Sampling, Taxonomic Description, and Our Evolving Knowledge of Morphological Diversity

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Sampling, taxonomic description, and our evolving knowledge of morphological diversity

Mike Foote

Abstract.—Morphological analysis of four higher taxa of fossil marine invertebrates shows that, over the history of paleontology, there is no general tendency for morphologically extreme or modal species and genera to be described preferentially early or late. Reconstructing the expected evolutionary sequences of morphological disparity that would have been estimated at various times during the past century and a half reveals features that are sensitive to sampling (for example, peak trilobite disparity in the Ordovician, peak of post-Paleozoic crinoid disparity in the Triassic, and peak blastoid disparity in the Permian), as well as more robust features (for example, increase in trilobite disparity from the Cambrian to the Ordovician, continued increase in trilobite disparity despite a drop in taxonomic diversity after the Early Ordovician, decrease in blastoid disparity from the Devonian to the Carboniferous, and increase in crinoid disparity from the Jurassic to the Cretaceous followed by decline during the Cretaceous). Although we still have much to learn about the evolution of form, in many respects our view of the history of biological diversity is mature.

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Sampling and Increased Knowledge

We rarely know all that we would like, but when do we know enough? An idealistic interpretation of this question would ask when our knowledge allows a sufficiently close approximation to the empirical truth. A more pragmatic view would ask when increased study yields such exceedingly diminishing returns that our knowledge is relatively stable in the face of modest investments of effort (even if this stability simply reflects reliable sampling of an unreliable record). Assessing the sensitivity of paleontological patterns, either as sampling increases or as data are compiled independently, is an important step in evaluating the reliability of such patterns, whether they concern, for example, diversity, evolutionary rates, or genealogy (Williams 1957; Paul 1980; Sepkoski et al. 1981; Raup 1991; Sepkoski 1993; Blackburn and Gaston 1994; Hughes and Labandeira 1995; Weishampel 1996).

This paper will explore the growth of our knowledge of morphological diversity in a few well-known fossil groups. We would like to know whether we have a representative sample of morphological diversity, and therefore can rely on patterns documented in the fossil record. On the basis of the date of publication of fossil species and genera, I construct sampling curves relating morphological diversity to the number of taxa described. I use these to address whether and how the increase in observed morphospace occupation reflects sampling of taxa nonrandomly with respect to their contribution to morphological disparity. In particular, addressing the claim that early systematists preferentially studied morphologically extreme forms (McGhee 1995), I find little evidence for such a secular trend. We would also like to know whether our view of macroevolutionary patterns is likely to change substantially as we increase our sample of fossil species. I document how perceived secular patterns of morphological disparity have changed as our knowledge has increased. This gives some clues as to which patterns are robust in the face of variable sampling.

Morphological Sampling Curves for Species and Genera

To estimate how the observed diversity of form has grown over the history of paleontology, we need to quantify organismic morphology and to estimate when each particular form in our present sample was first known. It is not feasible to reconstruct each instance
Figure 1. Cumulative morphospace occupation relative to cumulative sampling of 660 trilobite species. Species are arranged by year of publication; species described in the same year are randomly arranged within that year. A, Range of cumulative sample (sum of ranges of 12 principal components). Dotted lines show limits within which lie 90% of random orderings of species; they are not a 90% confidence interval for the observed sampling curve. Solid lines show ten alternative within-year randomizations; variation among these is relatively small. Unlabeled ticks on abscissa mark increments of 25 taxa. Logarithmic scale is used on abscissa to make the sampling curve easier to read; arithmetic coordinates would yield the same relationship between observed sampling curve and limits of random sampling. B, Variance of cumulative sample (sum of variances of 12 principal components). Dotted lines and solid lines as in A. C, Euclidean distance of species from multivariate mean (centroid). Letters at the top of the graph correspond with letter labels in A. A single within-year randomization is randomly chosen. To allow
in which a systematic biologist recognized a specimen in hand as distinct in some interesting way from previously known material. However, an operational approach can be based on the date of publication of taxonomic names.

**Morphological Data and Sampling of Taxa.**—Morphological data for this study were drawn from previous analyses of disparity in four major groups of marine invertebrates, namely trilobites, blastozoans, blastoids, and crinoids (Foote 1989, 1991a,b, 1992b, 1995a,b, 1996b). Trilobite form was quantified on the basis of Fourier analysis of the cranial outline (Foote 1989), blastoid form was measured as the Cartesian coordinates of thecal landmarks (Foote 1991b), and the form of blastozoans and crinoids was quantified with discrete characters (Foote 1992b, 1995a,b, 1996b). All data were converted to orthogonal dimensions using principal components analysis on the variance-covariance matrix for continuous variables and principal coordinates analysis on the interspecies phenetic distance matrix for discrete characters. The data were originally collected to study evolutionary patterns of disparity, and various sampling approaches and stratigraphic subdivisions were used. For Paleozoic crinoids (Foote 1995a,b) and blastozoans (Foote 1992b), only one species per genus per stratigraphic interval was sampled, whereas no such restriction was applied to trilobites, blastoids, or post-Paleozoic crinoids. As described below, this particular sampling restriction limits the analysis of expanding knowledge of evolutionary patterns. Species- and genus-level analyses used species and genus averages, respectively. (That is, in cases where multiple specimens were sampled for a species, that species was represented by its mean form, and similarly for genera in which multiple species were sampled.) For this study, I generally excluded material not identified to the species level (for example, *Asaphus sp.* and “unidentified scutelluid”), but I did consider new but unnamed species as valid (for example, *Acidaspis sp.* A Ross 1979). For material compared to a particular species with “cf.”, I considered the material to belong to the species in question. I generally treated subspecies as distinct species and subgenera as genera.

**Assigning Dates to Species.**—I used the accepted date of publication of a species name as a proxy for the time at which the form corresponding to the name was first known. In most cases, this proxy is reasonable, since publication follows the study of newly collected material by just a few years or less. There are exceptions, of course, such as Brezinski’s (1992) publication of trilobite species that J. Marvin Weller had earlier recognized, but these are relatively rare. I determined dates of publication using original descriptions, museum labels and catalogues (e.g., Morris and Fortey 1985), later systematic works and revisions (e.g., Macurda 1983; Morris 1988), bibliographic and synoptic works, such as Vogdes (1890, 1917, 1925a,b), Bassler and Moorey (1943), Webster (1969, 1977, 1986, 1988, 1993), and pertinent volumes of *The Zoological Record*, *Fossilium Catalogus*, and *The Treatise on Invertebrate Paleontology*. I considered all species described within a given year to have the same date of publication (that is, I made no attempt to determine sequence of publication within a year). To construct sampling curves, I randomized the order of species within a given year. As shown below (Fig. 1), the effect of ordering within a year is small compared with the effect of ordering from year to year.

**Sampling Curves for Trilobite Species.**—As more species are sampled, the observed range of morphology increases monotonically on average (provided that not all species are identical in the traits measured) (Pearson 1926; Foote 1992a), whereas variance is not thus constrained. Figure 1 depicts how these measures of morphological dispersion change as
more trilobite species are sampled. Several solid lines show results for alternative randomizations of species within years. The effect of randomizing within years is small compared with larger-scale patterns involving the growth of our knowledge as the years go by. Therefore, in all further examples, the sampling curve will be represented by a single within-year ordering. For selected points on the curve, years are indicated, along with one or more authors of works published in the corresponding year.

To compare the observed sampling curve with the expectations of random sampling, I randomized the order of all species 200 times and constructed a corresponding curve for each randomization. The dotted lines in Figure 1A, B show the envelope containing the inner 90% of the resulting distribution of random-sampling curves. However, note that interpreting the deviation of sampling curves beyond this envelope is difficult, because each point on the curves depends on the previous points. Thus, several adjacent points on the sampling curve that lie beyond the random-sampling envelope do not represent independent deviations from randomness. They could reflect just one or a few species whose effects propagate up the sampling curve.

For much of the history of trilobite studies, the cumulative known range of form is within the limits of what would be expected if species had been sampled at random morphologically. However, there are a few interesting exceptions. There are periods of time (e.g., from about 1850 to just after 1900) when the cumulative range of form increases slowly and the cumulative variance decreases. This reflects a preferential sampling of morphologically central taxa, mainly Cambrian ptychoparioids, over morphologically peripheral taxa (at least in the data at hand, which emphasize North American and British material). The increase in range and variance in the early 1950s largely reflects sampling of Ordovician Asaphina and Cheirurina (e.g., Ross 1951; Cooper 1953; Whittington and Evitt 1953; see Foote 1993b). At some points, when a few extreme species are sampled, there are jumps in range and variance, since both statistics are sensitive to extremes.

Because sampling curves are cumulative, certain features may be constrained. For example, in Figure 1A and some additional cases below, the observed curve has a slope less than that of the expectation of random sampling. However, because all sampling curves for a given set of data must end up in the same place, this lower slope could simply reflect the fact that, at low sample sizes, the empirical curve starts out higher than the expected random curve. Because cumulative curves can be difficult to interpret, the distance of each species from the multivariate mean (centroid) of the complete sample is shown in Figure 1C. There are a few periods of time during which several morphologically peripheral species are sampled, but there is no substantial trend. Although range and variance are above the random expectation early on, this is at a very low cumulative sample size; the observed sampling curve quickly falls within the range of patterns expected for random sampling. It is true that the first century or so depicted on this sampling curve is responsible for a greater increase in total range than is the second century, as is the case for the other examples documented below. However, the progressively smaller increase in range per unit increase in sample size is a general expectation of random sampling (see Pearson 1926; Foote 1992a). Thus, there is little support for the claim (McGhee 1995: p. 362) that, "[i]n the evolution of the classification of most fossil groups the most striking and divergent morphologies are usually the first to be formally described," whereas "new discoveries and descriptions tend to fill in finer morphological distinctions between the major morphological endmembers described in the earlier stages of classification."

Because cumulative curves have somewhat constrained shapes, it is conceivable that they must resemble those documented here. However, hypothetical, nonrandom sampling schemes clearly result in substantially different sampling curves. For example, if trilobite species were sampled in stratigraphic or taxonomic order, the increase in our knowledge of form would bear little resemblance to the actual pattern (Figs. 2 and 3). Moreover, observed sampling curves do not resemble what
we would obtain if species were described in order of either increasing or decreasing distance from the average form (Figs. 4 and 5). Thus, sampling falls between the extremes of highly structured and random, but is apparently closer to the latter.

Note that the empirical sampling curve for morphological range would give the impression of leveling off if cumulative sample size were plotted arithmetically rather than logarithmically. However, this and other sampling curves continue to increase at an ever decreasing rate. Thus, an apparently level curve does not imply that we have discovered the full range of form that existed or that can be known (i.e., that the curve is near its maximum). Rather, it implies that substantial effort will be required to extend the known range of form even slightly.

*Sampling Curves for Trilobite Genera.*—Species concepts may not be stable (Labandeira and Hughes 1994; Hughes and Labandeira 1995), and the material sampled here is not always the material available to the author of the species. However, because variation within species and genera is small relative to variation within all trilobites, the particular specimens I measured for a currently recognized species should not greatly affect the sampling curves. Nevertheless, there are a number of reasons to explore the sampling of genera in addition to species. For example, the genus is often treated as the operational unit of morphology, with characters distinguishing genera rather stable.
and easily agreed upon compared with the finer, possibly more arbitrary distinctions among species (Allmon 1992). In addition, it is possible that incomplete sampling of known species may preferentially include forms described later in time. For example, stratigraphic and geographic information in older museum collections is generally less detailed than in newer collections. Therefore, more extensive effort would be needed to locate usable material in older collections. Because genera may contain numerous species, it is more likely for a given genus than for a given species that incomplete sampling of available collections will yield at least some material with adequate collecting information.

There are several problems with estimating the date at which the form corresponding to a genus was first known. The date of publication of the genus name could be used, but genera are commonly based on species that have been known for many years. Using the date of publication of the type species is problematic because, in a new genus with several species, it is common to select a newly described species as the type. Ideally, the date would be the oldest date of publication among the genus name and all the species names assigned to the genus. However, in a large group like trilobites (with on the order of $10^4$ described species), it can be a daunting task to compile the dates of publication of all species in a large sample of genera. As an operational solution to this problem, I estimated the date for each genus as the earliest of the three dates corresponding to the publication of the genus name, the publication of the type-species name, and the oldest published name among the species that...
happen to have been sampled for the morphological data on which this study is based. These three dates typically differ by less than five years, but they differ in some cases by over 100 years.

To test whether the oldest of these three dates is a reasonable proxy for the oldest of all names applicable to a genus, I determined the dates of publication of all species within a random sample of twenty-five Paleozoic crinoid genera that I had previously used in a study of morphological diversity (Foote 1995a,b). Crinoids were chosen for this test because the publication of a series of bibliographic compilations (Bassler and Moohey 1943; Webster 1969–1993) allows an essentially complete inventory. I should emphasize that this test case is biased against finding a good correspondence between estimated and actual dates. This is because I sampled only one species per genus per stratigraphic interval, and therefore forwent many chances to sample the oldest published name for a genus. Thus, if there is a good correspondence between estimated and actual dates even in this biased sample, the proposed proxy is probably even better in cases where the number of species sampled was not constrained (trilobites, blastoids, and post-Paleozoic crinoids).

For about half (13 of 25) of the genera tested, the estimated date of the oldest assigned name is exactly the same as the actual date (Fig. 6). The difference between estimated and actual dates for most (7 of 12) of the remaining genera is less than 15 years. Therefore, this operational approach represents a reasonable, albeit imperfect, way to estimate the date of the oldest name assigned to a genus. (The results
presented below are based on this method of assigning a genus date, but using the date of publication of the genus name or the type-species name yields similar sampling curves.

The sampling curve for trilobite genera shows the same large-scale trend of declining cumulative variance seen in the species-level curve, as well as intervals of time with little increase in the known range of form (Fig. 7). Likewise, there is no major, long-term trend in the morphological distance of trilobite genera from the centroid. The general agreement between species- and genus-level sampling curves is at least partly a consequence of the fact that 254 of 384 genera are represented in the morphological data by a single species, for, of these 254 genera, 164 have the same date as the corresponding single species that was sampled. However, the sampling curve for the 130 genera represented by multiple species is also similar to the species-level curve (Fig. 8). Thus, the agreement among these various sampling curves suggests that they are detecting robust patterns in the growth of our knowledge of morphological diversity, and that changing species concepts (e.g., Labandeira and Hughes 1994; Hughes and Labandeira 1995), which might be expected to influence sampling curves for species more than for genera, are not responsible for the patterns observed.

Changes in Perceived Evolutionary Patterns

The foregoing analyses focused on changes in observed morphological diversity with all species in a group combined into a single sample. However, sampling also affects cumulative morphological diversity for particular stratigraphic intervals, and heterogeneities in smaller-scale sampling curves may be masked

To reconstruct morphological disparity on the basis of data available at various times during the history of systematic paleontology, I culled morphological data to omit all species described after the date in question. To the extent that new species are based on the study of new material, rather than splitting off of previously described material attributed to older species names, this culling procedure should yield a reasonable estimate of what the disparity history would have looked like to a paleontologist of a previous generation using the same methods employed today.

For trilobites, I reconstructed disparity histories for the years 1896, 1924, 1948, and 1954, corresponding to roughly one-fourth, one-third, one-half, and two-thirds of the cumulative species sampled as of 1996 (Fig. 9). In addition, I calculated disparity for species described after 1948, a sample that is independent of the 1896, 1924, and 1948 cumulative samples. Although the patterns vary as sampling increases, certain features are relatively stable, such as the increase in disparity from the Cambrian to the Ordovician (Whittington 1954; Foote 1991a), and the sharp decline after the Devonian (Foote 1993a). However, the substantial rise in disparity within the Ordovician might not have been evident to a paleontologist a century ago, nor would the subequal disparity of the later Ordovician and Silurian. Breaking disparity down into the contributions made by various taxa reveals that much of the high level of disparity in the later Ordovician can be attributed to the suborders Asaphina and, especially, Cheirurina (Foote 1993b). Although knowledge of the Ordovician record of these groups extends back well into the 19th century, sampling has been especially intense more recently (for example, in the monographs of Ross [1951], Cooper

Figure 6. Comparison between actual and estimated date of oldest name applicable to 25 randomly chosen Paleozoic crinoid genera. Actual date is the oldest of the genus name, type species name, and all species names assigned to the genus. Estimated date is the oldest of the genus name, type species name, and all species in the genus that were sampled for morphological analysis. A, Scatterplot of estimated and actual dates. Open squares each denote two genera, closed squares a single genus. B, Frequency distribution of differences between actual and estimated dates. In nearly all cases, the estimated date is a reasonable proxy for the actual date.
Figure 7. Cumulative morphospace occupation relative to cumulative sampling of 384 trilobite genera. See Figure 1 for explanation. In this and all subsequent figures portraying cumulative sampling, taxa are arranged by year of publication, with a single within-year randomization randomly chosen (solid line). Note that year of publication for genera is not the year of publication of the genus name, but the estimated date of the oldest name applicable to the genus (see Fig. 6). A, Range of cumulative sample (sum of ranges of 12 principal components). B, Variance of cumulative sample (sum of variances of 12 principal components). C, Euclidean distance of genera from centroid. Note similarity to Figure 1.
Figure 8. Cumulative morphospace occupation relative to cumulative sampling of 130 trilobite genera represented by more than one species. See Figure 7 for explanation. Note similarity to Figures 1 and 7.

[1953], and Whittington and Evitt [1953], which largely reflect increased knowledge through acid preparation of silicified material. These results suggest that continued sampling is unlikely, for example, to make Cambrian disparity appear as high as that in the Ordovician, but how Middle–Late Ordovician and Silurian disparity will compare when studied by future paleontologists cannot be predicted. (N. C. Hughes [personal communication 1996] has suggested that genal spines may have an undue influence on my measures of Ordovician trilobites. To test this possibility, I modified the cranial outlines of all trilo-
bites so that the outline was completely truncated posterior to the occipital ring. This effectively eliminates genal spines, but other features as well. Recomputing Fourier descriptors of these modified cranidia, I find that spineless disparity is lower in the Middle–Late Ordovician than in the Silurian [variance ± 1 standard error: Middle–Late Ordovician 0.068 ± 0.0058, unmodified, 0.056 ± 0.0066, modified; Silurian 0.065 ± 0.0075, unmodified, 0.069 ± 0.0088, modified].

**Additional Examples**

I also computed sampling curves and reconstructed disparity histories for the other fossil taxa. However, in the case of blastozoans and Paleozoic crinoids, the sampling protocol used in the original data collection was such that no stratigraphic interval is represented by more than one species per genus. Therefore, it is difficult to reconstruct, by simple resampling of the available data, what a species-level disparity history would have looked like to a paleontologist of an earlier generation. For example, a species not sampled now because its currently accepted genus is already represented may once have been considered to belong to a different genus and therefore could have been sampled if the study had been done at an earlier date. Likewise, a species not sampled now because its genus is already represented by a species could have been sampled in the past if, at that time, it was the only species known from the stratigraphic interval in

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**Figure 9.** Change in disparity histories for Trilobita as sampling increases. Each panel shows temporal pattern of morphological variance (sum of variances of 12 principal components), with error bars giving ± 1 standard error, based on bootstrap resampling. Sample variance is undefined for a sample size of unity, so disparity is not plotted for such samples. Panels A–E include species described through the year at the top of the panel; number of species within stratigraphic intervals (see Foote 1993a) is shown above or below error bars. Panels A–E portray roughly one-fourth, one-third, one-half, two-thirds, and 100% of the cumulative sample. Panel F represents all species described after 1948, i.e., roughly the second half of the cumulative sample. Note that some features, such as the increase in disparity after the Cambrian and the decrease after the Devonian, are stable, whereas others, such as the peak of disparity in the middle Ordovician, are not.
question. Many other complications arising from factors such as stratigraphic range extensions and changing species- and genus-level synonymies can easily be imagined.

**Blastozoaa.—**With the exceptions of *Pentremites* and *Gogia*, each genus was represented by only one species. Thus, species- and genus-level sampling curves, while not identical because of the different procedures used to assign dates to species and genera, are very similar, and only the species curve is shown here (Fig. 10). (In 115 of 145 genera in which only one species was sampled, this species is the type of the genus.) For most of the history of blastozoan studies, cumulative morphological diversity is within the expectation of random sampling, and there appears to be no strong tendency for preferential sampling of morphological extremes early or late.

One conspicuous feature of the blastozoan data (as well as those of crinoids, below) is the lack of species at small or even moderate distances from the centroid. This is simply a consequence of using a large number of morphological dimensions. For example, in a circle of radius $r$, one-fourth of the area lies within a distance $r/2$ of the center, whereas, in a sphere of radius $r$, one-eighth of the volume lies within a distance $r/2$ of the center, and so on. Therefore, if points are substantially dispersed in many dimensions, it is increasingly unlikely to find points close to the centroid. This effect is not seen in the case of trilobites or blastoids, however. This is because most of the total variance is summarized by a few principal components, i.e., the points are substantially dispersed in just a few dimensions. With little variation in the higher principal components, species are constrained to be near the centroid along those higher axes (i.e., the shape of the distribution is more elongate), and the effective dimensionality of the space is much smaller than the number of axes used (Van Valen 1974). In the case of blastozoans or crinoids, where it takes many more principal coordinates to represent interspecies distances accurately (e.g., Foote 1995a,b), the effective dimensionality is much higher.

**Blastoida.—**Sampling curves for blastoids are largely within the expectations of random sampling (Figs. 11, 12). Unlike the trilobite and blastozoan cases, this is true even at small sample sizes. Considering the magnitude of sampling error at such small sample sizes, however, it would be premature to conclude that early sampling of trilobites and blastozoans was substantially less random than early sampling of blastoids. There is no long-term trend in distance from the centroid. Note that the largest single increase in morphological range corresponds to the sampling of *Timoroblastus* Wanner (1924a) and its type species, *T. coronatus* Wanner (1924a), yet this taxon is barely farther from the overall centroid than many other species (Figs. 11C, 12C), and its addition to the cumulative data does not result in a large jump in variance. This is because *Timoroblastus*, while not anomalously far from the centroid, is far from the centroid in an unusual direction, i.e., it is separated by a pronounced gap from the previous cumulative sample (Foote 1991b: Fig. 2).

Reconstructed disparity histories (Fig. 13) suggest that the increase in disparity from the Silurian to the Middle Devonian and the decrease from the Middle Devonian to the Carboniferous are relatively robust. Maximal observed disparity in blastoids occurs in the Permian (Foote 1991b), but this result is very sensitive to sampling, since most of the Permian material comes from a small geographic area, the island of Timor and neighboring Australia (Waters 1990), and was described only in the 20th century.

**Paleozoic Crinoidea.—**Although the known range of form tends to fall on the low side of what would be expected from random sampling, cumulative variance among Paleozoic crinoids is remarkably stable over the past century and a half, despite an increase in sample size of more than an order of magnitude (Figs. 14, 15). In accord with this, there is essentially no trend in distance from the centroid.

**Post-Paleozoic Crinoidea.—**From the middle to the late 1800s, morphological diversity is somewhat lower than would be expected for a random subsample drawn from the forms currently known (Figs. 16, 17). Starting in the late 19th century, there is a long-term increase in cumulative variance, reflected in a greater proportion of sampled taxa further from the
FIGURE 10. Cumulative morphospace occupation (based on 20 principal coordinates) relative to cumulative sampling of 147 blastozoan species. There is no trend in distance from centroid, and cumulative range and variance largely lie within the limits of random sampling.
overall centroid (starting at about \( n = 175 \) for species and \( n = 75 \) for genera). Many of these more extreme taxa are in the order Cyrtocrinida, which is well known for many unusual forms, such as reduced, bilaterally symmetrical cups (Arendt 1974). Although what we perceive as "bizarre"—perhaps a quality more in our minds than in an organism's
Figure 12. Cumulative morphospace occupation (based on 17 principal components) relative to cumulative sampling of 47 blastoid genera. Open square in C is *Timoroblastus*. Note similarity to Figure 11.
body—need not be morphologically extreme in general, in this case the correspondence may hold.

Several features of the post-Paleozoic history of disparity in crinoids persist as more species are sampled (Fig. 18). For example, disparity increases from the Jurassic to the Early Cretaceous, and disparity declines within the Cretaceous. One interesting feature that would not have been seen even half a century ago, however, is the peak of disparity in the Late Triassic (Foote 1996b). This raises the obvious question of whether the apparently rapid rise in disparity during the Triassic is a robust enough pattern to be reliably interpreted. To a large extent, the estimate of disparity in an interval is a function of the number of higher taxa (in this case, orders and suborders) that are sampled (Foote 1993b, 1995a,b, 1996a,b). For example, now that the mutually disparate orders Encrinida, Millericrinida, Isocrinida, Roveacrinida, and Camatulida are known to range into the Late Triassic (Hagdorn 1995), and all but Millericrinida are present in the morphological data, future sampling seems unlikely to greatly reduce estimated disparity in the Late Triassic. In addition, it is noteworthy that as soon as the Late Triassic sample is large enough to allow us to calculate disparity (which is undefined for a sample of one species), the estimated value is high, even if highly uncertain. In contrast to Permian blastoids, high disparity in Late Triassic crinoids does not depend so strongly on a single deposit (even though the Muschelkalk is important in our view of Middle Triassic disparity). The blastoid and post-Paleozoic crinoid cases illustrate how strong an influence a small number of species can have on our view of macroevolutionary patterns.

**Discussion and Conclusions**

Sampling of form from the fossil record certainly has nonrandom aspects, but there is no clear evidence of a general tendency to sample more extreme species preferentially earlier or later during the history of systematic paleontology. This is bad news if we hope to see nearly the full range of forms in a group with just a limited sample (McGhee 1995), but is
FIGURE 14. Cumulative morphospace occupation (based on 30 principal coordinates) relative to cumulative sampling of 588 Paleozoic crinoid species. There is no trend in distance from centroid. Although cumulative range sometimes falls outside the limits of random sampling, cumulative variance is relatively stable.
Figure 15. Cumulative morphospace occupation (based on 30 principal coordinates) relative to cumulative sampling of 469 Paleozoic crinoid genera. Note similarity to Figure 14.
Figure 16. Cumulative morphospace occupation (based on 30 principal coordinates) relative to cumulative sampling of 385 post-Paleozoic crinoid species. There is no trend in distance from centroid, but cumulative range and variance at times fall below the expectations of random sampling.
good news if we are interested in a relatively representative sample in order to explore, for example, the relative frequency of various morphotypes (Raup 1967; Saunders and Swan 1984; McGhee 1995; Saunders and Work 1996). It should be emphasized that this study has used a multivariate approach to quantifying form. Univariate studies may show that some
particular aspects of form are more subject to sampling bias. For example, Blackburn and Gaston (1994) demonstrated a tendency for species with smaller body size to be discovered and described preferentially later in a number of groups of living animals.

These results still leave open the possibility that extreme or modal forms have been preferentially sampled consistently over the past two centuries, a possibility that is difficult to test since we have only the cumulative sample, not what has been left in the field. However, a more interesting, and probably more realistic, problem is not sampling bias, but rather bias in the publication of names. For example, Kummel and Steele (1962) synonymized a number of Lower Triassic ammonoid species based in part on morphometric analysis. They found that type and figured specimens of species they considered invalid tended to fall near the periphery of the distribution of specimens within the species they considered valid. Apparently, extremes of a continuum had been singled out and given new names. If this were a general practice, then choosing forms from a list of published names would yield a biased morphological sample. (This pattern certainly is not universal. In a Cambrian trilobite genus, Labandeira and Hughes [1994] document that early types were well within a continuous distribution of form. Evidently, early workers perceived gaps in the distribution that were later filled in by improved sampling. In a Miocene foraminiferan genus, Tabachnick and Bookstein [1990] also found continuous variation with types dispersed throughout the range of variation.)

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**Figure 18.** Change in disparity histories for post-Paleozoic crinoid species as sampling increases. See Foote (1996b) for explanation of stratigraphic intervals. Panels A–E portray roughly one-third, one-half, two-thirds, three-fourths, and 100% of the cumulative sample. Panel F represents species described after 1894, i.e., the second half of the cumulative sample. Note that some species range through more than one interval; thus the within-interval sample sizes sum to more than the total number of species. Increase in disparity from the Jurassic to the Cretaceous and subsequent decline through the Cretaceous are stable features. Peak of disparity in the Late Triassic is a more recently documented feature.
Although the bias Kummel and Steele documented in the attachment of names to forms may be important at the species level, it seems unlikely to affect studies at a larger scale. First, the variation within a species or genus is generally small compared with the variation within an entire class. Thus, in estimating disparity within a class, it matters little whether the sampled forms are near the center or the periphery of the within-species or within-genus distribution. (A similar argument would hold if the largest specimens within a species were preferentially sampled, since the spectrum of size of the higher taxon could still be reasonably represented by the distribution of species maxima; but see Blackburn and Gaston [1994].) Second, there is no obvious reason to think that an analogous bias operates at higher levels, i.e., that forms at the periphery of the morphological distribution of an entire class are singled out and given taxonomic names. Rather, the data presented here show that the number of names decreases away from the overall centroid of morphology (Figs. 1C, 7C, 8C, 10C, 11C, 12C, 14C, 15C, 16C, 17C). Nevertheless, it is conceivable that the number of names far from the centroid, while not greater than the number of names near the centroid, is greater than it should be by an unbiased scheme of taxonomic naming. This possibility can be tested in the case of trilobites, where I deliberately included unidentified specimens and specimens identified but not to the species level. All 1125 specimens taken together have a mean Euclidean distance from the centroid of 0.201 (standard error = 0.00292, based on bootstrap resampling), the 980 named specimens have a mean Euclidean distance from the same centroid of 0.200 (standard error = 0.00334), and the 145 unnamed specimens have a mean Euclidean distance from this same centroid of 0.212 (standard error = 0.00916). The differences among these mean distances are not significant; thus, at the scale of all trilobites, there is no prevailing tendency for collected material to be assigned a taxonomic name if it is morphologically more (or less) extreme.

Unbiased sampling at the gross scale clearly does not imply that any documented pattern is unbiased, because sampling is partitioned stratigraphically and geographically. Williams (1957) demonstrated this clearly when he showed that the geological period of maximal taxonomic turnover in brachiopods has shifted over the history of paleontology, depending on the stratigraphic interests of the leading workers of each generation. Similarly, certain features of morphological diversity, such as the level of trilobite disparity in the later Ordovician, have shifted to some extent as more species have been sampled. Nevertheless, as paleontologists have sampled more, many large-scale patterns of disparity have become rather stable, just as Sepkoski (1993) found for diversity, origination, and extinction of animals throughout the Phanerozoic. The insensitivity of evolutionary patterns to increased sampling, different sampling methods (Sepkoski et al. 1981), or different principles of taxonomic definition (Wagner 1995) obviously does not ensure the empirical accuracy of these patterns. Increased random sampling of a biased record will tend to entrench a biased result. However, the degree of stability of paleontological patterns can at least shed light on the empirical maturity of our science, on the relative likelihood that further study will substantially change our picture of the history of life.

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Literature Cited

Austin, T., and T. Austin Jr. 1843. Descriptions of several new


Miller, J. S. 1821. A natural history of the Crinoidea, or lily-shaped animals. 897:1; with observation on the genera Asteria, Euryale, Comatula, and Marsupites. C. Frost, Bristol.

Miller, S. A., and W. F. E. Gurley. 1890. Description of some new
genera and species of Echinodermata, from the Coal Mea-
sures and Subcarboniferous rocks of Indiana, Missouri, and
Iowa. Indiana Department of Geology and Natural History

Moore, R. C., and F. B. Plummer. 1940. Crinoids from the Upper
Carboniferous and Permian strata in Texas. University of Tex-
as Publication 3945:1–459.

Morris, S. F. 1988. A review of British trilobites, including a syn-
optic revision of Salter’s monograph. Palaeontographical So-
ciety Monograph 140(574):1–316.

Morris, S. F., and R. A. Fortey. 1985. Catalogue of the type and
figured specimens of Trilobita in the British Museum (Natural

Nielsen, K. B. 1913. Crinoideer i Danmarks Kridtagefringer.
Danmarks Geologiske Undersøgelse, Ser. 2, 26:1–120.

new species of Crinoidea from the sub-carboniferous lime-
stone of Iowa, collected during the U. S. Geological Survey
of Wisconsin, Iowa, and Minnesota in the years 1848–1849.
Academy of Natural Sciences of Philadelphia Journal, new se-
ries, 2:57–70.

——. 1850b. Descriptions of seven new species of Crinoidea
from the sub-carboniferous limestone of Iowa and Illinois.
Academy of Natural Sciences of Philadelphia Journal, new se-
ries, 2:89–94.

ntographical Society Monograph 127(536):1–64.

——. 1980. The natural history of fossils. Weidenfeld and

——. 1984. British Ordovician cystoids, Part 2. Palaeonto-

Pearce, J. C. 1843. On an entirely new form of Encrinute from
the Dudley Limestone. Proceedings of the Geological Society
of London 4:160.

Pearson, E. S. 1926. Further note on the distribution of range
in samples taken from a normal population. Biometrika 18:173–
194.

Peck, R. E. 1943. Lower Cretaceous crinoids from Texas. Journal
of Paleontology 17:451–475.

Rasmussen, H. W. 1961. A monograph on the Cretaceous Cri-

Raup, D. M. 1967. Geometric analysis of shell coiling: coiling in

——. 1991. The future of analytical paleobiology. In N. L. Gil-
insky and P. W. Signor, eds. Analytical paleobiology. Pale-
ontological Society Short Courses in Paleontology No. 4: 207–
216. University of Tennessee, Knoxville, Tenn.

Raymond, P. E. 1925. Some trilobites of the Lower Middle Or-

Resser, C. E. 1938. Cambrian system (restricted) of the southern
Appalachians. Geological Society of America Special Paper
15:1–140.

Ross, R. J., Jr. 1951. Stratigraphy of the Garden City Formation
in northeastern Utah, and its trilobite faunas. Bulletin of the
Peabody Museum of Natural History, Yale University 6:1–161.

——. 1979. Additional trilobites from the Ordovician of Ken-
13.

Saunders, W. B., and A. R. H. Swan. 1984. Morphology and mor-
phologic diversity in mid-Carboniferous (Namurian) ammo-

Saunders, W. B., and D. M. Work. 1996. Shell morphology and
suture complexity in Upper Carboniferous ammonoids. Pa-

Say, T. 1825. On two genera and several species of Crinoidea.
Academy of Natural Sciences of Philadelphia Journal, series 1,

Schultze, L. 1867. Monographie der Echinodermen des Eifler
Kalkes. Denkschriften der Kaiserlichen Akademie der Wis-
senschaften (Mathematisch-Naturwissenschaftliche Klasse)

Sepkoski, J. J., Jr. 1993. Ten years in the library: new data con-

1981. Phanerozoic marine diversity and the fossil record. Na-

Shumard, B. F. 1855. Palaeontology. Description of new species
of organic remains. Missouri Geological Survey Annual Re-
port 1:2(2):185–238.

Simms, M. J. 1989. British Lower Jurassic crinoids. Palaeont-

Sowerby, G. B. 1825. Note on the foregoing paper, together with
a description of a new species of Pentremites. Zoological Jour-
nal 2:316–318.

Springer, F. 1920. The Crinoidea Flexibilis. Smithsonian Insti-
tution Publication 2503:1–486.

——. 1926a. American Silurian crinoids. Smithsonian Institu-
tion Publication 2871:1–239.

——. 1926b. Unusual forms of fossil crinoids. Proceedings,

Sprinkle, J. 1973. Morphology and evolution of blastozoan echi-
noerms. Special Publication of the Museum of Comparative
Zoology, Harvard University, Cambridge.

——. 1982. Echinoderm faunas from the Bromide Formation
(Middle Ordovician) of Oklahoma. University of Kansas Pa-
leontological Contributions, Monograph 1:1–369.

Strimple, H. L. 1961. Late Desmoinesian crinoid fauna from

Tabachnick, R. E., and F. L. Bookstein. 1990. The structure of
individual variation in Miocene Globorotalia. Evolution 44:
416–434.

Trautschold, H. 1867. Einige Crinoideen und andere Thiere
ster des jüngeren Bergkalks im Gouvernement Moskau. Bulletin
de la Société Impériale des Naturalistes de Moscou 40(2):3:
1–49.

Troost, G. 1835. On the Pentremites reinwardtii, a new fossil;
with remarks on the genus Pentremites (Say), and its geog-
nostic position in the state of Tennessee, Alabama and Ken-
231.


Vogdes, A. W. 1890. A bibliography of Paleozoic Crustacea

——. 1917. Paleozoic Crustacea. Transactions of the San Di-
ego Society of Natural History 3:1–141.

——. 1925a. Paleozoic Crustacea. Part I, A bibliography of
Paleozoic Crustacea. Transactions of the San Diego Society
of Natural History 4:88–115.

——. 1925b. Paleozoic Crustacea. Part II, A list of the genera
and subgenera of the Trilobita. Transactions of the San Diego
Society of Natural History 4:5–88.

Wachsmuth, C., and F. Springer. 1897. The North American Cri-
noidea Camerata. Harvard College Museum of Comparative

Wagner, P. J. 1995. Diversity patterns among early gastropods:
contrasting taxonomic and phylogenetic descriptions. Pale-


Walcott, C. D. 1916a. Cambrian geology and paleontology, Ill,
No. 3, Cambrian trilobites. Smithsonian Miscellaneous Col-
lections 64:157–258.

——. 1916b. Cambrian geology and paleontology, Ill, No. 5,