their proper stratigraphic intervals, and the morphological diversity trajectory and clade-shape statistics recomputed. A similar procedure was used for taxonomic diversity. Given  $M$ , the total number of occurrences of species (trilobites) or genera (blastoids), bootstrap samples of  $M$  occurrences were drawn with replacement and assigned to their proper stratigraphic intervals, and the taxonomic diversity trajectory and clade-shape statistics recalculated. Following Efron (1982), the standard error of an observed clade-shape statistic was estimated by the standard deviation of the distribution of bootstrapped clade-shape statistics. Standard errors calculated in this way are similar to those obtained with the method developed by Ericson (presented in Foote 1991b). To compare morphological and taxonomic clade-shape statistics nonparametrically, sums were computed of the number of bootstrap runs with the morphological statistic greater than and less than the taxonomic statistic. The smaller of these two sums was doubled and divided by the number of bootstrap values to give the two-tailed probability that the two statistics could have been drawn from the same sampling distribution. Previous work shows that such tests for clade-shape differences based on the exact distribution of bootstrapped statistics are largely consistent with those based on the assumption that these bootstrapped distributions are normal (Foote 1992b).

### **Idealized Clade Histories**

Before examining actual clades, it is helpful to consider some idealized relationships between morphological and taxonomic diversity during the diversification of a clade and

during its decline (fig. 1; Foote 1991b, 1992a). Because decreases in diversity may take place over several million years, and because the level of stratigraphic resolution used here does not permit examination of morphological and taxonomic diversity immediately before and after a major extinction event, I mainly consider attrition, i.e., the loss of taxonomic diversity over some extended period of time.

Morphological diversity need not increase as taxonomic diversity increases; such morphological stagnation indicates taxonomic diversification that is highly constrained morphologically (fig. 1A; Foote 1992a). If morphological steps are large early in the history of a clade and subsequently become smaller (Stanley 1979: pp. 132–134; Valentine 1980; Valentine and Erwin 1987), the result is an initially rapid increase in morphological diversity that outstrips a simultaneous increase in taxonomic diversity (fig. 1B; Foote 1992b). If, on the other hand, there is neither a temporal trend in the size of morphological steps nor a major constraint on the direction of morphological evolution, morphological diversity will tend to increase more or less concordantly with taxonomic diversity (fig. 1C; Raup and Gould 1974; Fisher 1986). Considering the phase of the clade's history during which it declines in taxonomic diversity, there are several possibilities. If morphological extremes (fig. 1D) or large regions in morphospace (fig. 1E) preferentially experience enhanced extinction and/or reduced origination, then morphological diversity will tend to decrease with taxonomic diversity. However, if the newly originating lineages and the lineages that become extinct are randomly distributed with respect to morphology, then morphological diversity will be maintained for some time (fig. 1F). In fact, if origination continues near the edges of the morphological distribution, it is even possible for morphological diversity to rise for some time as taxonomic richness falls (fig. 1F; Foote 1991b). Finally, it is possible for heterogeneities in morphospace to yield an increase rather than a decrease in morphological diversity, as measured by average dissimilarity. If morphologically modal forms are preferentially selected against (whether by en-

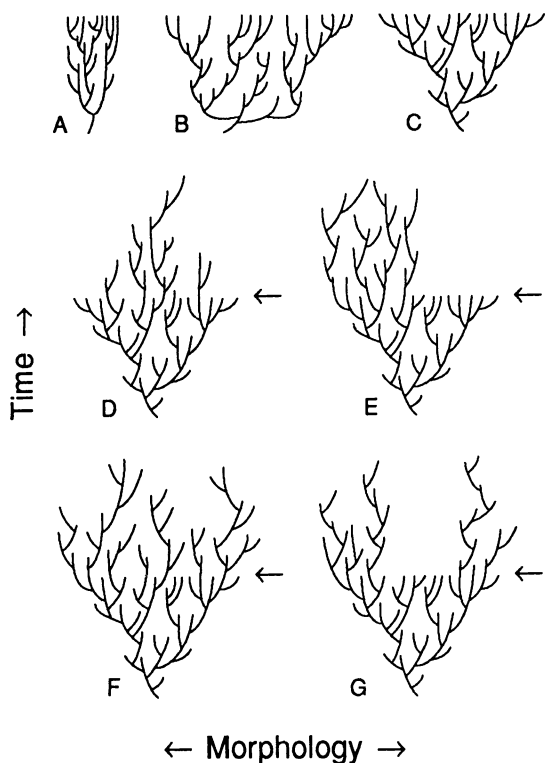


FIGURE 1. Idealized diversity histories. A-C depict three of the ways a clade may diversify, while D-G represent four of the ways a clade may decline. A, Morphological evolution is constrained (in this case so that morphological extremes are forbidden), with the result that taxonomic diversity increase is not accompanied by corresponding increase in morphological diversity (cf. Proetida). B, Morphological transitions are large early and subsequently become smaller. Morphological diversity continues to increase over time, but morphological diversity relative to taxonomic diversity is highest early in the clade's history (cf. Blastozoa, Foote 1992b). C, With no constraint on morphological transitions, and no secular trend in morphological step size, a clade diffuses through morphospace as it diversifies, leading to largely concordant increases in taxonomic and morphological diversity (cf. Blastozoa, Trilobita, and most trilobite subclades). Arrows in D-G indicate time of maximal taxonomic diversity. D, Selection against morphological extremes causes morphological diversity to decrease with taxonomic diversity (cf. Proetida, Phacopida, and Scutelluina). E, Selection against a broad region in morphospace has a similar effect as selection against extremes. F, If taxonomic attrition is nonselective with respect to morphology, morphological diversity remains high and may even increase as taxonomic diversity falls (cf. Trilobita, Libristoma, Asaphina, and Blastozoa). G, Selection against morphological intermediates causes an increase in morphological variance, analogous to disruptive selection within populations (cf. Blastozoa).

hanced extinction or inhibited origination) in a manner analogous to disruptive natural selection, the result is an increase in the variance of the morphological distribution (fig. 1G). Although the foregoing scenarios are highly idealized, they represent a few major, distinctive evolutionary possibilities, and provide a useful backdrop against which to compare large-scale diversity patterns in the fossil record.

## Results

*Blastozoa*.—Temporal patterns of morphological and taxonomic diversity documented here agree with those reported previously from a smaller morphological sample (Foote 1991b). Blastozoa increase in both morphological and taxonomic diversity from the Late Ordovician to the Devonian (figs. 2, 3). Many genera and species proliferate in the Early Carboniferous, but without an equally large increase in the total range of morphospace occupation (cf. fig. 1A). Thus, morphological diversity in the Early Carboniferous is relatively low. The decline in taxonomic richness after the Early Carboniferous is not accompanied by a corresponding reduction in morphological diversity. Morphological diversity continues to increase into the Permian, and the morphological diversity profile is significantly more top-heavy than the taxonomic diversity profile, suggesting continued diffusion through morphospace without attrition of morphological extremes.

*Trilobita*.—As shown previously (Foote 1991a), there is a general increase in morphological diversity from the Cambrian to the Ordovician (figs. 4, 5). This morphological diversification accompanies a large increase in taxonomic diversity, which peaks in the Early Ordovician and declines rather steadily for the rest of the Paleozoic. Morphological diversity continues to increase from the Early Ordovician to the Mid-Late Ordovician, even as taxonomic richness declines. And even though taxonomic diversity drops substantially from the Ordovician to the Permian, rather high levels of morphological diversity are maintained through the Devonian, after which only trilobites of the order Proetida

Blastoidea

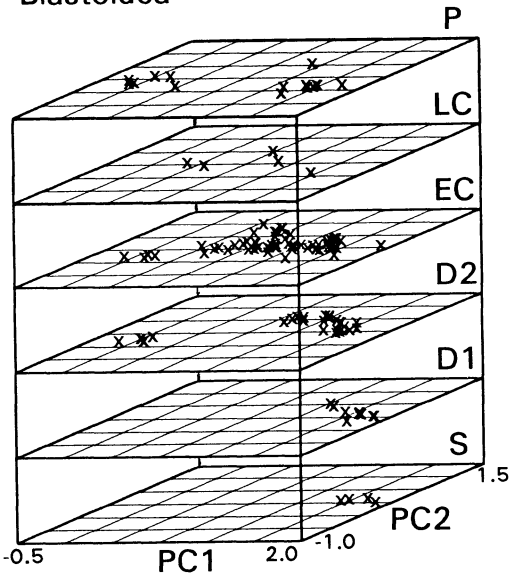


FIGURE 2. Temporal pattern of morphospace occupation in Blastoidea. Note overall increase in range of morphospace occupied. Early Carboniferous taxonomic diversification appears to be constrained morphologically. Despite decline in taxonomic diversity, blastoids remain morphologically diffuse in the Permian. Principal components (PC) 1 and 2 summarize 81.5% of total variance. Because the basals on the lone Ordovician species, *Maurcudablastus uniplicatus*, are poorly preserved (Broadhead 1984), this species is omitted from the figure. Note that, with only one species in the Ordovician, there is no morphological variance among species regardless of the actual morphology. In this and all subsequent morphospace plots: each point represents a single specimen (trilobites) or species (blastoids); and principal components are calculated separately for each clade figured. Therefore, positions in morphospace are not comparable from figure to figure, but are comparable among stratigraphic levels within a figure. Abbreviations regarding stratigraphic intervals are given in table 1 and used throughout the figures.

remain. Morphological diversity is strikingly more top-heavy than taxonomic diversity. Such a temporally forward displacement of morphological diversity suggests taxonomic attrition that is largely nonselective with regard to morphology (fig. 1F; Foote 1991b). This interpretation is corroborated by figure 4, which seems to show the transition from a relatively dense and broad occupation of morphospace in the Ordovician to a much sparser but only somewhat narrower occupation of morphospace in the Silurian. Fortey and Owens (1990b) have argued that the bio-

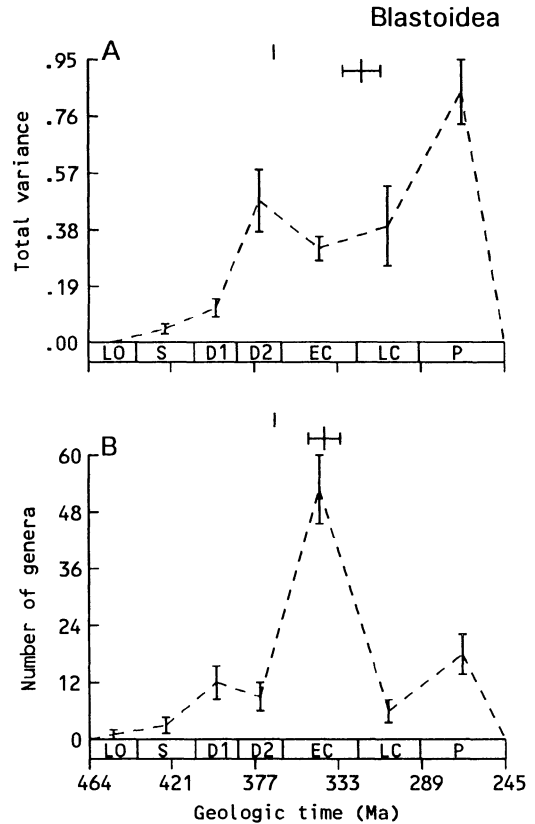


FIGURE 3. Comparison of morphological and taxonomic diversity in Blastoidea. Morphological diversity in this and all subsequent figures is measured as total variance in original morphospace, not principal-component space. Error bars on diversity measures are  $\pm 1$  standard error. Standard error of total variance is estimated by conventional bootstrap resampling of the data (200 iterations) for each interval (Efron 1982). Standard error of taxonomic diversity is estimated as the square root of number of taxa. Single vertical line gives position of center of gravity inherent in time scale. Vertical line with error bars gives position of observed center of gravity for diversity path ( $\pm 2$  standard errors). Despite drop in taxonomic diversity after the Early Carboniferous, morphological diversity remains high and is concentrated later in time than taxonomic diversity. Note that, with only one species in the Ordovician, there is no morphological variance among species regardless of the actual morphology. Clade-shape statistics ( $\pm 2$  standard errors):  $CG_m = 319.9 \pm 10.0$ ;  $CG_t = 339.9 \pm 8.5$ ;  $CG_i = 366.2$ ;  $A_m = 0.291 \pm 0.377$ ;  $A_t = -0.163 \pm 0.326$ ;  $A_i = -0.225$  (subscripts m, t, and i refer to morphological and taxonomic statistics, and statistics inherent in time scale). See text for calculation of standard error of clade-shape statistics. Based on exact distributions of bootstrapped clade-shape statistics, morphological diversity is more top-heavy than taxonomic diversity; this difference is significant for CG ( $p = 0.016$ ), but only marginal for A ( $p = 0.118$ ). All tests are two-tailed.

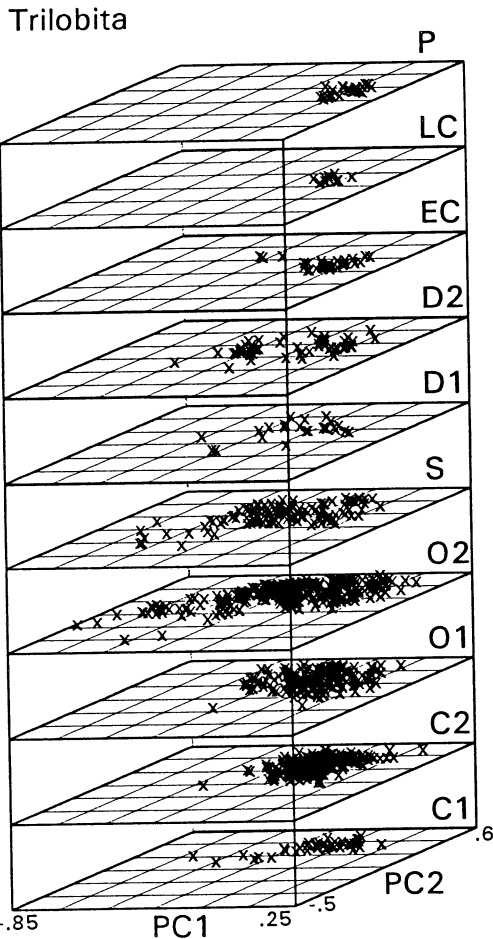


FIGURE 4. Temporal pattern of morphospace occupation in Trilobita. Note diversification into Ordovician, apparent increase in morphological diversity from Early Ordovician to Mid-Late Ordovician, and maintenance of dispersed morphological distribution into Silurian and Devonian. Only Proetida, occupying a relatively small range in morphospace, survive past the Devonian. First two principal components summarize 80.1% of variance.

geographic differentiation of trilobites in the earliest Cambrian indicates an interval of time in which some important evolutionary steps are missing from the record. Although such a gap in the trilobite record would affect the details of clade shape, it would not affect the most striking aspect of the trilobite pattern, namely the discordance between morphological and taxonomic diversity after the Cambro-Ordovician diversification of trilobites.

*Libristoma*.—Since *Libristoma* represents the largest trilobite clade (Fortey 1990), it is per-

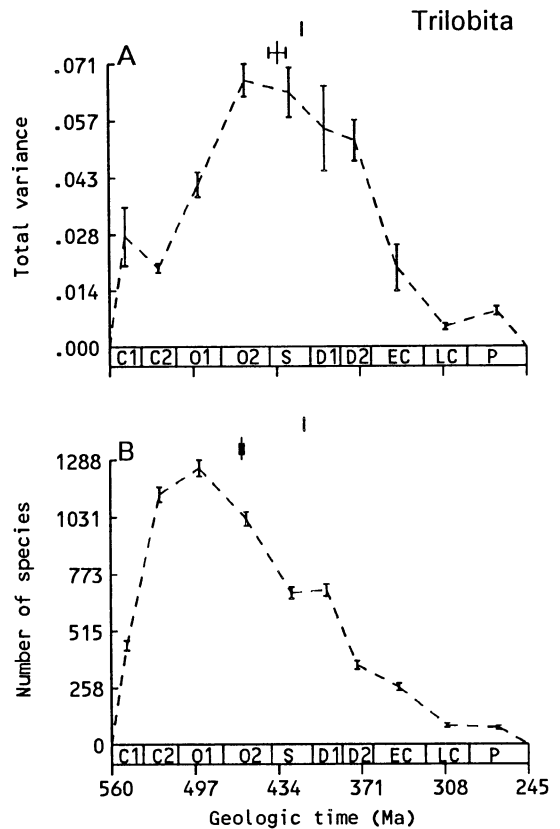


FIGURE 5. Comparison of morphological and taxonomic diversity in Trilobita. Morphological diversity is displaced forward in time relative to taxonomic diversity, reflecting high levels of morphological diversity despite substantial decline in taxonomic richness after the Early Ordovician. Clade-shape statistics:  $CG_m = 432.2 \pm 6.6$ ;  $CG_i = 460.7 \pm 1.6$ ;  $CG_s = 413.3$ ;  $A_m = -0.065 \pm 0.148$ ;  $A_i = -0.682 \pm 0.051$ ;  $A_s = -0.056$ . Morphological diversity is more top-heavy than taxonomic diversity for both  $CG$  ( $p < 0.002$ ) and  $A$  ( $p = 0.002$ ).

haps not surprising that the taxonomic diversity profile for libristome trilobites roughly resembles that for the whole class (fig. 7). The history of morphological diversity in libristomes, however, does not parallel that for trilobites as a whole (figs. 6, 7). Nevertheless, two similarities are noteworthy. First, morphological diversification continues through the Ordovician despite a decline in taxonomic diversity after the Early Ordovician. Second, moderate levels of morphological diversity are maintained into the Devonian in the face of a post-Ordovician decrease in species richness. Again we see a temporally forward dis-

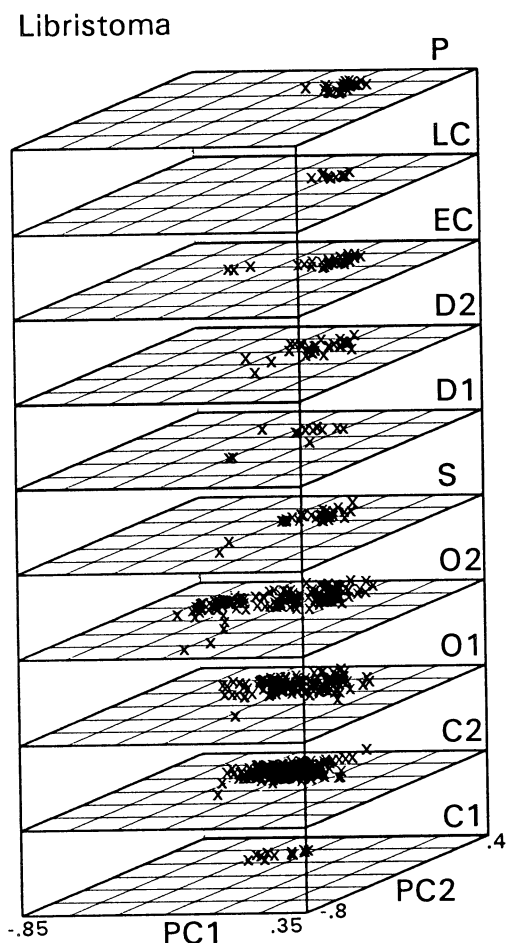


FIGURE 6. Temporal pattern of morphospace occupation in Libristoma. Note increase in morphospace occupation from Cambrian to Mid-Late Ordovician. Principal components 1 and 2 summarize 80% of total variance.

placement of morphological diversity, which suggests a nonselective vacating of morphological space during the clade's decline.

*Asaphina*.—Because this libristome subclade is relatively short-lived, its diversity profiles should be interpreted with more caution. Furthermore, although there are a few species of the trinucleacean family Raphiophoridae known from the Silurian, well preserved specimens were unavailable, so there are currently no morphological data representing this interval. It is very likely that morphological diversity in Silurian *Asaphina* was rather low, since the Raphiophoridae represents a limited variety of form compared to

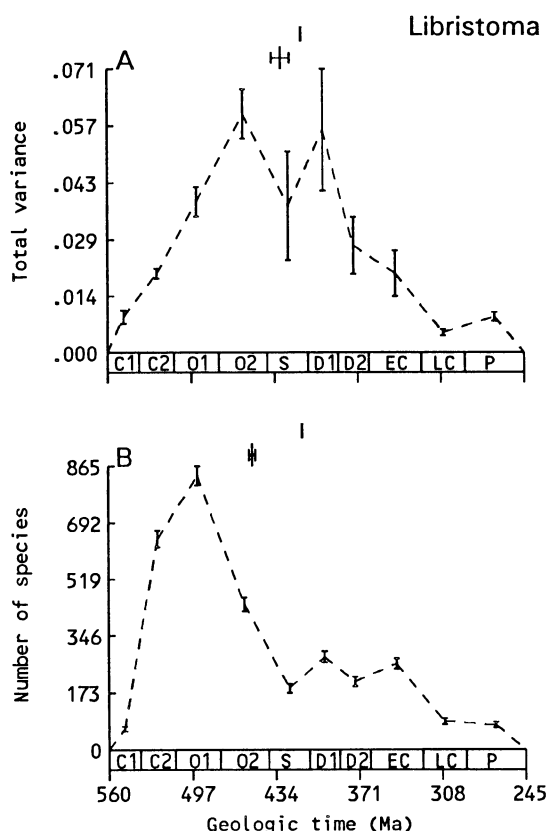


FIGURE 7. Comparison of morphological and taxonomic diversity in Libristoma. Morphological diversity increases from the Early to the Mid-Late Ordovician, and is fairly high through the Early Devonian, despite decrease in taxonomic diversity. Morphological diversity is therefore more top-heavy than taxonomic diversity for both CG ( $p < 0.002$ ) and A ( $p = 0.002$ ). Clade-shape statistics:  $CM_m = 429.1 \pm 6.8$ ;  $CG_i = 451.3 \pm 2.5$ ;  $CG_c = 413.3$ ;  $A_m = -0.290 \pm 0.244$ ;  $A_i = -0.808 \pm 0.068$ ;  $A_c = -0.225$ .

the array of Ordovician *Asaphina* that includes remopleuridaceans, trinucleaceans, asaphids, nileids, and cyclopygids. It is still worth considering the diversity profiles of *Asaphina* for the Cambro-Ordovician only. As with Trilobita and Libristoma, the increase in taxonomic diversity from the Cambrian to the Ordovician is accompanied by an increase in morphological diversity (figs. 8, 9). Also like Trilobita and Libristoma, morphological diversity continues to increase after the Early Ordovician, despite a decline in taxonomic richness. Again, continued morphological diffusion and nonselective taxonomic attrition can be inferred.

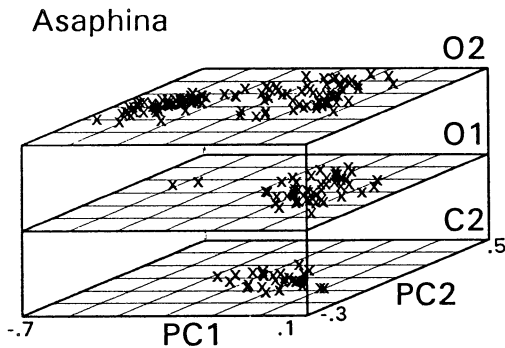


FIGURE 8. Temporal pattern of morphospace occupation in Asaphina. Note steady increase in amount of morphospace occupied. Principal components 1 and 2 summarize 84.5% of total variance.

*Proetida*.—Proetida represents the longest-lived libristome subclade, and the only trilobite group to endure beyond the Devonian. It is peculiar in a few respects (figs. 10, 11). (1) It is the only trilobite clade examined here in which maximal taxonomic diversity falls after the Ordovician. (2) It is the only trilobite clade studied for which maximal morphological diversity does not fall in the Mid-Late Ordovician. (3) It has the least peaked morphological diversity profile of all clades studied; morphological diversity is greatest in the Early Devonian, but is nearly as high in the surrounding stratigraphic intervals. That this taxon remains at about the same level of morphological diversity for most of its history may suggest some form of constraint on the magnitude and direction of morphological change (fig. 1A). Such an interpretation would be in accord with the general view of the proetids as a morphologically conservative group. After the Early Carboniferous there are corresponding drops in morphological and taxonomic diversity, which may reflect selection against morphological extremes (figs. 1D, 10).

*Phacopida*.—This, the largest non-libristome clade (Fortey 1990), is like the other trilobite clades in that the initial taxonomic diversification is accompanied by an increase in morphological diversity, and that maximal morphological and taxonomic diversity both occur in the Mid-Late Ordovician. In contrast with Trilobita, Libristoma, and Asaphina, however, the decline in taxonomic diversity

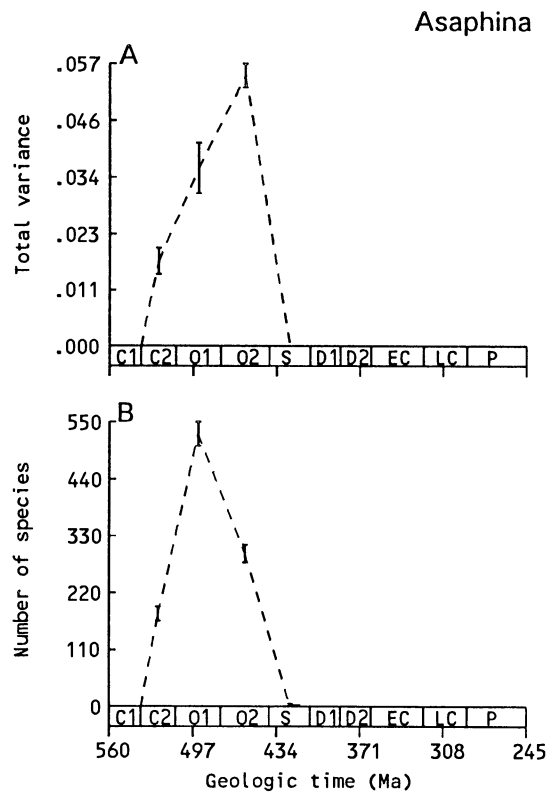


FIGURE 9. Comparison of morphological and taxonomic diversity in Asaphina. Despite decrease in taxonomic diversity from Early to Mid-Late Ordovician, morphological diversity continues to increase, and thus is concentrated later in time than taxonomic diversity. Because morphological data are lacking for the Silurian, clade shape statistics are not calculated.

after the Ordovician, and especially after the Silurian, is accompanied by a decrease in morphological diversity (figs. 12, 13), despite evolutionary bursts at smaller scales (e.g., Calmoniidae; Eldredge and Braniša 1980). Consistent with this pattern, figure 13 shows what appears to be a truncation of morphological extremes.

*Scutelluina*.—Sample sizes are quite small for this clade, so interpretations of morphological diversity patterns must be treated with caution. Despite the large uncertainties in morphological diversity and clade shape, however, it seems clear that taxonomic diversification in Scutelluina is at least equaled by morphological diversification, with both aspects of diversity maximal in the Mid-Late Ordovician (figs. 14, 15). Morphological diversity appears initially to increase more rap-

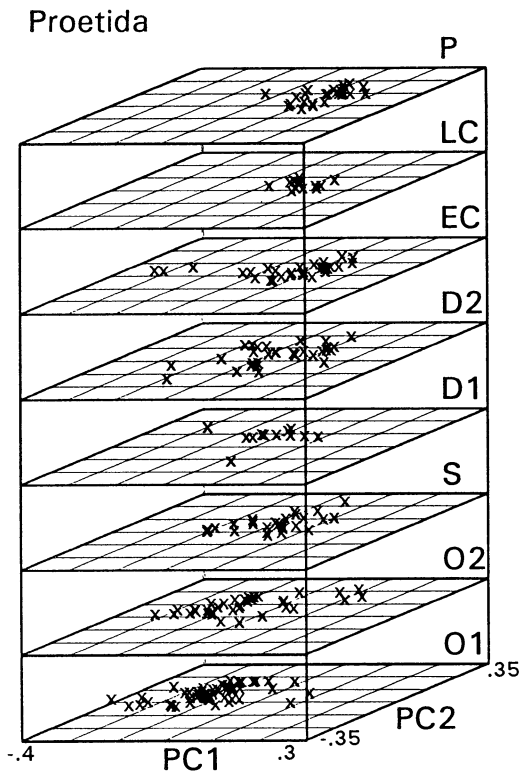


FIGURE 10. Temporal pattern of morphospace occupation in Proetida. Morphological diversification after the clade's initial appearance in the Early Ordovician is rather subdued. Note contraction in morphospace occupation after the Early Carboniferous. Principal components 1 and 2 summarize 82% of total variance.

idly than taxonomic diversity, but the very large uncertainty associated with the diversity metric in the Early Ordovician makes this pattern suspect. Morphological diversity drops after the Ordovician, although not as steadily as does species richness. Consistent with this pattern, figure 14 suggests selective elimination of morphological extremes. Morphological selectivity is in accord with the limited range of styginids that survived the Ordovician in contrast to the range of illaenids, panderiids, phillipsinellids, and styginids present in the Ordovician (Harrington et al. 1959; Lane and Thomas 1983).

*Overview.*—During the taxonomic diversification of a clade, morphological diversity tends to keep up with taxonomic diversity. However, a fundamental asymmetry between these two aspects of diversity is that morphological diversity does not always decrease

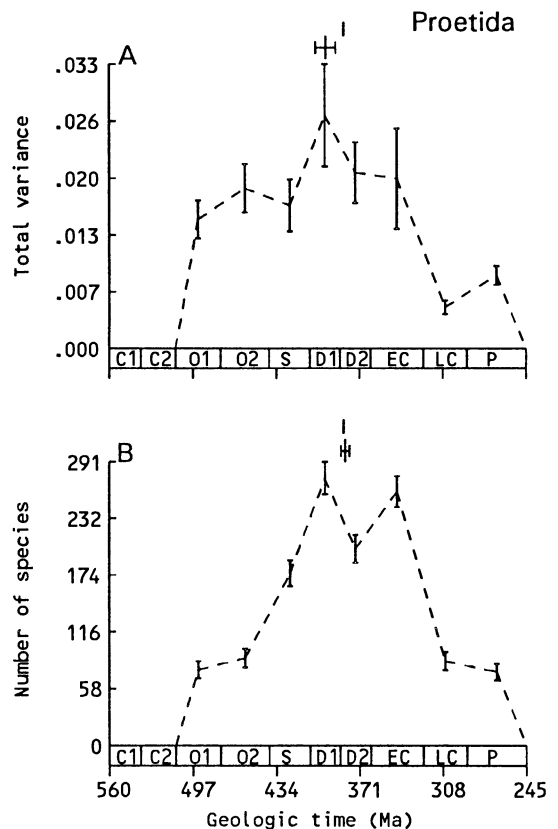


FIGURE 11. Comparison of morphological and taxonomic diversity in Proetida. Morphological diversity is nearly constant for much of the group's history, with a rough tendency for taxonomic diversity decrease to correspond with decrease in morphological diversity after the Early Carboniferous. Consequently, morphological diversity is more bottom-heavy than taxonomic diversity ( $CG$ ;  $p < 0.002$ ;  $A$ ;  $p = 0.008$ ). Clade-shape statistics:  $CG_m = 396.6 \pm 7.6$ ;  $CG_t = 381.9 \pm 3.2$ ;  $CG_i = 382.8$ ;  $A_m = -0.253 \pm 0.238$ ;  $A_t = -0.036 \pm 0.092$ ;  $A_i = -0.075$ .

as rapidly as taxonomic diversity during the decline of a clade. In fact, morphological diversity often continues to increase after the time of peak taxonomic diversity has been passed. Clades that show roughly concordant decreases in morphological and taxonomic diversity appear to exhibit truncation of morphological extremes. Nearly all the trilobite clades studied are most diverse morphologically during the Mid-Late Ordovician, and most diverse taxonomically sometime in the Ordovician; this is true also of blastozoan echinoderms (Foote 1992b). Although apparent changes in amount of morphospace occupied can reflect changes in sampling (Foote

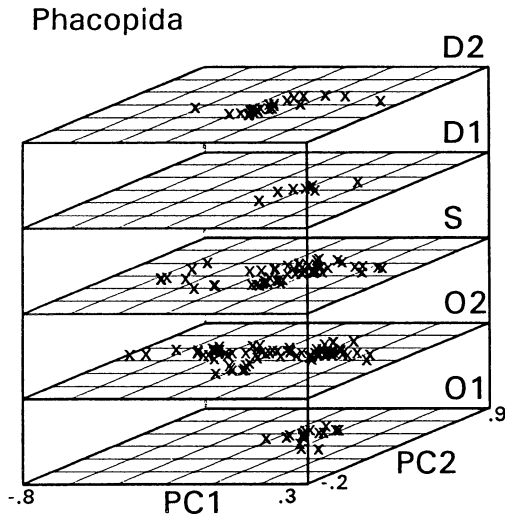


FIGURE 12. Temporal pattern of morphospace occupation in Phacopida. Note maximal extent of morphospace occupation in Mid-Late Ordovician and contraction of morphospace occupation in Devonian. Principal components 1 and 2 summarize 77.3% of total variance.

1992a), contractions in morphospace occupation in Proetida, Phacopida, and Scutellina are accompanied by decreases in the unbiased diversity metric used here, suggesting that the truncation of morphological extremes is not simply an artifact of poor sampling.

### Discussion

The history of morphological diversity in Trilobita portrayed here is similar to that presented by Fortey and Owens (1990a,b) in that morphological variety increases profoundly to an Ordovician maximum and trails off thereafter. To assess morphological diversity, Fortey and Owens considered the number of morphotypes and the number of families representing these morphotypes. Thus, their measure is effectively a joint index of morphological and taxonomic diversity. According to their measure, the post-Ordovician decline in diversity is much greater than it would appear from a strict analysis of morphology alone, because taxonomic diversity, which contributes heavily to their metric, declines much more substantially than does the variety of realized forms. Interestingly, inspection of Fortey and Owens' figures suggests that the raw number of morphotypes, re-

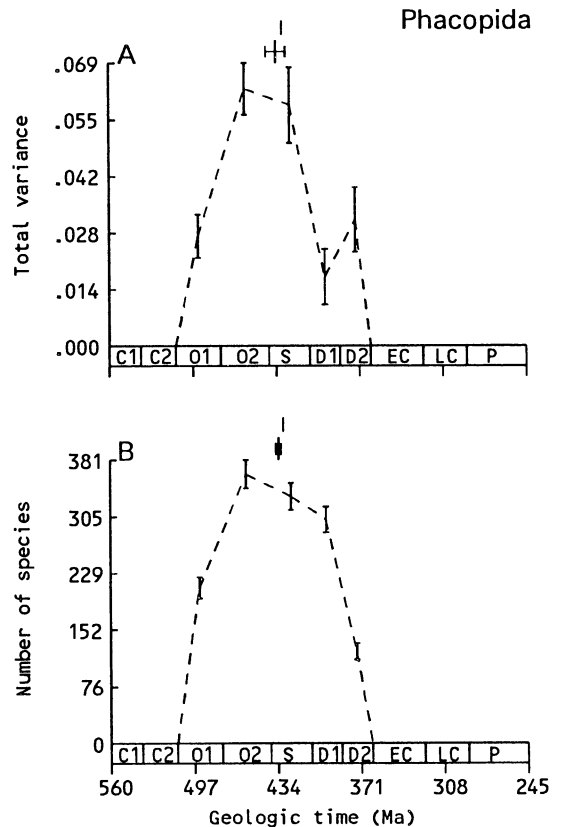


FIGURE 13. Comparison of morphological and taxonomic diversity in Phacopida. Overall shape of two diversity paths agrees rather well. CGs do not differ ( $p = 0.686$ ), but the asymmetry statistic indicates that morphological diversity is more skewed toward early times than is taxonomic diversity ( $p = 0.01$ ). However, this may largely reflect poor sampling (no Cheirurina) of morphological data in the Early Devonian. Clade-shape statistics:  $CG_m = 434.0 \pm 7.4$ ;  $CG_t = 432.9 \pm 2.0$ ;  $CG_i = 429.2$ ;  $A_m = -0.119 \pm 0.225$ ;  $A_t = 0.159 \pm 0.076$ ;  $A_i = -0.225$ .

gardless of the number of taxa representing them, yields a pattern of morphological diversity more in agreement with that presented here.

The recognition that various measures of taxonomic diversity yield similar temporal patterns over the Phanerozoic (Sepkoski et al. 1981) has served to strengthen the notion that different diversity metrics can detect a common signal. At the same time, it has become increasingly apparent that temporal patterns of morphological and taxonomic diversity often disagree with each other. An initial response to this discrepancy may be to explain the discordance away as the result of some

Scutelluina

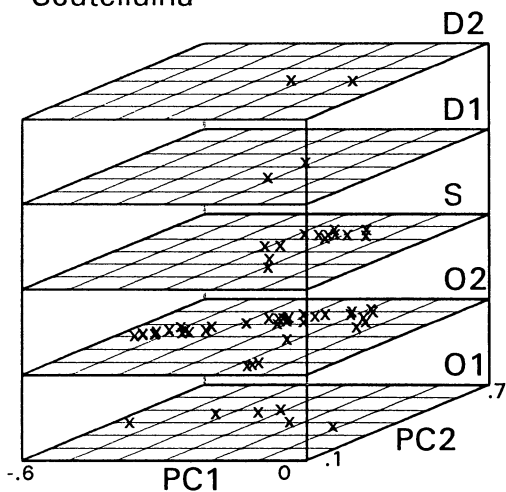


FIGURE 14. Temporal pattern of morphospace occupation in Scutelluina. Note maximal occupation of morphospace in Mid-Upper Ordovician, and truncation of morphospace occupation in the Silurian and Devonian. Principal components 1 and 2 summarize 92.5% of total variance.

procedural artifact. However, a major component of the discordance, i.e., the persistence of morphological diversity in the face of taxonomic decline, is perfectly consistent with the geometry of branching. Unless origination is highly constrained morphologically, diffusion through morphospace is likely to occur as a clade diversifies, and once it has spread out in morphospace, only highly selective taxonomic attrition can curtail morphological variety as rapidly as taxonomic diversity decreases (Foote 1991b). Ironically, it may be that a close correspondence between morphological and taxonomic diversity demands more of an explanation than a systematic difference between the two aspects of diversity. For in such a case, selective elimination of morphological extremes or whole regions in morphospace is suggested, and we would like to understand the ecological and microevolutionary basis of such heterogeneities.

Comparing morphological and taxonomic diversity to infer selectivity in extinction and/or origination may seem absurdly indirect, but is reasonable in light of the temporal distribution of extinctions and originations and the uncertainty with which evolutionary trees

Scutelluina

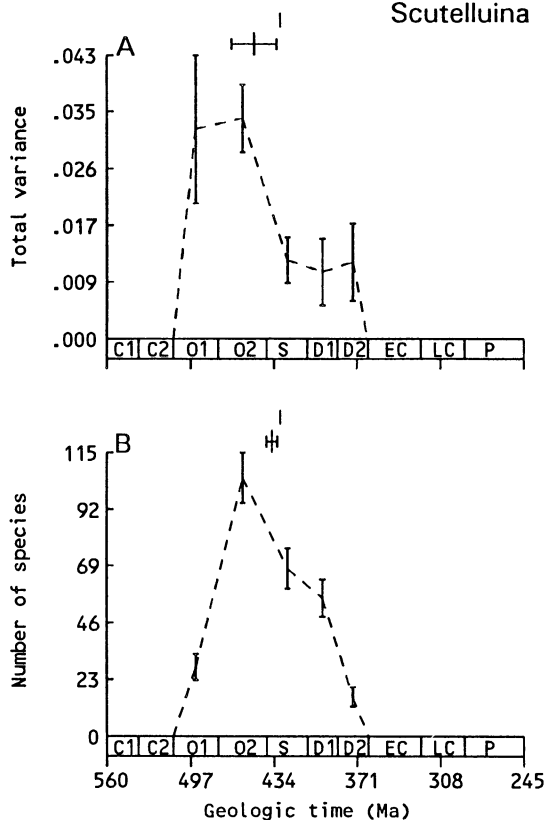


FIGURE 15. Comparison of morphological and taxonomic diversity in Scutelluina. Morphological diversity appears initially to increase faster than taxonomic diversity, but there is great uncertainty in the estimate of morphological diversity for the Early Ordovician. Decline in taxonomic diversity is accompanied by decline in morphological diversity. Morphological and taxonomic clade-shape statistics do not differ significantly (CG:  $p = 0.616$ ; A:  $p = 0.824$ ). Clade-shape statistics:  $CG_m = 466.8 \pm 14.5$ ;  $CG_l = 473.7 \pm 4.9$ ;  $CG_s = 459.6$ ;  $A_m = -0.218 \pm 0.524$ ;  $A_l = -0.156 \pm 0.141$ ;  $A_s = 0.050$ .

are known. Studies of selectivity in extinction have tended to focus on major extinction episodes, comparing survivors and victims of the event (Jablonski 1986; Kitchell et al. 1986). However, if most extinctions and originations can be attributed to background rates and minor pulses (e.g., Raup 1992), it is useful to ask whether the many smaller events add up to a general pattern of selectivity. Comparison of morphological and taxonomic diversity patterns allows this question to be addressed. If we had detailed evolutionary trees such as those in figure 1, then it would be relatively obvious whether extinction were selective. But we usually have only samples of

a clade at successive intervals of time. Comparing morphological and taxonomic diversity allows some inference about evolutionary mechanisms given only larger-scale patterns.

This paper has sought to detect morphological heterogeneities, not to suggest their ultimate explanation. In this respect, the approach is similar to that of Raup (1978) and Valentine and Walker (1987), who examined taxonomic selectivity in extinction by comparing extinction rates at different taxonomic levels. Some previous studies have addressed the issue of selectivity at finer scales, stressing explanation rather than the pattern itself. Among numerous examples, Kitchell et al. (1986) suggested the importance of diatom resting spores in surviving ecological catastrophe, and Jablonski (1986) demonstrated the effect of geographic range on taxonomic longevity. Such explanations are important, but equally valuable is the demonstration that morphological heterogeneities even exist. At the coarsest scale (that adopted here), the concordant decline of morphological and taxonomic diversity in the Scutelluina, for example, suggests a bias against certain regions in morphospace. This bias could reflect higher extinction and/or lower origination rates. At a finer scale, we can trace the morphological decline of Scutelluina to the loss of panderiids, phillipsinellids, most illaenids, and the majority of forms in the broad and variable Styginidae (Lane and Thomas 1983). At a finer scale still, we may ask why these particular forms became extinct, but this question requires data of a different kind than presented here. Again looking at the coarse scale, the post-Devonian decline in morphological diversity in Trilobita seems clearly tied to the ultimate loss of all groups except the order Proetida by this time. Why this conservative order should have survived is not clear, however. If one were willing to assume that morphologically extreme forms are ecologically more specialized, and that specialization increases extinction risk, then selection against morphological extremes would make sense.

The maintenance of morphological diversity in the midst of taxonomic attrition is con-

sistent with morphologically nonselective extinction. As has been stressed before (Raup et al. 1973; Valentine and Walker 1987; Foote 1991b), this perspective is not meant to suggest that extinction is fundamentally random, but that the causes of extinction are so many and varied that taxonomic attrition over the broad expanse of morphological space shows no obvious pattern. Moreover, if clades overlap in morphological space (which they often do), it is conceivable for extinction to act selectively in a phylogenetic sense without effecting as strong a morphological selectivity.

I have discussed increases in morphological diversity as consistent with undirected diffusion through morphospace (Raup and Gould 1974; Fisher 1986), but at least two other processes can cause an increase in morphological diversity. (1) Classic adaptive radiation, involving the (rapid) occupation of radically new adaptive zones, should lead to wide exploration and colonization of morphological space (Simpson 1953; Van Valen 1971). Considering the extensive proliferation of whole new morphological themes in Ordovician trilobites, such an explanation may seem virtually inescapable (Fortey and Owens 1990b). Of course, even the notion of diffusion through morphospace does not deny that changes are adaptive, and the distinction between the two processes may reflect differences of scale and emphasis (Erwin 1992). Adaptive radiation serves as a possible explanation at one level, but at a finer scale one may still ask why particular forms were established at a particular time and place. Other kinds of studies, such as the functional analyses of Stanley (1968), are needed to explain such radiations.

(2) Selective extinction of modal forms can cause an increase in morphological variance, a measure of diversity, without increasing the total range of realized forms (fig. 1G). Such a process, analogous to disruptive selection at the population level, may be partly responsible for high morphological diversity in Permian blastoids. It seems as though much of the interior region in morphospace (at least as represented by principal components), once richly occupied by Carboniferous forms, was vacated by the Permian. Bias against inter-

mediates serves as a potential explanation at one scale. If there is such a bias, finer scale studies are needed to explain why the intermediates were not favored.

One striking discordance between morphological and taxonomic diversity not shown by the clades studied here, but documented for other groups, is early morphological diversification that greatly outstrips taxonomic diversification (fig. 1B). The echinoderm subphylum Blastozoa (the larger group that includes the blastoids studied here) increases dramatically in morphological diversity in the Cambrian, despite very low taxonomic diversity, and only in the Ordovician does it greatly increase in taxonomic diversity (Foote 1992b). Briggs et al. (1992) have argued that morphological diversity in Recent arthropods is about the same as that in the Cambrian, even though taxonomic diversity has increased enormously since the Cambrian. Both the blastozoan and arthropod patterns strongly suggest a change in patterns of constraint, with morphological transitions becoming smaller after the Cambrian (Foote and Gould 1992). A similar change has been discussed for echinoderms (Sprinkle 1980; Campbell and Marshall 1987), stenolaemate bryozoans (Anstey and Pachut 1992), and the Metazoa as a whole (Valentine and Erwin 1987).

An important asymmetry between morphological and taxonomic diversity not discussed above is their differential sensitivity to incomplete preservation and sampling. Changes in taxonomic diversity may commonly reflect monographic and geologic biases (Raup 1972). For example, it seems clear that taxonomic diversity in blastoids increased from the Devonian to the Carboniferous, but this increase may be exaggerated by the abundance of shallow-water carbonates on the North American midcontinent. Changes in morphological diversity, on the other hand, are generally less sensitive to such biases. This is because, given the measure of morphological diversity as average dissimilarity rather than maximal dissimilarity or amount of morphospace occupied, a simple change in sample size does not bias diversity toward higher or lower values (Foote 1992a).

It is primarily severely nonrandom sampling, with some regions in morphospace overrepresented relative to others, that has such an effect. Thus, even if one does not trust taxonomic diversity data, temporal patterns of morphological diversity are relatively reliable. However, given the scale of analysis and the purposes for which they are used here, taxonomic diversity data probably also convey a reliable picture.

Further insight into the determinants of diversity is gained by considering time-specific versus clade-specific patterns. For example, blastozoan echinoderms (Foote 1992b) and all trilobite clades studied except *Proetida* show maximal morphological diversity in the Mid-Late Ordovician. Guensburg and Sprinkle (1992) discuss the importance of cratonic flooding and habitat diversity in the Ordovician radiation of echinoderms, factors likely to be of importance in trilobite diversification as well. Furthermore, the Ordovician is generally recognized as a time of high provinciality, although trilobite faunas became more cosmopolitan from the Early to the Late Ordovician (Whittington and Hughes 1972; Hallam 1973). In contrast to this similarity shared among clades, it is noteworthy that the class Trilobita does not show the same early diversification pattern as that claimed for the arthropods as a whole (Whittington 1980; Gould 1989, 1991), and demonstrated for blastozoan echinoderms (Foote 1992b), namely, an initial morphological diversification that far exceeds lower-level taxonomic diversification. That different major biologic groups do not behave exactly alike at the same time may argue for an interplay between common ecological, geological, and genetic factors, and those unique to particular clades.

Differences in taxonomic level may also contribute to differences in diversity patterns among various groups (Valentine 1969). For example, it appears as though the arthropod phylum generated many new body plans in or just before the Cambrian (Whittington 1980), but the Trilobita, one of the most prolific arthropod designs and one of the dominant arthropod groups of the Cambrian, did not generate its greatest array of form early in its history. In fact none of the trilobite

subgroups studied produced such a pronounced initial diversification of forms. Likewise, the echinoderm subphylum Blastozoa experienced much greater morphological than taxonomic diversification early in its history (Foote 1992b), whereas early morphological and taxonomic diversification were more concordant in the blastozoan subclade Blastoidea (Foote 1991b; this study). It has long been appreciated that the same taxonomic rank does not "mean the same thing" among groups, but this does not imply that different taxonomic ranks mean nothing within a group. Nested diversification patterns may differ predictably up and down the taxonomic hierarchy, with the highest-level taxa showing early morphological bursts as major body plans are established, and lower-level taxa showing concordant morphological and taxonomic diversity increases as simple variations on those body plans are generated (Gould 1989; Sprinkle 1980; Valentine 1986). This suggests some measure of significance for the taxonomic ranks that are occasionally regarded as arbitrary and "meaningless."

The foregoing discussion is replete with qualifiers and hedges. There are two main reasons for this. First, there is no unique correspondence between a pair of morphological and taxonomic diversity profiles and a particular set of ecological and evolutionary mechanisms. Concordant morphological and taxonomic diversification are consistent with diffusion through morphospace, but adaptive radiation cannot be ruled out. Maintenance of morphological diversity during taxonomic decline suggests effectively nonselective extinction and continued origination, but a shift in morphological distribution (elimination at one morphological extreme and enhanced origination that extends the opposite extreme, for example), could also be responsible for such a pattern. Concordant declines in morphological and taxonomic diversity strongly suggest heterogeneity in morphospace, either enhanced extinction or inhibited origination, but this may be a matter of sawing a few large branches off the evolutionary bush, or pruning off many of the branch tips. Although the style of analysis presented here can effectively narrow down the possibilities, investigations at finer scales

are needed to provide ultimate (or penultimate) explanations.

Second, some general patterns in the history of morphological diversity are beginning to emerge, but very few clades have been studied, other than with taxonomic proxies. Therefore, it would be imprudent to predict which kinds of patterns—early morphological bursts, morphological top-heaviness, and so on—will prove to predominate, and under which historical circumstances. This study represents a very modest step toward increasing our data base on the history of morphological diversity, but there are many more clades that deserve our attention. We may hope that analysis of more clades at various taxonomic levels will eventually allow us inductively to formulate macroevolutionary laws of morphological and taxonomic diversity.

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