CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

THE UNIVERSITY OF MICHIGAN

VOL. 28, NO. 6, PP. 101-140 September 30, 1991

MORPHOLOGICAL AND TAXONOMIC DIVERSITY IN A CLADE'S HISTORY: THE BLASTOID RECORD AND STOCHASTIC SIMULATIONS

BY

MIKE FOOTE

MUSEUM OF PALEONTOLOGY
THE UNIVERSITY OF MICHIGAN
ANN ARBOR

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

Philip D. Gingerich, Director

This series of contributions from the Museum of Paleontology is a medium for publication of papers based chiefly on collections in the Museum. When the number of pages issued is sufficient to make a volume, a title page and a table of contents will be sent to libraries on the mailing list, and to individuals on request. A list of the separate issues may also be obtained by request. Correspondence should be directed to the Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan 48109-1079.

VOLS. 2-27. Parts of volumes may be obtained if available. Price lists are available upon inquiry.

MORPHOLOGICAL AND TAXONOMIC DIVERSITY IN A CLADE'S HISTORY: THE BLASTOID RECORD AND STOCHASTIC SIMULATIONS

By

MIKE FOOTE

Abstract.— Ordovician-Permian Blastoidea are used to compare morphological and taxonomic diversity. Morphological diversity, based on the locations (in three dimensions) of homologous landmarks on the theca, is compared to published estimates of generic richness. Rarefaction of morphological distributions with respect to sample size (number of species) is presented as one way to analyze the structure of diversity, i.e., the relationship between morphological and taxonomic diversity. This allows the assessment of morphological diversity per unit taxonomic diversity. Any subset of a clade is less diverse than the clade as a whole. However, Permian blastoids occupy morphospace more extensively than the entire class in the sense that small, random subsamples from the whole class are not as diverse morphologically as are similar samples from the Permian.

Whereas maximal generic richness occurs in the Lower Carboniferous, maximal morphological diversity is found in the Permian. Generic richness rises from the Ordovician to the Lower Carboniferous, then drops off, but morphological diversity may increase essentially until the group's demise. Artificially degrading the record so that each stratigraphic interval is represented by a narrow temporal and geographic window does not substantially alter observed diversity patterns. Silurian and Devonian morphological diversification may outpace taxonomic diversification, but this observation depends on how morphological diversity is measured. Use of the center of gravity and the median to describe clade shape suggests that morphological diversity in the Blastoidea is concentrated later in time than taxonomic diversity. Because unequal time intervals bias measures of central tendency, such measures should be compared to the central tendency inherent in the time scale, rather than to the temporal midpoint of a clade's history.

Stochastic simulations of taxonomic and morphological evolution yield clades whose morphological diversity is concentrated later in time than their taxonomic diversity. The prevalence of this difference between morphological and taxonomic diversity increases with the duration of the simulated clade and the number of morphological characters. By their very nature, randomly evolving clades exhibit diffusion through morphospace and extinction acting randomly with respect to morphology. This combination allows clades to maintain and even increase their morphospace occupation in the face of declining taxonomic diversity. Although it cannot be concluded that the blastoids represent a randomly evolving clade, smaller-scale directionalities may "cancel out" when the clade is viewed at a sufficiently large scale, so that large-scale evolutionary patterns are not readily distinguishable from randomness.

INTRODUCTION

One of the principal goals of paleobiology is interpretation of the bewildering variety of organisms in the fossil record. This variety has been assessed by reference to at least two concepts, the number of entities (diversity) and the morphological differences among them (distinctness or disparity) (e.g., Yochelson, 1978, 1979; Jaanusson, 1981; Runnegar, 1987; Gould, 1989). Despite the importance of both notions of variety in the history of life, large-scale evolutionary patterns are often documented primarily in terms of taxonomic diversity (e.g., Valentine, 1969; Bambach, 1977; Sepkoski et al., 1981; Sepkoski, 1984). At least two reasons can be given for this: (1) whereas taxonomic richness is readily quantified by simple counting of what are believed to be biologically comparable entities, morphological variety can be more difficult to measure consistently. There are relatively few studies in which many, distantly related lineages within a higher taxon have been described by a single morphometric system (e.g., Raup, 1966, 1967; Cain, 1977; Cherry et al., 1985; Saunders and Swan, 1984; Swan and Saunders, 1987; Foote, 1991). Even when it is possible to establish a morphospace for all forms, this generally results in a loss of morphological resolution, as all forms are reduced to the "least common denominator." Furthermore, the larger the scale of analysis, the greater the loss of resolution. Raup's (1966) molluscan coiling parameters, for example, describe the general form of the shell fairly well, but do not consider features such as ornamentation and apertural angle. (2) In contrast to taxonomic diversity studies, in which there *may* be a rough correspondence among, say, genera in different classes, morphological descriptions tend to be more idiosyncratic, making the comparison of morphological variety among different higher taxa difficult if not impossible.

In discussing diversity I will use the following terminology: *richness* refers to the number of taxa; *morphological diversity* or *morphological variety* refers to the variance in form or the amount of morphospace occupied (see discussion below), irrespective of taxonomic richness; and *diversity* (unqualified) refers to any of the foregoing concepts. I avoid the term *disparity* because it has been used to refer to variation among phylum- or class-level body plans (Runnegar, 1987), whereas this study focuses on morphological variation within a body plan.

One may be quick to reason that taxonomic richness and morphological variety *must* correlate positively, since taxa are based on morphology. Let me emphasize that I do not mean to imply that the erection of fossil taxa is independent of morphology. Our ability to recognize two species implies that these species must be morphologically different from each other; but it implies little if anything about the *magnitude* of that difference. At a larger scale, we may have scores of species built upon the same morphological theme (less variety), or just a handful of species, each of which is morphologically very different from the others (greater variety).

It is often assumed that taxonomic richness is in some way a proxy for the magnitude of morphological variety. This equation of taxonomic diversity and morphological variety is perhaps most striking in discussions of "adaptive radiation." In a summary, Stanley (1979) follows Simpson's (1953) definition by referring to adaptive radiation as a proliferation not just of many taxa (richness) but of many kinds of organisms (morphological variety). However, his ensuing discussion refers primarily to richness for documentation of adaptive radiation. It is probably true that the proliferation of taxa, particularly higher taxa, generally represents a proliferation of morphological variety (Valentine, 1969). However, such a correlation may be only approximate, as the morphological nature of higher taxa is not uniform. For example, the proliferation of trilobite families is most striking in the Cambrian (Stubblefield, 1960; Harrington, 1959). But the proliferation of morphological variety is more pronounced in the Ordovician, as the morphological differences among higher taxa (superfamilies) are greater in the Ordovician than the Cambrian (Whittington, 1954, 1966; Fortey and Owens, 1990; Foote, 1991 and references therein). Although a lack of concordance between morphological and

taxonomic diversity may be an artifact of taxonomic practice, such discrepancies need not imply that either morphological or taxonomic diversity measurement is somehow "wrong." As with richness and evenness in ecology, the two concepts concern different aspects of diversity.

In this study I present a comparison between taxonomic and morphological diversity for a single clade, the echinoderm class Blastoidea. I will show that the large-scale patterns in these two aspects of diversity are not identical. For example, maximal generic richness and maximal morphological variety do not coincide temporally. It appears as though generic richness waxes and wanes (Waters, 1988), whereas morphological diversity increases more steadily even in the face of declining taxonomic richness. Therefore, there may be a tendency for morphological diversity to be preferentially concentrated later in the clade's history than generic richness. Computer simulation indicates that this asymmetry between taxonomic richness and morphological diversity may be the expected outcome of a time-homogeneous, stochastic model of clade evolution. This asymmetry can be attributed to diffusion through morphospace and to extinction that is effectively random with respect to morphology. These factors allow morphological variety to be maintained, and even to increase, in the face of reductions in taxonomic richness.

BLASTOIDEA AND MORPHOMETRICS

General Considerations

A higher taxon treated as an evolving entity should possess several characteristics. (1) For many kinds of studies, it should be strictly monophyletic (i.e., holophyletic). The theoretical basis of some analyses, such as that presented here, involves the fate of all and only descendants of a common ancestor. This does not argue against the utility of paraphyletic or even polyphyletic taxa for the study of patterns such as the timing of extinction or the occupation of adaptive zones. (2) For some analyses, the clade should be extinct. There are two principal reasons for this requirement, the relative importance of which varies from case to case: (a) for some studies, such as the present one, the *entire* evolutionary history of a clade may be of interest, something that simply cannot be known for an extant clade, and (b) the Pull of the Recent and related factors (Raup, 1979) complicate temporal comparisons of diversity if extant taxa are involved. (3) The systematic treatment of the group should be stable and consistent, so that changes in taxonomic richness can be reliably assessed. (4) Morphology should be readily measurable in a way that is informative and consistent from species to species within the clade. Finally, (5) all else being equal, it may be preferable to study a clade with a relatively long duration and many subtaxa. There is nothing uninteresting about clades that are short-lived or not very diverse, but sampling error is generally more significant for such clades. The echinoderm class Blastoidea satisfies these five conditions well.

The evolutionary history of the blastoids has been summarized most recently by Waters (1988). The class Blastoidea, which is generally considered to be monophyletic (e.g., Sprinkle, 1973, text-fig. 20), attained a total diversity of over 90 genera, and endured some 200 million years, from the upper Ordovician to the late Permian. Because the description and revision of genera and species has been done by a relatively small group of paleontologists, often working in collaboration, taxonomic concepts below the family level are reasonably consistent and allow temporal changes in generic richness to be reliably documented.

The theca is the principal source of morphological information for blastoids. Despite great variation in thecal morphology, blastoids differ from most other echinoderm classes in having an essentially stable number and arrangement of major thecal plates. Thus, the morphology of nearly all blastoids can be readily assessed with a single set of descriptors, as will be discussed below.

TABLE 1 – Geologic time scale, generic richness, and number of species measured in Blastoidea

Interval	Base[1]	Duration	Midpoint	Genera[2]	N[3]
Caradocian-Ashgillian	464	25	451.5	1	1
Silurian	439	30.5	423.8	3	4
Devonian	408.5	46	385.5	17	25
Lower Carboniferous	362.5	39.7	342.7	53	42
Upper Carboniferous	322.8	32.8	306.4	6	3[4]
Permian	290	45	267.5	18	13

[1] Ages in million years before present; durations in million years. Based on Harland et al. (1990).
[2] Number of genera in interval, based on Waters (1988).
[3] Number of species measured.
[4] Based on range-through method described in text.

Generic Richness

Compiled estimates of species richness are not yet available, but await further revision of spiraculate blastoids. However, because most genera have either one or two species (Waters, 1988), the history of species richness is likely to be similar to that of generic richness. To obtain estimates for the number of genera through time, *independent of the number of genera sampled for morphological measurements*, I used the compilation of stratigraphic ranges published by Waters (1988), based on a previous compilation by Horowitz et al. (1985). Although some details of this compilation may be open to question, it seems close to a consensus. I have included both named genera and entries in Waters' list such as "Fissiculate genus 1" (many of the unnamed genera are in the process of being described or have been described since publication of Waters' compilation; Horowitz, personal communication). For the patterns to be discussed below, it makes relatively little difference if such unnamed genera are included or excluded.

Although generic ranges are given by Waters (1988) to the series level, the small sample sizes (for both generic richness and morphological data) for most series make the analysis of data at the system level more prudent for the present study. The time scale employed in this study (Table 1) is based on Harland et al. (1990). Also given in this table are the generic diversity data from Waters (1988) and the number of species measured. Placement of some Namurian genera in the stratigraphic framework used here is not without uncertainty, partly because of difficulties in global correlation (Macurda and Mapes, 1983; Macurda, personal communication). Because the genera *Artuschisma*, *Dolichoblastus*, *Kazachstanoblastus*, and *Mastoblastus* are considered by their authors to be early Namurian in age (Arendt et al., 1968), I have placed them in the Lower Carboniferous. As just a few genera are involved, this decision has little effect on the analysis. Similarly, use of the time scale employed by Horowitz et al. (1985) does not alter any of the patterns appreciably.

Morphometric Description and Sampling

Morphometric analysis of blastoids has concerned primarily the vault:pelvis ratio (e.g., Waters et al., 1985) and ontogenetic regressions of plate measurements (e.g., Macurda, 1966, 1983). The vault:pelvis ratio is useful for comparisons within species or among similar species, but does not provide sufficient detail for the study of all blastoids simultaneously. Macurda's ontogenetic studies embody more information, but there are questions of strict homology of the measures among genera. Furthermore, Macurda's approach is potentially un-

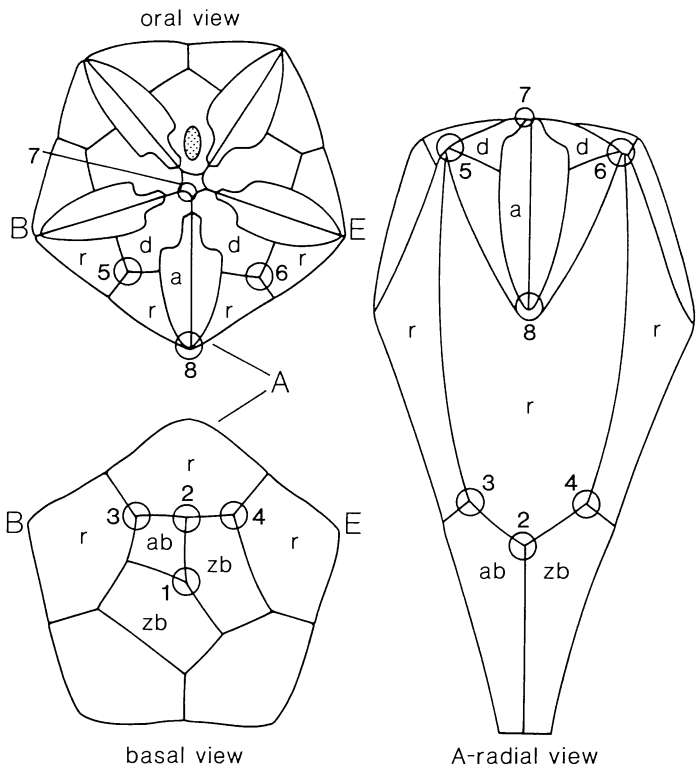

FIG. 1— Generalized blastoid theca showing morphological landmarks. 1, conjunction of three basal plates; 2, conjunction of A-radial, E-zygous basal, and azygous basal; 3, conjunction of A-radial, B-radial, and azygous basal; 4, conjunction of E-radial, A-radial, and E-zygous basal; 5, conjunction of A-radial, B-radial, and AB deltoid; 6, conjunction of E-radial, A-radial, and EA deltoid; 7, most adoral point on AB deltoid; 8, most aboral point on A-ambulacrum. Abbreviations: a, ambulacrum; ab, azygous basal; d, deltoid; r, radial; z, zygous basal; A, B, and E refer to rays.

wieldy in the sheer number of measures and regressions involved. Therefore, this approach is not best suited for the present problem of considering all blastoids in a single morphospace.

Of the several kinds of blastoid thecal plates, three types, deltoids, radials, and basals, are generally well preserved and largely determine the overall shape of the theca. The importance of measuring features that are homologous among all forms is widely recognized, but at the class level this can often be a difficult requirement to satisfy. Because of their conservative plate arrangement, blastoids have the uncommon advantage that the principal aspects of variation in the theca can be captured with a reliable set of homologous landmarks, i.e., discrete points on the theca that correspond from species to species.

Morphometric description

Morphometric description of blastoids is based on the locations of eight landmarks, six of which represent the conjunction of three plates, and two of which represent extremal points (Fig. 1). These landmarks were chosen to give coverage to the whole theca, and because they can be located on virtually all blastoids. An example of a form that could not be accommodated would be *Astrocrinus*, having only two basals (Macurda, 1977b). In order to reduce redundancy associated with the near-pentameral symmetry of most blastoids, only a single ray, the A-ray, was measured (another advantage to measuring a single ray is that incomplete thecae can be measured, thus increasing sample size). This particular ray was chosen because

it is one of the rays (the other being the B-ray) in which both types of basals, zygous and azygous, are found. In nearly all blastoids the azygous basal lies in the AB interray. In the unusual case of basal inversion (where the azygous basal lies in either the CD or the DE interray), the ray between the azygous basal and the zygous basal clockwise to it (as seen from the basal view) was measured, rather than the A-ray. In the current study only a single specimen, representing the species *Diploblastus glaber* (which characteristically has the azygous basal in the DE interray; Macurda, 1978), has inverted basals. Because only a single specimen is involved, the operational decision to treat the D-ray as pseudo-homologous with the A-ray has little effect on the analysis of evolutionary patterns. Although the A-radial plate appears superficially to be bilaterally symmetrical, some asymmetry results from the abutment of both types of basals. This warrants measurement of both sides of the ray. On the other hand, preliminary analyses suggested that the location of the most adoral point on the EA deltoid is sufficiently similar to the corresponding point on the AB deltoid, that only one of these deltoids need be measured.

Having chosen the locations of landmarks, it is necessary to establish a morphospace in which all blastoids can be accommodated. I have used the raw coordinates of the landmarks, after scaling the thecae to a common size and placing them in a common orientation. Each theca is scaled individually, based on the distance between a pair of thecal landmarks. (The orientation and scaling of thecae are described more fully below.) The morphometric variables are the Cartesian coordinates themselves, not distances among landmarks. This approach is similar to the use of shape coordinates (Tabachnick and Bookstein, 1990; Bookstein, 1991), but is somewhat more simplified than the formal extension of shape coordinates to three dimensions (Tabachnick, personal communication).

Each theca is translated so that landmark 1 is the origin and landmark 7 is on the z-axis. The axis from landmark 1 to landmark 7 approximates the long axis of the theca. To scale to a common size, this axis is assigned unit length. Thus, landmark 1 is constrained to have coordinates (0,0,0) and landmark 7 to have coordinates (0,0,1). (Other means of scaling, such as centroid-averaging, were investigated and found to yield similar results.) Because this standardization still allows the theca to rotate about this axis, a unique description of the theca is not obtained unless the orientation is further specified. To do so, I constrained landmark 4 to lie in the X-Z plane, in such a way that $x > 0$; thus its coordinates in the new system are $(x,0,z)$. Because the coordinates of landmarks 1 and 7 are not free to vary, and only two of the coordinates of landmark 4 are free to vary, there are a total of 17 coordinates (as opposed to the original 24 coordinates) describing the morphology of each theca. These coordinates represent 17 morphological variables defining the blastoid morphospace. Three-dimensional Cartesian coordinates were digitized using a Reflex Microscope (Reflex Measurement Ltd.). The orientation of the theca during measurement is arbitrary; reorientation and scaling of thecae are performed by computer, using standard geometric transformations.

To assess the repeatability of measurements, a single specimen of *Heteroschisma canadense* was measured twenty times (the species and specimen were chosen randomly from those available in the collections of the University of Michigan Museum of Paleontology). Replication variance (not presented here) is small compared to variation within species, and can be safely disregarded.

Sampling

Specimens were selected, based on availability, from collections of the University of Michigan Museum of Paleontology (UM) and the United States National Museum of Natural History (USNM). No attempt was made to limit sampling to particular genera and species; rather, any specimen was considered if it was sufficiently well preserved to be measured. Because the number of specimens per species varies widely (in the present study from 1 to 10), allowing each specimen to represent a single observation may cause just a few species to dominate perceived patterns (see Foote, 1991). Therefore, each species was represented in this study by its average morphology. A total of 113 specimens, 85 species, and 45 genera (about half of all described genera accepted as valid by Waters, 1988) were measured. This coverage

is broad enough that it should allow a reasonably accurate documentation of large-scale evolutionary patterns in the blastoids. It should be noted that the patterns documented using replicates within species are broadly similar to those documented using species averages. This also suggests that minor uncertainties due, for example, to misidentification or synonymy are unlikely to have substantial effects on the analysis. A list of specimens measured is given in Appendix A. A table of average measurements for each species is given in Appendix B.

It is well known that Lower Carboniferous and Permian blastoids are diverse and locally abundant, whereas blastoids in the Upper Carboniferous are rather rare (e.g., Waters, 1988). The suggestion that the dearth of Upper Carboniferous blastoids is preservational has been based on the observations (1) that some genera are well known in the Lower Carboniferous and Permian (and therefore must range through the Upper Carboniferous), but unknown or poorly known in the Upper Carboniferous (Breimer and Macurda, 1972; Macurda and Mapes, 1983), and (2) that more intensive sampling of Upper Carboniferous, non-carbonate facies has yielded an increasing number of blastoids (Macurda and Mapes, 1983). On the other hand, it has been argued that, because (presumably) ecologically and taphonomically similar crinoids are common in the Upper Carboniferous, the rarity of blastoids is evolutionary (Strimple and Mapes, 1977). In the absence of compelling evidence for greater generic richness in the Upper Carboniferous, I have considered the record at face value.

Given the paucity of Upper Carboniferous blastoids, there are currently no morphological data representing this stratigraphic interval. In contrast to the case of generic richness, we know that morphological variety is greater than observed, i.e., greater than zero! In order to estimate morphological variety for the Pennsylvanian, I have used the range-through method commonly employed in biostratigraphy. Three of the six genera known or inferred to occur in the Upper Carboniferous (*Angioblastus*, *Orbitremites*, and *Pentremites*) are represented in the morphological data. I have taken the average morphology of each of these genera, to yield three data points for the Upper Carboniferous. This is a crude approximation, but it is probably not extremely unreasonable, as the morphology of a genus is not likely to vary appreciably relative to variation in the class as a whole. As will be seen below, morphological variety so estimated for the Upper Carboniferous tends to fall between the values observed for the Lower Carboniferous and Permian.

ANALYSIS OF MORPHOLOGICAL DIVERSITY

Preliminary Investigation of Morphospace Occupation

In order to allow graphical depiction of morphological data, I have determined the principal components (PCs) of the blastoid morphospace, based on the covariance matrix of the Cartesian coordinates. PCs 1-3 summarize over 94% of the total variance in the 17 coordinates, and PCs 1-6 summarize over 99% of the total variance. Figure 2 shows the positions of 31 fissiculate species and 53 spiraculate species ordinated along the first three PCs, as well as the position of the oldest known blastoid, *Macurdablastus uniplicatus* (of unknown ordinal affinity), from the Caradocian of Tennessee (Broadhead, 1984). Neither the Fissiculata nor the Spiraculata can be analyzed separately as a clade, because the former is paraphyletic and the latter polyphyletic (Breimer and Macurda, 1972, pp. 358-360; Horowitz et al., 1986). Nevertheless, the two orders occupy relatively distinct regions in morphospace.

The locations of several genera are depicted along with sketches of the thecae. As would be expected, forms with different general appearance do fall in different regions in the PC space. The landmarks also allow the discrimination of two superficially similar forms, one (*Globoblastus*) with very long radials, the other (*Nucleocrinus*) with very long deltoids. Thus, both gross thecal form and the form of individual plates are captured in this morphometric framework.

If the species are arranged by stratigraphic interval (Fig. 3), it appears as though the Lower Carboniferous is represented by the greatest morphological variety, as measured by the extent

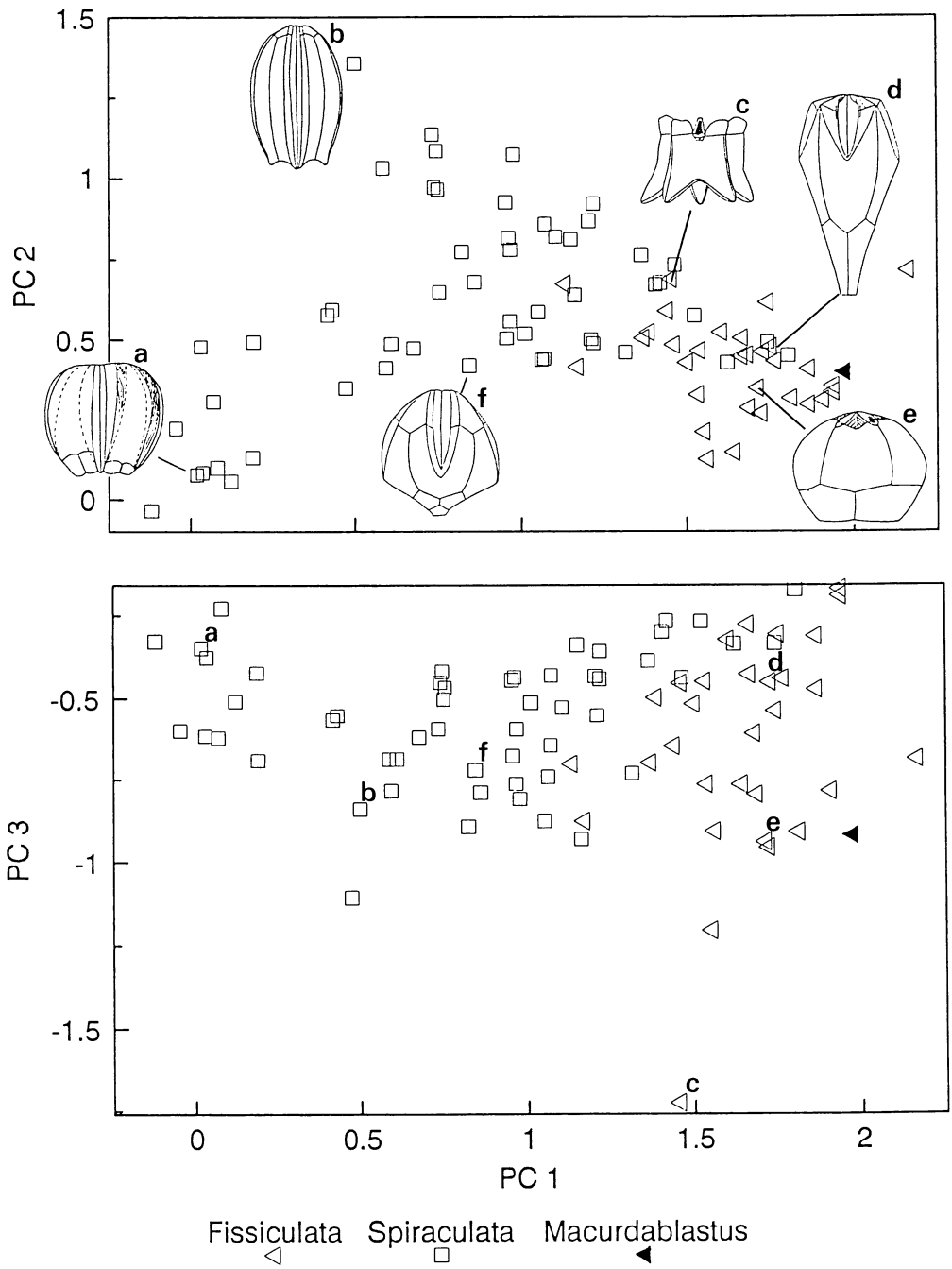

FIG. 2— Ordination of 85 blastoid species along first, second, and third principal components (PCs). PC scores unstandardized. Locations of six genera also indicated. a, *Nucleocrinus*; b, *Globoblastus*; c, *Timoroblastus*; d, *Phaenoschisma*; e, *Angioblastus*; f, *Pentremites*. Note different locations of *Nucleocrinus* and *Globoblastus*, because of different individual plate shapes, despite overall resemblance of entire theca. Also note relatively distinct regions occupied by fissiculates and spiraculates. Sketches of blastoid genera from Fay and Wanner (1967).

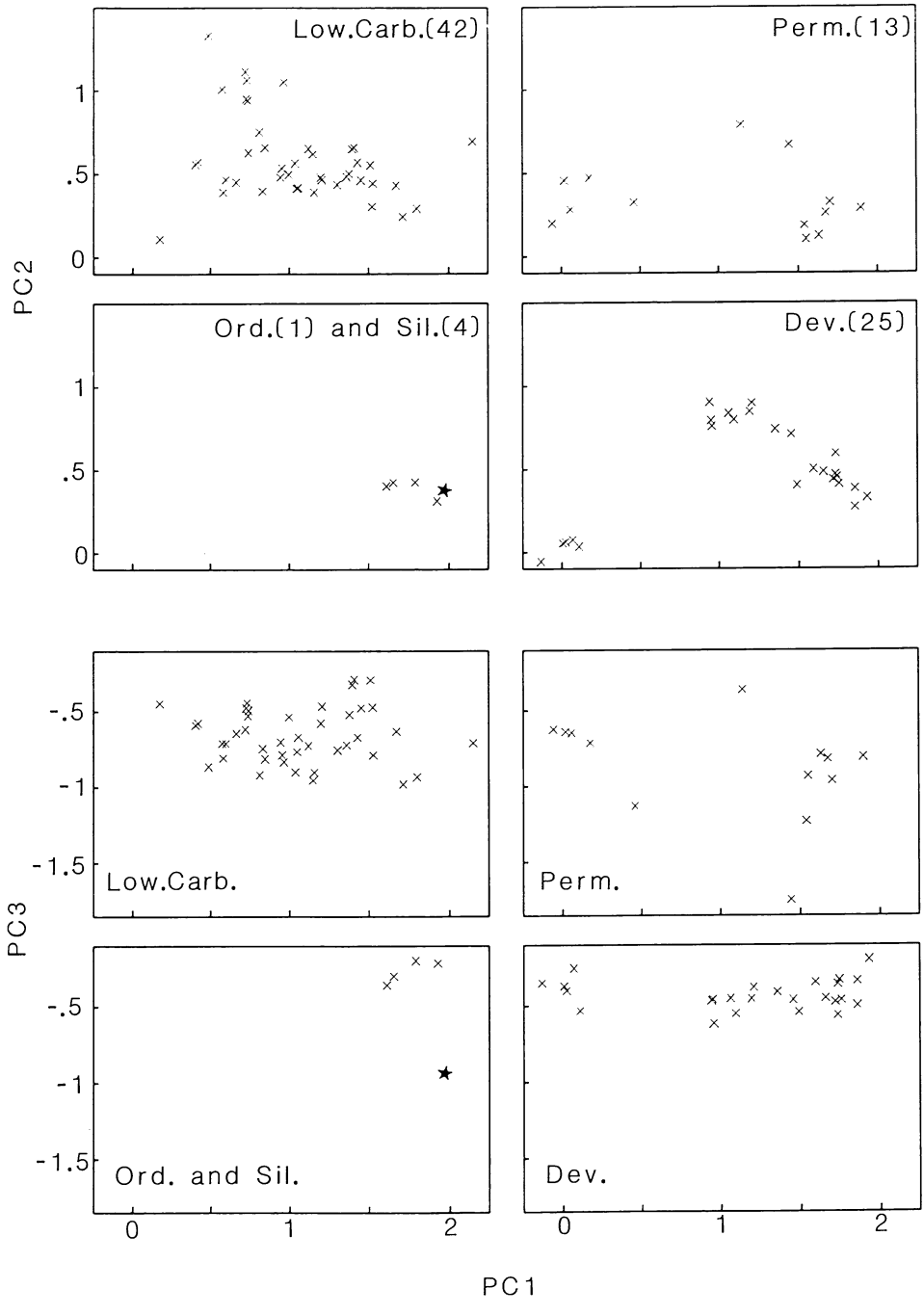

FIG. 3— Ordination of 85 blastoid species along first three principal components, arranged by stratigraphic interval. (Number of species measured in parentheses.) The oldest known blastoid, *Macurdablastus uniplicatus*, from the Caradocian of Tennessee (Broadhead, 1984), is indicated by the solid star. Note increase in both morphological variety and sample size from Silurian to Devonian and Devonian to Carboniferous, while transition to Permian is marked by increase in morphological variety despite decrease in sample size.

of morphospace occupation (agreeing with its status as the interval with the greatest generic richness), followed by the Permian, Devonian, Silurian, and Ordovician. However, one's impression of morphological diversity, whether based on inspection of a bivariate plot or an array of actual specimens, inevitably depends on sample size. The greater the sample size, the larger, on average, will be the morphological range. Therefore, it will be very important, in choosing quantitative estimators of morphological diversity, to correct for differences in sample size.

Measuring Morphological Variety

At least two notions of morphological variety are commonly employed: (1) the average dissimilarity among forms, and (2) the amount of morphospace occupied. In the univariate case (1) is most obviously measured by the sample variance, and (2) by the range. (Multivariate extensions will be discussed below.) An exhaustive treatment of the measurement of morphological diversity will not be attempted here, but some advantages and disadvantages of different approaches should be mentioned. In the present context, the principal advantage of the variance is that it is relatively insensitive to sample size. On the other hand, the variance can be sensitive to taxonomic practice. Oversampling of a particular morphotype because of taxonomic splitting will tend to bias the variance downward if that morphotype is near the average morphology, and upward if the morphotype is far from the average morphology. The effect of taxonomic lumping is the opposite. The principal advantage of the range is that it is essentially insensitive to taxonomic practice; therefore, morphological diversity can be assessed for poorly monographed groups, or with little or no reference to taxonomic information (see Foote, 1990). However, the range is strongly dependent on sample size.

Because variation in taxonomic practice is unlikely to be very important within the Blastoidea, sample-size dependency appears to be the major concern. This would suggest the use of the variance. However, because the amount of morphospace occupied remains an important aspect of morphological variety, it will be useful to develop methods that enable the range of morphospace occupation to be assessed in a way that corrects for sample size. One such approach, rarefaction of samples, is outlined briefly below. Secular patterns of morphological diversity are therefore documented using both the variance and the range, corrected for sample size differences.

Bootstrapping (random sampling with replacement from the morphological distribution; Efron, 1982) was used to obtain an unbiased estimate of the variance, especially important when sample size is small as in the Silurian. All bootstrapped estimates were based on 1000 replications. In order also to correct for sample size effects (expected to be small for the variance) the bootstrapped estimates of variance were based on random samples of three species (equivalent to the number of data points represented in the Upper Carboniferous). (There is little appreciable difference between the variance calculated directly and that based on bootstrapping.)

Multivariate extension

Van Valen (1974) discusses the multivariate generalization of the univariate variance (see also Ashton and Rowell, 1975). The total variance, i.e., the sum of univariate variances, is equivalent to the average squared Euclidean distance of all points from the centroid (Van Valen, 1974). Because my interest here is in the use of a single metric to measure overall variability in a single group, approaches that consider the differences in within- and among-group variability are not immediately relevant.

As discussed above, one may be interested in some measure of the amount (i.e., volume or hypervolume) of morphospace occupied. The product of univariate variances as a measure of this volume has the disadvantage that the product vanishes or nearly vanishes if any of the variances are zero or nearly zero (Van Valen, 1974). Furthermore, redundancy in the variables causes overestimation of the volume of morphospace occupied. One solution to these difficul-

ties lies in the use of principal components (Van Valen, 1974). Redundancy can be reduced and the number of PCs limited, decreasing the probability that any dimension (PC) will have a variance of zero or nearly zero. Although the choice of how many PCs to include is arbitrary, this choice can at least be consistently made within a single analysis. Because the first six PCs summarize about 99% of the total variance, I have used these PCs to estimate both total variance and the product of variances. Analyses based on the first three PCs yield similar results, suggesting that observed patterns are not the consequence of small variances in the higher PCs

A further difficulty remains with use of the product of variances. Samples that differ only slightly in variance in each dimension will appear to differ progressively more as the number of dimensions increases. For example, two samples whose variances differ by a factor of 1.1 in each of six dimensions will differ by a factor of $(1.1)^6$, or 1.77, in the product of the variances. I have therefore used the geometric mean of variances (the k^{th} root of the product of k variances) as an indication of multivariate morphospace occupation scaled to a single dimension.

In addition to the foregoing measures of multivariate variability based on the variance, I calculated analogous measures of variability, the total range and the geometric mean range of samples *rarefied to a common sample size* (see below).

Morphological rarefaction

How much morphospace would be occupied by a taxonomic group if it were constrained to be represented by a particular number of species? This question is analogous to those addressed by Sanders (1968) (How many species are likely to be represented in an ecological sample of a particular number of individuals?) and Raup (1975b) (How many higher taxa are likely to be found in a paleontological sample of a specified number of lower taxa?). Although the problems addressed by Sanders and Raup have an analytical solution based on sampling theory, the question involving morphology can be solved analytically only if the distribution of data is well characterized (e.g., multivariate normal). In general, it is necessary to rarefy a sample (i.e., to estimate its likely diversity at smaller sample sizes) by brute force, repeatedly pulling random samples. As with rarefaction of diversity data, samples to be compared must represent similar sampling conditions and methods.

The technique of morphological rarefaction is illustrated in Fig. 4 for blastoids arranged by stratigraphic interval. For a particular sample, two species are chosen at random. Morphological variety (the range, total range, or geometric mean range) is then computed. (Sampling here is without replacement. One could also sample with replacement, with the effect that the range would be lowered.) Another random sample of two species is chosen and its diversity computed. This is repeated many times, and the average of the diversity values represents the estimate of the diversity one would expect to find at a sample size of two. The whole procedure is then repeated for three species, four species, and on up to the total number of species. Confidence intervals around this expectation can be empirically determined based on the distribution of randomized values. Here I have drawn the 90% confidence interval, i.e., the interval containing 45% of rarefied diversity values on each side of the mean. A complete discussion of morphological rarefaction is given by Foote (1992).

Taking sample sizes at face value, the total range of PCs 1-6 is similar for the Devonian and Lower Carboniferous, and somewhat higher for the Permian (Fig. 4A). However, if Carboniferous blastoids were represented by the same number of species as Permian forms, they would exhibit a much lower total range. Another approach is to compare the diversity within stratigraphic intervals to that of the entire class (Fig. 4B). Here we see that Silurian, Devonian, and Carboniferous blastoids are less diverse morphologically than is the class as a whole, while Permian blastoids are actually more diverse when normalized for sample size. Use of the geometric mean range reveals the same pattern.

Two issues need to be separated in the use of rarefaction: (1) the meaning and interpretation of the number of species sampled, and (2) the structure of diversity, i.e. the relationship between sample size and morphological diversity. The decision to rarefy a sample may be

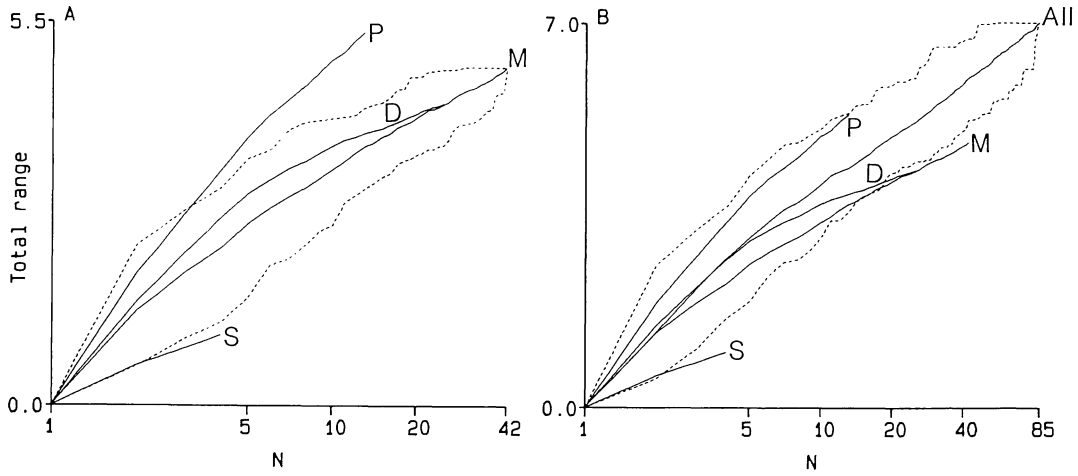

FIG. 4— Rarefaction of morphological distributions. Abscissa is the number of species sampled; ordinate is the expected total range of PCs 1-6 (unstandardized) at the corresponding sample size (based on 100 random samples of *N* species each). (Figs. 5-10 are also based on PCs 1-6.) Abscissa is logarithmic to account for decreasing proportional contribution of sample size to morphological variety. Dashed curves give 90% confidence interval for rarefaction curve. A: Silurian, Devonian, and Permian compared to Lower Carboniferous. B: Silurian, Devonian, Lower Carboniferous, and Permian compared to entire class (curve labeled "All"). Abbreviations: C, Lower Carboniferous; D, Devonian; P, Permian; S, Silurian. Devonian and Carboniferous diversity structure do not differ significantly, while Silurian and Permian blastoids occupy less morphospace and more morphospace, respectively, per unit taxonomic richness than Devonian or Carboniferous blastoids. Blastoids in each interval except the Permian not only occupy less morphospace than the entire class, but also less morphospace per unit taxonomic richness.

made because one suspects that differences in sample size (here, number of species) do not reliably indicate true differences in species richness. For example, the number of described genera in the Devonian and Permian is nearly the same (17 and 18, respectively), but nearly twice as many Devonian species are represented in the morphological data (25 vs. 13). This suggests that the Devonian is more thoroughly represented than the Permian. In such a case one would obviously want to rarefy the Devonian sample to the size of the Permian sample. Conversely, there are only three genera described from the Silurian, all of which are represented in the morphological data. To rarefy the Devonian sample to the size of the Silurian sample would seem to suggest that we can have no confidence whatsoever in sample size differences. Given the intensity of paleontological sampling, it seems unlikely that there are dozens more Silurian blastoid species waiting to be found. Thus we are tempted to say that the morphological range in the Silurian is low not just because it is represented by a small sample, but because there *really* were not many blastoid species around at that time.

The foregoing could be taken as an argument against rarefaction. However, I would suggest that rarefaction is desirable because it can more objectively distinguish differences in morphological variety correlated with sample size from those that are biologically "real" in the sense given above. Therefore, it is not necessary to try to determine a priori (and with some uncertainty) which differences are "real" and which are not. Note that rarefaction of the Devonian, Carboniferous, and Permian samples to the sample size of the Silurian does not impart the same morphological diversity to these four samples. It is the structure of diversity, rather than the interpretation of differences in sample size, that is of principal importance here. Differences in slope of the rarefaction curves suggest that Permian and Carboniferous morphological diversity are *qualitatively* different; they do not represent simply different numbers of species drawn from the same diversity structure. In contrast, the observed difference in

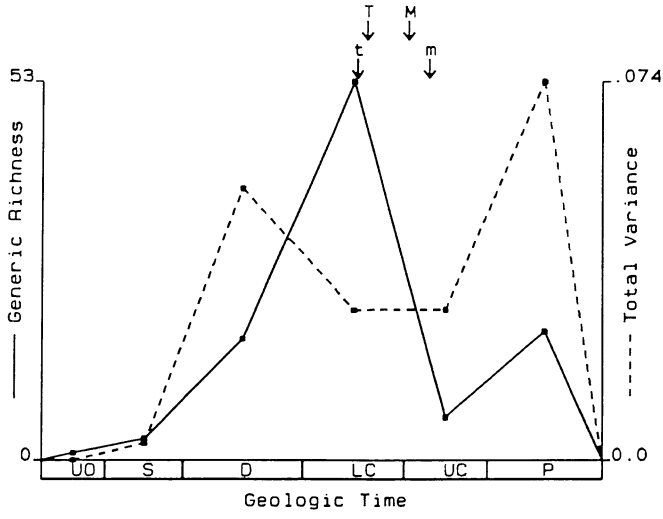

FIG. 5— Generic richness (from Waters, 1988) and total variance against stratigraphic interval. Arrows marked "T" and "M" show taxonomic and morphological *CG*s; arrows marked "t" and "m" show taxonomic and morphological medians. Note temporally forward displacement of morphological variety with respect to taxonomic richness. Abbreviations: UO, Upper Ordovician (Caradocian and Ashgillian); S, Silurian; D, Devonian; LC, Lower Carboniferous; UC, Upper Carboniferous; P, Permian.

total range between the Devonian and Carboniferous may reflect simply the sampling of different numbers of species from the same diversity structure.

COMPARING MORPHOLOGICAL AND TAXONOMIC DIVERSITY

Secular Pattern

The secular pattern of total variance is depicted in Fig. 5 along with generic richness data from Waters (1988). Discordances between the two aspects of diversity are obvious. For example, although maximal generic richness occurs in the Lower Carboniferous, both the Devonian and Permian exhibit higher morphological diversity. This reflects, in part, the fact that many Lower Carboniferous genera are variations on the ellipsoidal-globose theme (Macurda, 1977a). The genus concept in blastoids is probably sufficiently uniform that the amount of morphological variation within a genus does not change systematically through time (Macurda, personal communication). However, the magnitude of the gaps among genera and among species is far from constant, with the result that generic richness gives a poor indication of the magnitude of morphological variety in the class as a whole.

Measures of the extent of morphospace occupation (geometric mean variance, sum of ranges, and geometric mean range) suggest a temporal pattern in which morphological diversity is higher in the Silurian and Lower Carboniferous than indicated by total variance (Figs. 6-8). No single indication of morphological diversity can be considered the "correct" measure. A "consensus" among the different measures of morphological diversity was obtained by scaling

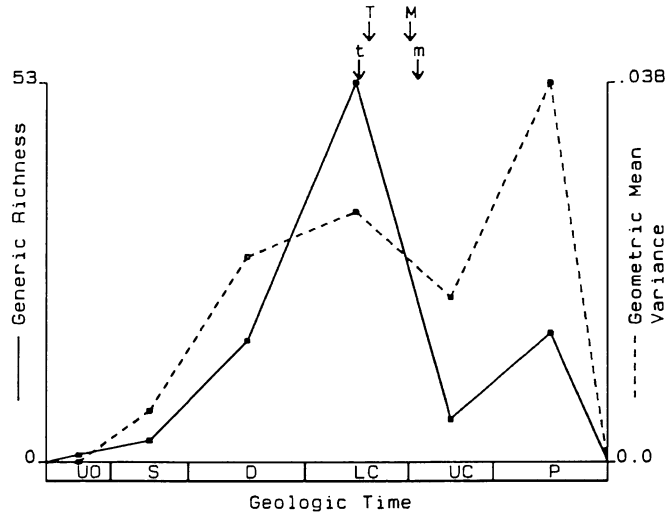

FIG. 6— Generic richness and geometric mean variance. Pattern of morphological and taxonomic central tendency similar to that in Fig. 5.

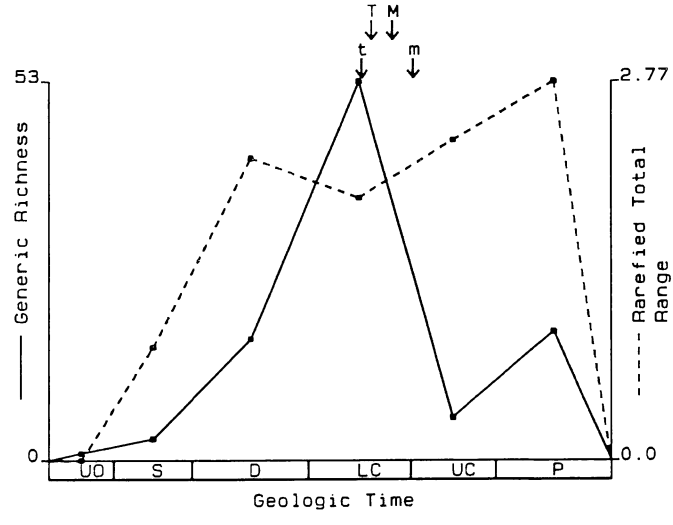

FIG. 7— Generic richness and total morphological range (rarefied to $n = 3$). Pattern of morphological and taxonomic central tendency similar to that in Fig. 5.

each measure from zero to unity and taking the mean for each stratigraphic interval. This normalized measure of morphological diversity suggests that, despite the nearly unimodal pattern of increase and decrease in generic richness, morphological diversity continued to increase until the extinction of the Blastoidea (Fig. 9). In addition to the overall increase in morphological diversity, the use of morphological range suggests early morphological diversification that outpaces taxonomic diversification (Figs. 7 and 8).

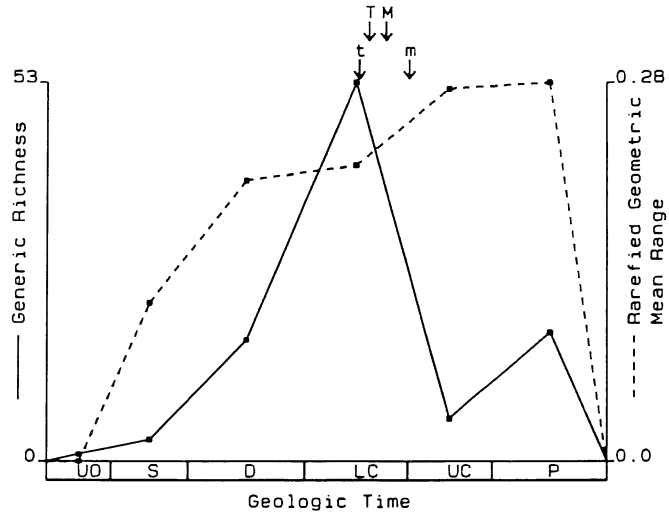

FIG. 8— Generic richness and geometric mean range (rarefied to $n = 3$). Pattern of morphological and taxonomic central tendency similar to that in Fig. 5.

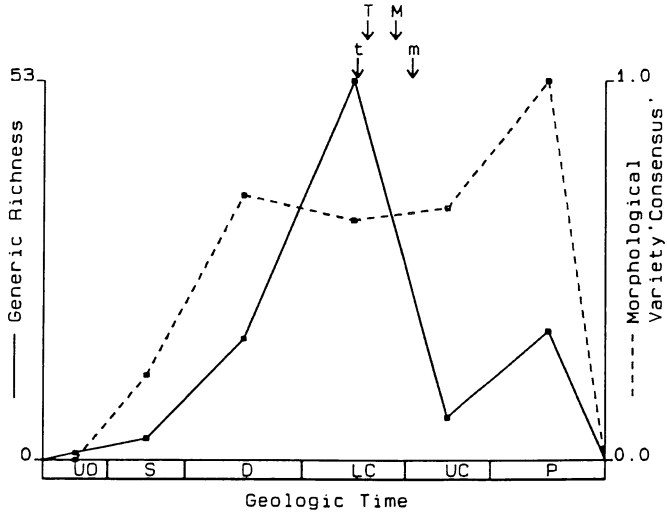

FIG. 9— Generic richness and normalized average of four measures of morphological diversity from Figs. 5-8.

Clade Shape

The temporal pattern of diversity can be treated more abstractly, so that the diversity histories of different clades, or different aspects of diversity in the same clade, can be compared. Gould et al. (1977) presented some clade shape descriptors to convey statistical properties of clade histories. The center of gravity (*CG*) statistic was presented as a "measure of the relative position in time of the mean diversity" of a clade (Gould et al., 1977, p. 26).

TABLE 2 – Clade center of gravity, *CG*, and median for generic richness of Blastoidea

Data	*CG*[1]	Scaled *CG*[2]	Median[1]	Scaled median[2]
Constant diversity[3]	362.9	0.462	362.5	0.463
Generic richness (Table 1)	337.7	0.577	341.7	0.559
One genus added to Ordovician	338.8	0.572	341.9	0.558
Two genera added to Ordovician	339.9	0.567	342.3	0.556
One genus added to Permian	336.9	0.580	341.2	0.561
Two genera added to Permian	336.3	0.583	340.8	0.563
One genus taken from Permian	338.4	0.574	341.9	0.558
Two genera taken from Permian	339.1	0.570	342.3	0.556
Constant diversity, Ordovician omitted[3]	345.2	0.484	342.7	0.497
Generic richness (Table 1), Ordovician omitted	336.5	0.528	341.2	0.504

[1] Million years before present.
[2] Duration of clade scaled to unit length.
[3] *CG* and median with constant diversity represent central tendencies inherent in time scale.

The taxonomic and morphological *CG*s are given by

$$CG_t = \sum_{i=1}^{n} d_i t_i \Big/ \sum_{i=1}^{n} d_i \quad \text{and} \quad CG_m = \sum_{i=1}^{n} w_i t_i \Big/ \sum_{i=1}^{n} w_i \tag{1}$$

where n is the number of stratigraphic intervals, t_i is the midpoint of the i^{th} stratigraphic interval, and d_i and w_i are the number of genera and the morphological diversity, respectively (Gould et al., 1987, equation on p. 1438). I have also calculated the median as a descriptor of clade shape, i.e. the point in time where the cumulative diversity is equal to half the total cumulative diversity.

Gould et al. (1987) discuss the problem of unequal interval lengths. If just a single diversity value is taken for each interval, then a series of short intervals will carry disproportionate weight in the calculation of central tendency compared to a single, longer interval. Conversely, if diversity values are interpolated every million years, then longer intervals carry disproportionate weight (Gould et al., 1987). Gould et al. (1987) approached this problem both by interpolation of values at million-year increments, and by treating interval lengths as uniform. As a compromise, each stratigraphic interval can be represented only once, at its midpoint, with the *CG* being compared to the *CG* inherent in the time scale. For equal interval lengths, a clade with constant diversity will have a center of gravity of 0.5. However, a clade with constant diversity in the time scale used here would have a center of gravity of 0.462, and a median of 0.463 (Table 2). The *CG* of a clade with constant diversity is the same as the *CG* obtained if the observed diversity values are repeatedly randomized with respect to stratigraphic interval, and the average *CG* taken over all the possible randomizations. This is also true of the median. Just as the periodicity inherent in the time scale must be evaluated when studying the timing of extinction events (Stigler and Wagner, 1987; Raup and Sepkoski, 1988), the central tendency inherent in the time scale must be taken into consideration when evaluating clade shape. Because this study compares temporal patterns to each other, rather than to a theoretical expectation, inaccuracies in the time scale are not of primary importance.

The median is sometimes considered preferable to the mean because slight variation in the tails of a distribution (particularly if it is asymmetric) can affect the mean more strongly. The mean also tends to be pulled by a long tail of a distribution, even if that tail accounts for little

of the cumulative frequency of the distribution. An example of this is the familiar case of one millionaire balancing a thousand paupers. Table 2 shows the effect of adding or subtracting a small number of genera in the tails of the generic richness history of the blastoids. Although the mean is affected more than the median by these variations, the effect in either case is rather small. This is because the duration of the clade (analogous to the range of the frequency distribution) is not affected. Omitting the Ordovician altogether (and thus changing the duration of the clade) has a small effect on both the mean and the median if these quantities are expressed in terms of absolute time. If time is scaled from zero to one the effect is more pronounced, but the mean and median are not affected extremely differently. This is in part because the clade history is not grossly asymmetrical. The mean and median should both be evaluated, particularly for very asymmetrical clades or clades in which large range extensions are likely. But in many cases (such as the present one) it may make relatively little difference which statistic is used.

Statistical testing of clade shape

Gould et al. (1977, 1987) compared the average centers of gravity of two large, empirical sets of taxa, whereas Kitchell and MacLeod (1988) determined the mean and variance of *CG*s of many simulated, randomly evolving clades. The statistical problem we face here is different: given only two diversity histories, one morphological and one taxonomic, how can we determine whether an observed difference in central tendency is significant? To do so requires calculation of the respective *CG*s and an estimate of the variance of each. The variance of CG_t is obtained by treating the diversity path as a frequency distribution (as was done to calculate CG_t). Thus

$$V(CG_t) = \frac{\sum_{i=1}^{n} d_i t_i^2 \; - \; (\sum_{i=1}^{n} d_i t_i)^2 \; / \; \sum_{i=1}^{n} d_i}{\sum_{i=1}^{n} d_i \; - \; 1} \qquad (2)$$

The estimated variance of CG_m is developed in Appendix C, based on the assumption that morphological diversity is measured as the variance, or the sum of variances, of a set of linearly uncorrelated variables, such as principal components. (I thank Prof. William A. Ericson, Statistics Department, University of Michigan, for providing this solution.) The *z*-statistic for the difference between CG_m and CG_t is equal to 2.46, which is significant at $P < 0.05$. In the Blastoidea, therefore, there is a significant, temporally forward displacement of morphological diversity relative to generic richness.

This result is similar to that obtained if one calculates the variance as for taxonomic diversity, while using the total number of species measured as the "sample size" to convert the variance to the standard error of the mean (i.e., CG_m). Although statistical tests for other measures of morphological variability are not developed here, one can gain some idea of the magnitude of differences in *CG* by inspection of Figs. 6-9.

The Restricted Permian Record

Most of the Permian blastoid record comes from the Eastern Hemisphere, principally Timor. Whether the geographic restriction of Permian blastoids indicates their actual biogeographic distribution during the Permian or is preservational in nature, the samples representing the different stratigraphic intervals are not strictly comparable. The Devonian and Carboniferous samples represent, to a first approximation, global diversity, while the Permian sample more nearly approximates within-province diversity. It would be helpful to compare more nearly equivalent samples for each interval. This is especially important because taxonomic richness

and morphological diversity are not equally affected by restricted sampling (see rarefaction analysis above). For example, suppose that various morphotypes were essentially globally distributed, but were represented by different genera in different provinces. Then preservation and/or sampling in a single province would likely yield a relatively large proportion of total morphological diversity, but a relatively small proportion of total generic richness. In the case at hand, this effect could bias the Permian record toward disproportionately higher morphological diversity, thus making the entire morphological history of the blastoids asymmetric. We cannot know what the morphological or taxonomic diversity would have been for the Permian had the Permian been represented by more extensive deposits. However, we can estimate how the Devonian and Carboniferous records would appear if they were similarly restricted geographically.

I artificially degraded the Devonian, Lower Carboniferous, and Permian records so that each would be represented by the single richest deposit (or closely related set of deposits), as judged by the availability of specimens in museum collections. The Ordovician is already represented by a single deposit. Because morphological data are available for no more than one genus in any Silurian formation, the Silurian record, paltry enough to begin with, was not artificially degraded. The Upper Carboniferous is omitted altogether, as no data are available. For the Devonian I considered only the Hamiltonian (mainly Givetian) deposits of the Michigan Basin; for the Lower Carboniferous only the Osagean (upper Tournaisian and lower Visean) Burlington Limestone; and for the Permian only the Upper Permian deposits of Timor. The number of genera known from these deposits was taken from Waters (1988) as 7, 20, and 12, respectively. Artificial degradation of the record changes the patterns of diversity, but not substantially (Fig. 10). It is important to keep in mind that the facies, geographic extent, and temporal scope representing each stratigraphic interval are not strictly comparable. Nevertheless, it is reassuring that the pattern based on within-province diversity is not very different from that based on global diversity.

Discussion

The imperfect correlation between morphological and taxonomic diversity is not a novel result. However, the magnitude of these discrepancies (comparing the Lower Carboniferous to the Permian, for example) raises the question of what exactly we are measuring when we count taxa. Taxonomic richness is simply an estimate of the number of definable biological entities in the world, with no particular reference to the magnitude of the morphological differences among them. Subtaxa among different higher taxa may not generally be comparable (Van Valen, 1973b). However, even within a single, well monographed clade, there is substantial variation in the nature of differences among subtaxa.

A discordance between morphological and taxonomic diversity does not imply that, say, a doubling or halving of generic richness is uninterpretable. Rather, such changes in diversity should not be assumed to represent changes in ecological or morphological diversity. As Erwin et al. (1987) suggested, it is possible for taxonomic richness to decline substantially, while leaving the world ecologically nearly saturated, at a coarse scale. Summaries of the evolutionary history of blastoids generally refer to the Lower Carboniferous as the time of maximal diversity. However, it is no less significant that the most extensive occupation of morphospace (and possibly, by implication, ecospace) occurred in the Permian.

The increase in morphological variety resembles a pattern of "diffusion" (e.g., Stanley, 1973; Fisher, 1986; Gould, 1988). This increase is seen when diversity is measured within geographically and stratigraphically restricted deposits, suggesting that the pattern is not an artifact of changes in the quality of the record.

Considering the inadequacy of the Upper Carboniferous data and the coarse level of stratigraphic resolution, we should interpret the foregoing analysis of clade shape with caution.

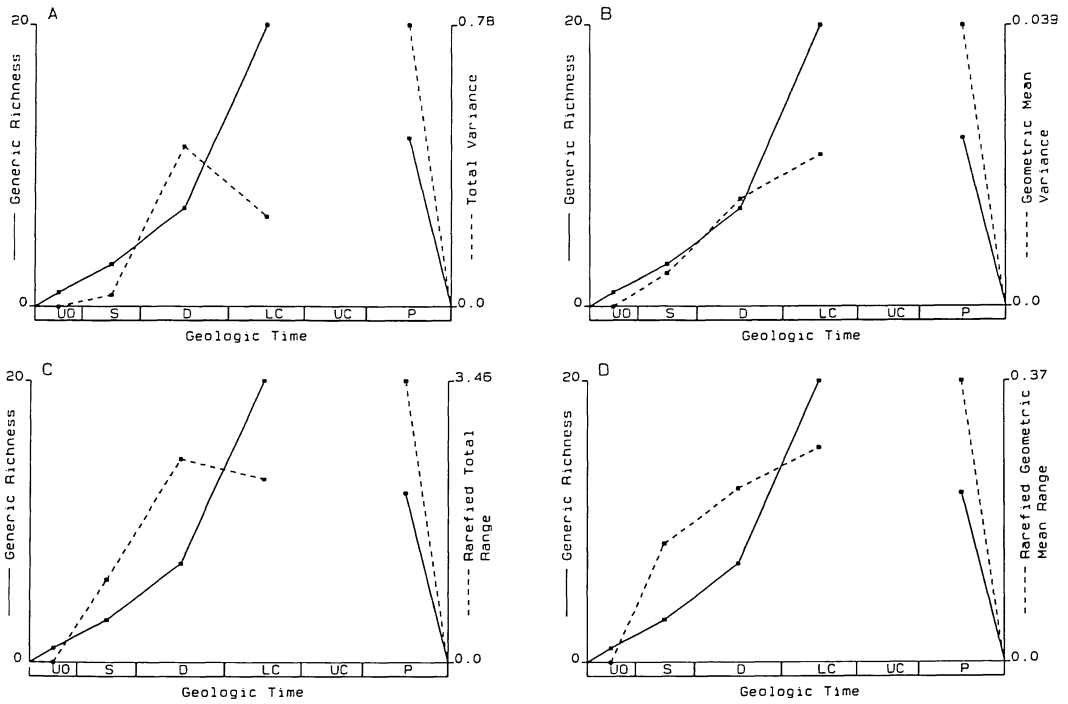

FIG. 10— Generic richness and morphological diversity for artificially degraded record, representing the single richest deposit or closely related group of deposits sampled in this study. Geographically restricted samples yield much the same pattern as does the entire data set. Note that the Upper Carboniferous is not considered; therefore samples are rarefied or bootstrapped to the Silurian sample size of 4, in contrast to Figs. 5-9. This accounts for the difference in the maximum value of the ordinate.

However, the possibility that morphological diversity is more heavily concentrated in the latter half of the history of the Blastoidea remains suggestive. As more morphological data are collected, perhaps allowing finer stratigraphic resolution and better estimates of Upper Carboniferous morphological diversity, the pattern may stand or fall. Although it is tempting to suggest that the late Permian extinctions truncated the clade's history, thereby making it asymmetric (as it is), it should be kept in mind that such a truncation should not be expected to affect taxonomic and morphological diversity differently, unless there is some real difference between the two. Whatever the case may be with the blastoids, the methods outlined above should serve as a foundation for comparing morphological and taxonomic diversity histories in other clades.

The Trilobita also appear to exhibit a forward displacement of morphological diversity relative to taxonomic diversity (Foote, 1991). However, it is instructive to focus less on particular cases and more on what such a difference between morphological and taxonomic diversity histories would imply in general. Because it has been suggested that the early history of animal life is marked by great morphological diversity and low taxonomic richness (Gould,

1989), it is worth considering reasons for the discrepancy between this perception and the pattern suggested by the trilobites and blastoids.

One explanation is that the claim for greater morphological diversity in the Early Phanerozoic is time-specific, having resulted because the world was relatively "empty" ecologically (Valentine, 1986; Gould et al., 1987; Gould, 1989). Another obvious explanation is simply that the trilobites and blastoids are exceptional. At this point it would be premature to conclude that the forward displacement of morphological diversity is a general phenomenon. (Of course, it could also be pointed out that the phenomenon of differential morphological diversification early in time has not been demonstrated rigorously.) Furthermore, it should be added that measures of diversity based on the morphological range indicate a radiation into morphospace that outpaced the initial taxonomic diversification of blastoids. But even if most clades proved to exhibit greater asymmetry of morphological versus taxonomic diversity histories, the discrepancy between this pattern and that of early morphological diversity may be more apparent than real. This is simply because the claim for early morphological diversity has been based on the number of phylum- or class-level *Baupläne* (disparity), rather than morphological variety within a single *Bauplan.*

Perhaps the most celebrated example concerns the Middle Cambrian Burgess Shale and related deposits. Here we see a diversity of organisms, apparently quite different from each other, which did not survive the Cambrian. Gould (1989) has used this observation to support the position that body plan diversity (disparity) has decreased over time. Briggs and Fortey (1989) demonstrate that gradations can be found among many arthropods of the Burgess Shale. However, the presence of intermediates does not make the most divergent forms any less divergent. Whereas morphological intermediates certainly indicate a different structure of diversity (which would be represented by shallower rarefaction curves), they do not affect the total extent of morphospace occupation.

We could, in principle, treat all the Burgess body plans as representatives of the single metazoan clade, but, in the absence of information on homology, it is difficult to measure the morphological diversity of the clade. It would be desirable to have a morphospace in which all Cambrian organisms could be ordinated, so that changes in morphological variety could be documented without reference to numbers of taxonomic units, whose significance is uncertain and not constant over geologic time. Although such an assessment is at this point quite subjective, it would seem that the Metazoa today, even if they are represented by fewer body plans, probably occupy more morphospace than did the animals of the Middle Cambrian. Of course, rarefaction of morphological diversity might reveal that, corrected for species richness (which is relatively low in the Middle Cambrian), morphological diversity in the Metazoa has in fact decreased over time.

SIMULATION STUDIES

Rationale

The foregoing analysis and discussion concerned methods of testing for directionality in the history of a clade. Simulation of randomly evolving clades is instructive for two reasons: (1) it provides a benchmark against which real clades can be compared, and (2) it allows us systematically to vary biologically important parameters, such as speciation and extinction rates, to determine their likely effects on the large-scale evolutionary properties of clades. It will be shown below that certain patterns appear often in simulated clades, and are maintained, or even enhanced, as conditions of the simulations are changed.

Procedure

Simulations of undirected evolution were based on the time-homogeneous approach presented by Raup et al. (1973) and Raup and Gould (1974). A simulation begins with a single lineage having an arbitrary morphology. At each time increment the lineage may branch into two daughter lineages (with probability p), become extinct (with probability q), or persist (with probability s). So that there is no directionality inherent in the model, p and q are assumed equal to each other. Furthermore, p, q, and s are stochastically constant over time. If the lineage branches, then one of the daughter lineages has the same morphology as its ancestor, while the other is allowed to evolve morphologically as follows. For each morphological character, a random number determines whether or not that character changes, based on the assigned probability of character change, u. If that character does change, it has equal probability of experiencing either an increment or a decrement in its value. (Probabilities of positive and negative change are constant and equal to each other in order to avoid inherent directionality.) Two different approaches were used to determine the magnitude of character change. (1) As in Raup and Gould's (1974) simulations, a constant value was added to or subtracted from the morphological value of the character. (2) In an alternative approach, the size of the change was taken as a constant fraction (x) of the existing character value. Because the latter mode of character evolution is probably biologically more realistic, at least for size characters (Haldane, 1949; Gingerich, 1983), all simulation results presented are based on this mode. However, with respect to the statistical properties of clades discussed here, there is virtually no difference whether morphological change is constant or proportional.

The model employed differs from early simulations (Raup et al., 1973; Raup and Gould, 1974; Gould et al., 1977) in two important respects. (1) Only strictly monophyletic clades were considered. Each simulation initiates with a single lineage. This lineage and all its descendants are considered a single clade. Thus, no decisions are made to form new clades arbitrarily. (2) Phyletic evolution can also be incorporated, with stochastically constant probability r. (The probability of persistence, s, is equal to $1 - p - q - r$.) In the event of phyletic evolution, the magnitude and direction of character change are determined exactly as in the event of branching described above.

Overall, the model of stochastic evolution is intended to be biologically reasonable (containing the principal elements of speciation, extinction, and morphological evolution), but to lack any inherent directionality (as all the parameters in the model are held stochastically constant through the duration of a simulation). The purpose of simulations is to determine whether any large-scale directionalities result from a process that is essentially non-directional at the smaller scale, *not* to try to replicate observed patterns by making the model progressively more realistic or "finely tuned." The use of time-homogenous taxonomic rates does not constitute belief that these rates are in fact constant (on the question of constancy of taxonomic rates, see, e.g., Van Valen, 1973a; Raup, 1975a; and Raup, 1988). Just as agreement between an empirical pattern and the results of a directional model does not indicate that the model explains the real world, the failure to distinguish between an empirical pattern and the results of a non-directional model does not indicate that there were no directional processes contributing to the empirical pattern.

Initial Choice of Parameters

Speciation and extinction rates

The importance of scaling simulations empirically has been cogently argued by Stanley et al. (1981). Reasonable estimates for speciation and extinction rates are available for particular higher taxa (e.g. Horowitz et al., 1985; Foote, 1988) as well as for larger assemblages of taxa (e.g. Raup, 1978). Published estimates of rates of speciation and extinction are often in the neighborhood of 0.1 events per lineage per million years. Based on survivorship analysis of blastoid genera, Horowitz et al. (1985) estimate the speciation rate at 0.2. Because the value

0.1 is closer to that for all invertebrates (Raup, 1978) I have used this value for most simulations. (The sensitivity analysis discussed below will investigate the effects of varying taxonomic rates.) The published estimates concern speciation and extinction rates, while the model employs probabilities. For sufficiently fine time increments and/or sufficiently small rates, the rates and probabilities are approximately equal. Simulations with the initial parameter choice were run with time increments of 1 m.y. Sensitivity analyses are based on simulations using 0.1 m.y. increments. At this level of resolution, the discrete-time simulation provides a reasonable approximation to the continuous process.

Phyletic evolution rate

Phyletic evolution rate, as employed here, refers to the number of "events" of phyletic evolution per lineage per million years, and is not equivalent to the magnitude of character change per unit time. The general importance of phyletic evolution, as opposed to morphological evolution associated with cladogenesis, has been inconclusively debated. For simplicity, not for realism, I first present simulations without phyletic evolution. Sensitivity analysis will later explore the effects of allowing the rate of phyletic evolution to vary from zero to ten times the speciation rate. It is likely that the actual prevalence of phyletic evolution lies somewhere in this interval.

Probability of character change, size of increment, and number of characters

Gingerich (1983) has tabulated data showing, for size at least, that morphological measurements on closely related species are typically within about 20% of each other, regardless of how much time was involved in the morphological transition. This is in rough agreement with an analysis of 17 coordinates in 12 species of *Pentremites*. If each species is compared to its nearest neighbor in morphospace, i.e. to the species morphologically most similar to it, the median character difference is 14%. As Gingerich points out, the commonly observed difference of 20% partly reflects the fact that species differing by very small amounts are unlikely to be discriminated in the first place, while species that are very different are unlikely to be compared. The expected difference between ancestral and descendant lineages per character is simply ux, where u and x are as defined above. In order to be conservative in choosing the average morphological step size, I have used intial values of $u = 0.5$ and $x = 0.1$. Sensitivity analyses presented below explore the effects of changing these values.

For initial simulations I have used 10 morphological characters, each starting with an arbitrary value of 10 (varying this value has no appreciable effect on the results). This number of variables was chosen because it is of the same order of magnitude as the number of features commonly measured in studies involving morphological evolution. The effects of changing the number of variables are discussed below.

Summary

Except for exploring the effect of varying single parameters, all simulations used speciation and extinction rates of 0.1 events per lineage per million years; phyletic evolution rate of zero; probability of character change of 0.5; morphological step size of 0.1 times the existent character value; and ten morphological variables.

Results Based on Initial Parameter Choice

It is well known that nearly any conceivable diversity history can result from a simulation of the type employed here. To gain insight into the expectation of the model, I have run 1000 simulations and determined for each simulation the center of gravity of taxonomic diversity and total morphological variance. Use of the median reveals the same patterns as those discussed here. Because clades consisting of a single lineage are constrained to have *CG*s of 0.5, they were excluded from consideration as essentially uninformative. All simulations were allowed

to run for 600 simulated million years (an arbitrary choice, corresponding approximately to the duration of the Phanerozoic). Clades extant at the end of the run were disregarded.

Neither taxonomic richness nor morphological diversity has any pronounced tendency toward asymmetry. Taxonomic and morphological *CG*s averaged over all simulations are 0.499 and 0.515, respectively. Because all time increments are of equal length, the *CG*s inherent in the time scale are both 0.5, and no correction for this is needed. Although the mean morphological *CG* is slightly larger than 0.5, the variance in CG_m is so great that the mean cannot be distinguished from 0.5. However, we can also ask, regardless of the central tendency, how often does one aspect of diversity have a higher central tendency than the other? Over 63% of all simulations yielded clades with CG_m greater than CG_t. This is significantly different from 50% at $P < 0.01$. Thus, a temporal asymmetry at a large scale results from a set of smaller-scale processes (speciation, extinction, and morphological change) that are time-homogeneous.

Interpretation

Why should morphological variety in randomly evolving clades be displaced later in time, on average, relative to taxonomic richness? The sensititivy analysis presented below strongly suggests that this is not an artifact. First principles and the inspection of many simulated clades point toward the importance of morphological diffusion (random walking), and extinction that acts randomly with respect to morphology. As Raup and Gould (1974) showed for randomly evolving clades, and as others have shown for real clades (see Gould, 1988), variance in morphology often tends to increase as a clade diversifies. Now consider what happens when taxonomic diversity decreases (Fig. 11). If extinction preferentially selected against morphologically extreme species, then we would expect morphological diversity to decrease as well. But if extinction were effectively random with respect to morphology (at a sufficiently coarse scale of analysis), much morphological variability could be maintained, despite a decrease in taxonomic diversity. In fact, a clade could even continue to diffuse through morphospace, because speciation and phyletic evolution would continue. Many simulated clades show this very pattern: morphological diversity is maintained or increases during declines in taxonomic richness (Fig. 12). Although it may be tempting to interpret such a buffering of morphological diversity as an immediate consequence of organismic adaptation, it should be stressed that it is simply a predictable effect of the geometry of branching.

Sensitivity Analysis

It is possible that the discrepancy between morphological and taxonomic diversity in the simulations results from the particular choice of parameters. To test for this possibility, several parameters were varied independently, leaving all other parameters the same as in the foregoing simulations. The results of these sensitivity analyses suggest that only the duration of a clade and the number of morphological characters have any appreciable effect. As the duration of a clade increases, the magnitude of CG_m increases, and the tendency for CG_m to be greater than CG_t becomes more pronounced. These same changes are likewise observed as more morphological characters are measured.

Duration of clade

The foregoing results summarized the history of multilineage clades of any duration, provided they had become extinct before the end of the simulation. To investigate the effects of clade duration, I culled the results of the foregoing set of simulations, choosing increasing values for minimum duration, and ignoring clades that failed to attain this minimum duration. The effect of duration on central tendency is depicted in Fig. 13. As the minimum duration increases, the taxonomic *CG* barely changes, whereas the morphological *CG* increases. Accompanying the increase in morphological *CG*, the percentage of simulations in which morphological *CG* is higher than taxonomic *CG* also increases. It would appear as though

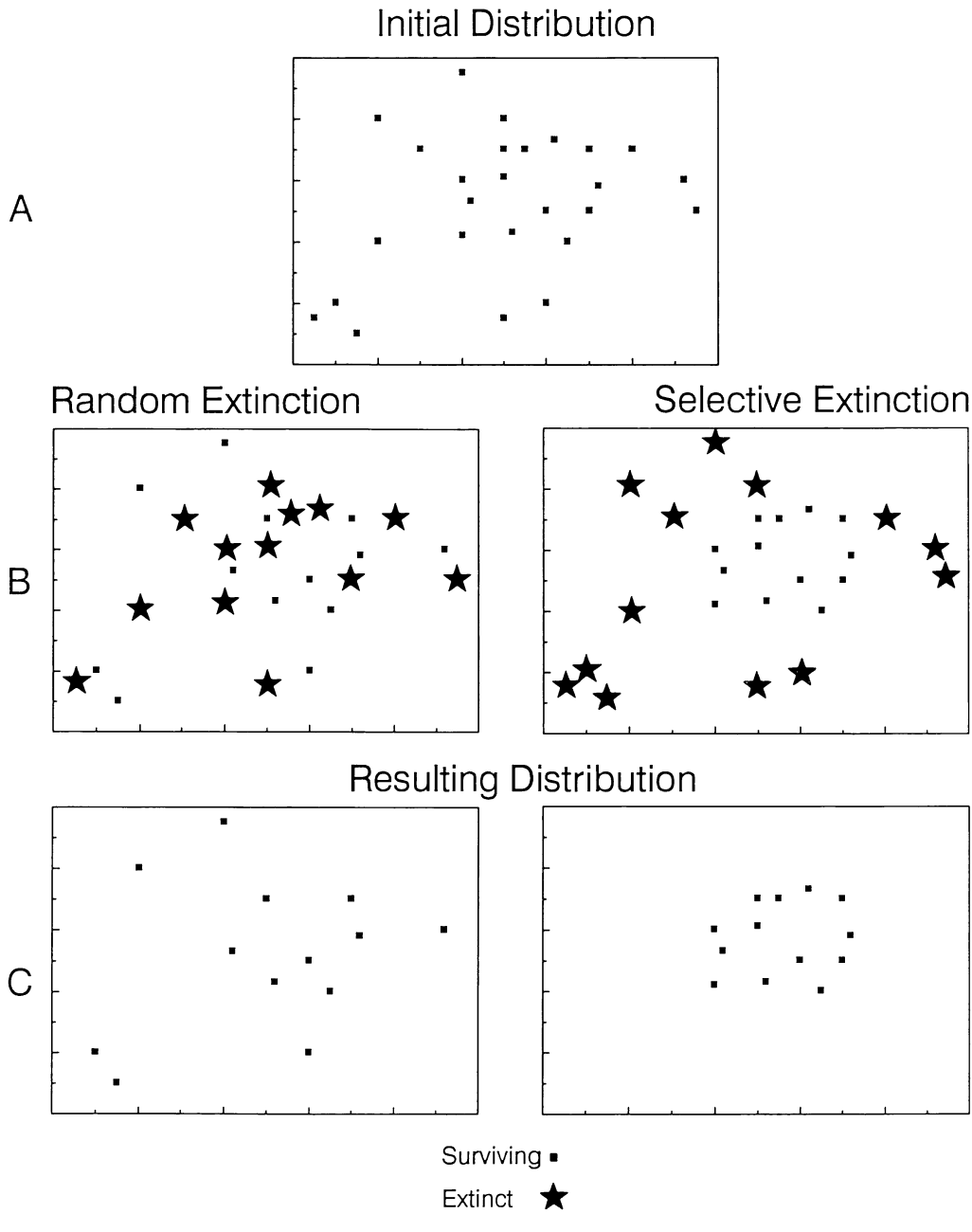

FIG. 11— Effects of random and selective extinction on morphological diversity, depicted in a hypothetical, two-dimensional morphospace. A: initial morphological distribution. B: imposition of extinction; extinct species indicated by stars, surviving species by squares. C: resulting morphological distribution. While selection against morphological extremes decreases both taxonomic and morphological diversity, random extinction allows morphological variety to be maintained despite decrease in taxonomic richness.

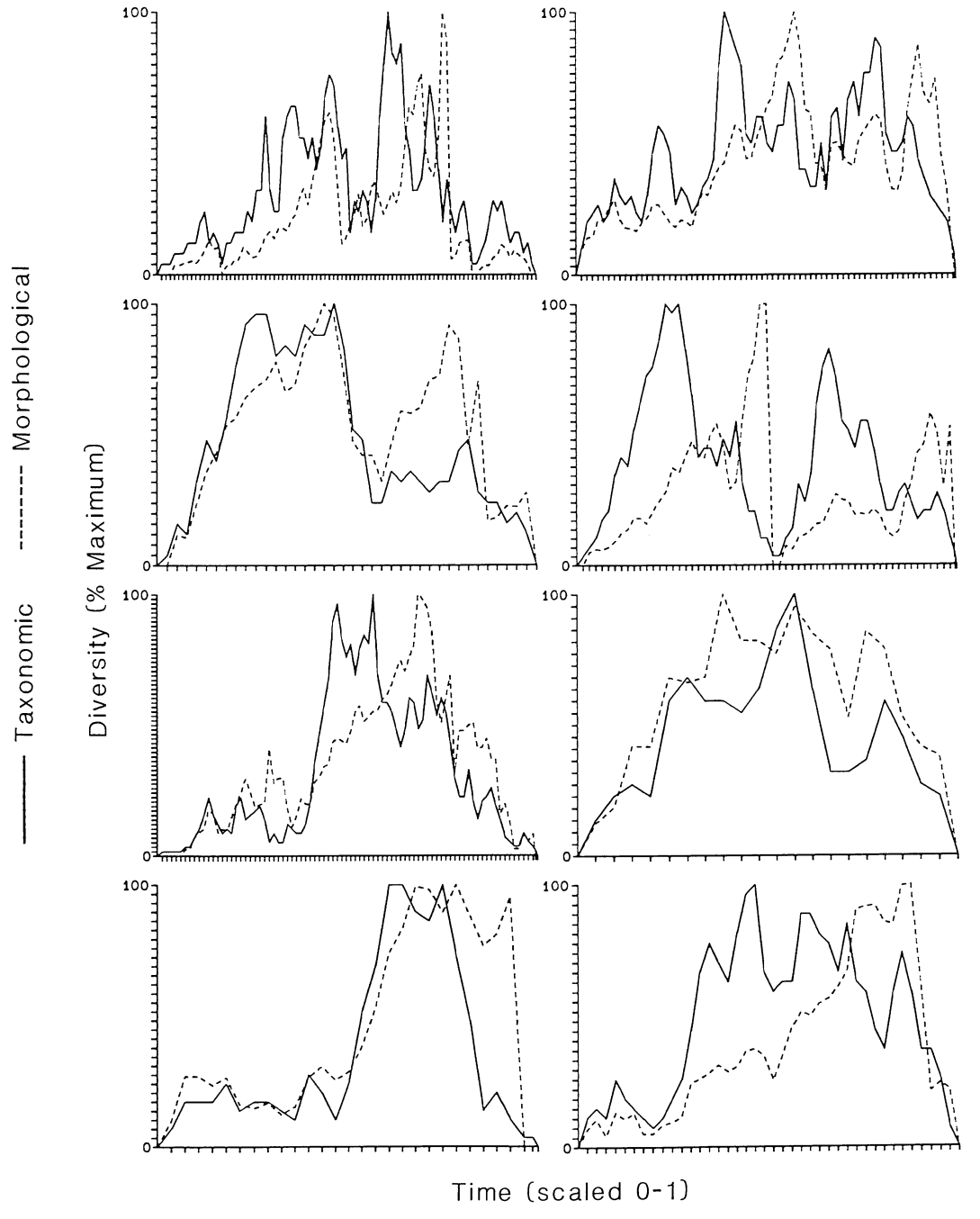

FIG. 12— Morphological and taxonomic diversity histories of simulated clades, based on initial parameter choice discussed in text. Data lumped into increments of 5 m.y. Clades presented are the first eight that attained richness of 20 or more lineages at any point during their history (to make clade history less volatile and therefore easier to follow). Morphological diversity (dashed curve) measured by total variance, taxonomic diversity (solid curve) by number of lineages. Each tick mark on time axis represents 5 m.y. Each tick mark on diversity axis represents one lineage. Note tendency for morphological diversity to be maintained and to increase despite decreases in taxonomic diversity.

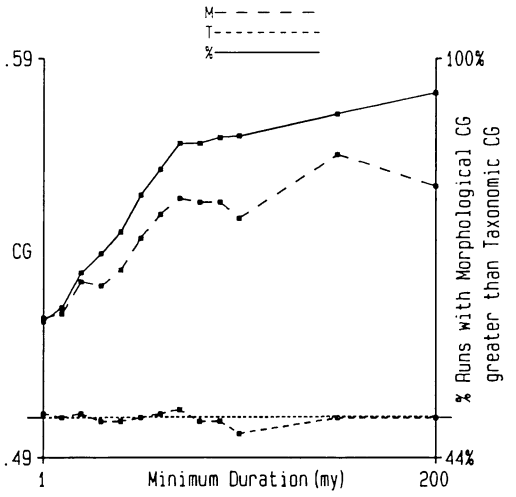

FIG. 13— Effect of minimum clade duration on simulation results. Clades that endure longer spread further through morphospace; their morphological variety is therefore more difficult to reduce by taxonomic extinction. In this and all subsequent figures, short-dashed line (T) gives taxonomic *CG*, long-dashed line (M) gives morphological *CG*, solid line (%) gives percent of runs with CG_m greater than CG_t, and dotted line indicates position at which *CG* = 0.5 and 50% of runs have CG_m greater than CG_t. Note that Figs. 13-18 are drawn to different scales.

short-lived clades have not had time to diffuse sufficiently through morphospace to enable them to maintain morphological diversity as taxonomic richness decreases.

Taxonomic rates

Estimates of median lineage duration tend to fall around 3 to 10 million years (Raup, 1978), corresponding to extinction rates of 0.23 to 0.07 events per lineage per million years, respectively. Simulations were performed at ten values of p (=q) between 0.07 and 0.25 (Fig. 14A). The published estimate of median lineage duration in blastoids lies in this range at about 3.5 m.y., or q = 0.2 (Horowitz et al., 1985).

Taxonomic rates are an important aspect of a clade's macroevolutionary dynamics. Because clades with higher turnover rates exhibit greater fluctuations in total diversity (see discussion in Stanley et al., 1981), at least one aspect of clade shape is affected by changes in taxonomic rates. However, in terms of central tendency and the relationship between morphological and taxonomic *CG*, the effect of taxonomic rates is small. There is a tendency for morphological *CG* to decrease as taxonomic rate increases. Intuitively it is not clear why this should be, but the magnitude of the change is quite small, particularly when we consider the great range of taxonomic rates covered. The dependence of *CG* upon clade duration was mentioned above. If we omit clades enduring less than the expected half-life of the clade, we find, as above, an enhancement of the tendency for morphological *CG*s to be higher than taxonomic *CG*s. As when short-lived clades are included, this tendency decreases as taxonomic rate increases, but the magnitude of the change is still very small (Fig. 14B). Therefore, for practical purposes, the effect of taxonomic rates on both morphological and taxonomic *CG* is neglible.

Rate of occurrence of phyletic evolution

Van Valen (1990, Table 3) presented data indicating that instances of phyletic transition are about as common as branching events in some Cenozoic mammalian lineages. The likely upper limit on the rate of phyletic evolution is difficult to estimate, but a value of twice the speciation rate (which, in the model, would mean that on average 2/3 of all morphological

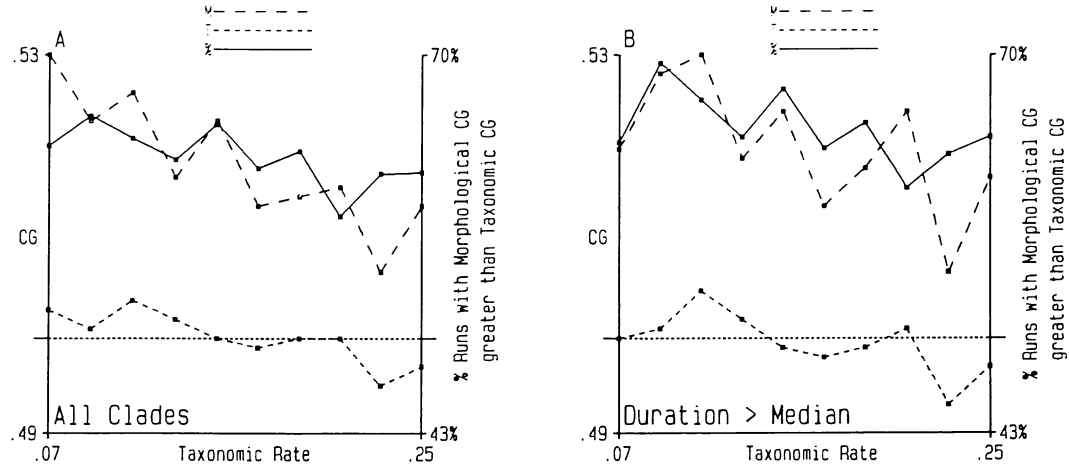

FIG. 14— Effect of taxonomic rates of evolution on simulation results. A: all clades. B: only clades enduring longer than median clade duration (i.e., clade half-life). Effect of taxonomic rate is small considering the magnitude over which this rate is varied.

change is independent of speciation) may be a reasonable guideline. Simulations were run for ten values of r varying from 0 to $2p$, as well for eight values from $3p$ to $10p$ (corresponding to the occurrence of over 90% of morphological evolution independent of speciation) (Fig. 15). Although there is a decrease in CG_m and in the tendency for CG_m to be greater than CG_t as r increases, the magnitude of these changes is small, especially considering the wide range over which r is varied. As with the results when taxonomic rates were varied, it is not intuitively obvious why these changes should occur. Even pushing r to a value that might stretch the belief of many a paleontologist, there is still a significant tendency for morphological diversity to be more heavily concentrated later in time than taxonomic diversity. Therefore, variation in the rate of phyletic evolution is unlikely to alter substantially the relationship between morphological and taxonomic *CG*.

Probability of character change and size of morphological change

The theoretical lower limit on u is zero and the upper limit unity. If u were very near zero, then it is unlikely that sufficient morphological evolution would occur for us to recognize different species. Keeping x constant at 0.1, I varied u from 0.1 to 1.0. This corresponds to an expected degree of character change ranging from 1% to 10%. The value of x is not permitted to reach unity, according to the model, as this would imply that a character could decrease by 100%, i.e., take on a value of zero. Because character change is multiplicative, no subsequent character evolution would then be possible. I therefore varied x from 0.05 to 0.9, with u constant at 0.5. This corresponds to a range of expected character change of 2.5% to 45%, probably covering the true biological range for most circumstances. (Recall that interspecific character differences in *Pentremites* are about 14%.) Neither changes in u nor changes in x have any substantial effect on CG_m or on the tendency for CG_m to be greater than CG_t (Figs. 16 and 17).

Number of characters

No presumption is made in the model regarding the nature of morphological characters, i.e. whether they represent size, meristic counts, or some other feature. That the simulation results are relatively insensitive to the size of character changes suggests that it matters little what kind of characters are involved. However, we need also to consider the dimensionality of the morphospace, i.e., number of characters. To do so I varied the number of simulated morpho-

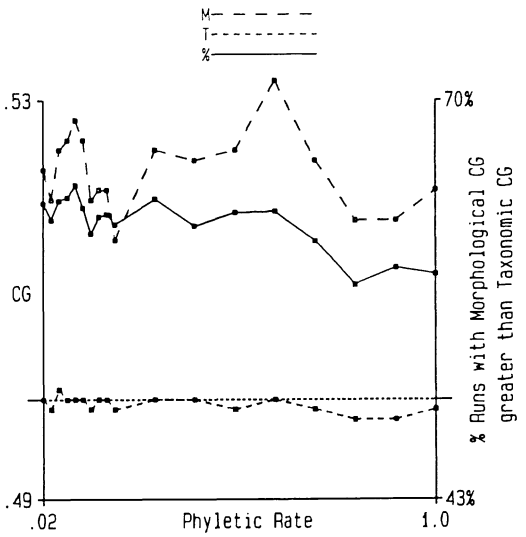

FIG. 15— Effect of phyletic rate of evolution on simulation results. Phyletic rate is the frequency of occurrence of phyletic morphological change, not the rate of character change per unit time. Effect of phyletic rate is small considering the magnitude over which this rate is varied.

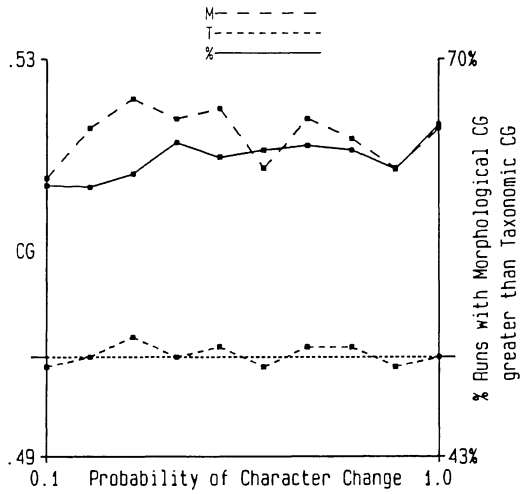

FIG. 16— Effect of probability of morphological change on simulation results. Virtually no effect is observed.

logical characters from 1 to 20 (Fig. 18). The percentage of simulations with CG_m greater than CG_t is significantly different from 50% regardless of the number of characters. There is an increase in morphological *CG* with the number of characters. Likewise, the tendency for morphological *CG*s to be higher than taxonomic *CG*s also increases with the number of characters.

Given that it is never possible to study the entire morphology of an organism, this result has obvious significance (G. Smith, personal communication): measuring the morphology increasingly more thoroughly only enhances the pattern observed, so the perceived displacement

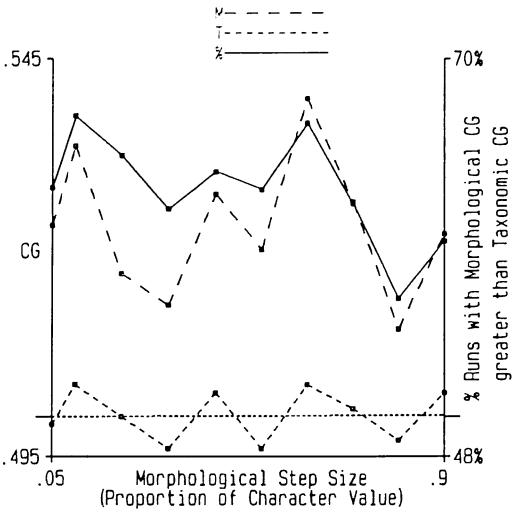

FIG. 17— Effect of morphological step size on simulation results. Despite variation in results, no clear, systematic effect is observed.

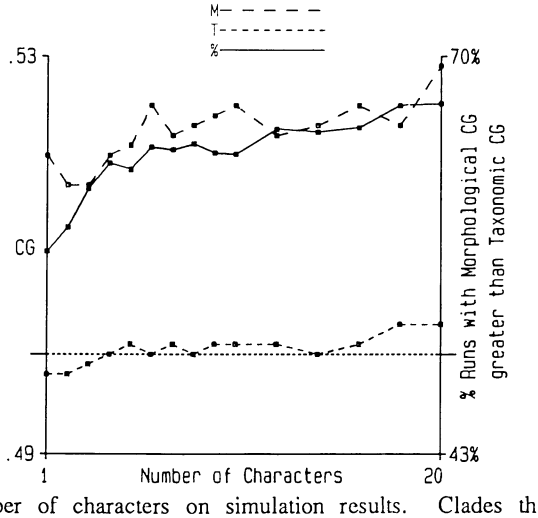

FIG. 18— Effect of number of characters on simulation results. Clades that diffuse through more dimensions in morphospace have stronger tendency to maintain morphological variety in the face of taxonomic extinction.

of morphological diversity later in time is unlikely to be an artifact of incomplete specification of morphology. The greater the dimensionality of the morphospace, the more extensively a clade diffuses and, therefore, the more likely it is to maintain morphological diversity as taxonomic diversity declines. This result is intuitively appealing, as random walks in one or two dimensions are bound to cross infinitely often, while random walks of higher dimensionality have a non-zero probability of never meeting (Feller, 1968, p. 360).

DISCUSSION

The sensitivity analysis demonstrates the robustness of the suggested pattern that morphological *CG*s tend to be higher than taxonomic *CG*s for randomly evolving clades. The two factors that have a substantial effect on this pattern are the number of morphological characters and the duration of the clade. Because very short-lived clades have not yet diffused extensively through morphospace, we cannot expect them to exhibit this pattern. If we take speciation and extinction rates to be 0.1, then fully half of all randomly evolving clades are expected to suffer total extinction in 10 million years or less (Raup, 1985, equation A7). Yet we commonly study clades enduring tens if not hundreds of millions of years. Consider the Blastoidea, which endured some 220 million years. If speciation and extinction rates were each equal to 0.2 (Horowitz et al., 1985), the probability that the clade would have endured this long with time-homogeneous branching and extinction is less than 0.03 (Raup, 1985, equation A11). The mere fact that we study a clade over some substantial history suggests that it was extraordinarily lucky, that speciation rates were higher than extinction rates, or that there was some non-randomness in its evolution, perhaps the opening of a new adaptive zone. While many of us would tend to favor the last explanation, the possibility of blind luck should not be discounted. Because every species is, in essence, the founder of a clade, there are scores of millions of trials from which to pick a few lucky clades that happen to endure longer than a few million years.

This study has analyzed a single aspect of clade shape. One problem with using the center of gravity is that there is in a sense a bias (inherent in a time scale of equal-length increments) toward symmetry. Clades of very different shape can all have the same *CG*, so information is lost. It is for this reason that I have focused on the *difference* between morphological and taxonomic *CG*s. Assessing the uniformity (*sensu* Gould et al., 1977) might allow greater resolution in comparing morphological and taxonomic diversity.

It was shown above, and by Kitchell and MacLeod (1988), that taxonomic *CG* tends to fall around 0.5. This initially seems to disagree with Gould et al. (1977), who found that *CG* increased with branching probability. However, Gould et al. (1977) were able to explain their result, partly by reference to their use of the "damped equilibrium" model.

How do the simulations relate to the history of the Blastoidea? I do mean to suggest that forward displacement of morphological diversity is a possibility in the blastoids, that this pattern is the expected result of a non-directional branching process, and that extinction acting randomly with respect to morphology is an important cause of this pattern (in the model). However, I wish to stop far short of suggesting that the model *explains* the evolution of the Blastoidea or any other clade, that forward displacement of morphological diversity is the rule in real clades, or that extinction in the Blastoidea or any other clade is random with respect to morphology. As has been stressed by previous authors, the use of stochastic models does not imply belief in randomness at all scales. Rather, it reflects the idea that smaller-scale events may be quite deterministic, but so multifarious in their causes, that they are not fully predictable when viewed at a larger scale (Raup et al., 1973).

The class Blastoidea was chosen for its monophyly and systematic treatment, the quality of its fossil record, and the measurability of its morphology. Nevertheless, it may be argued that the Blastoidea are not representative of clades on the whole. The only way to assess the generality of the proposed discrepancy between morphological and taxonomic central tendency is to study the problem in many clades. The Trilobita seem to agree with the pattern (Foote, 1991), and R. Wood (personal communication) suspects that the Archaeocyatha may do so as well. On the other hand, preliminary analysis of Raup's coiling parameters for 405 ammonoid genera suggests that morphological diversity is displaced backward in time relative to generic richness. Assessment of the pattern in ammonoids is hampered by the fact that only planispiral ammonoids are included.

The importance of the distinction between taxonomic richness and morphological diversity is well recognized. However, the former has generally been more objectively quantified, while the latter is assessed more subjectively and anecdotally. By appropriate choice of morphospace it should be possible to obtain nearly equally reliable estimates of morphological variety and taxonomic richness. Finally, neither morphological variety nor taxonomic richness should be considered the "right" measure of diversity. In general it is the comparison between the two aspects of diversity, not the choice of one over the other, that is of interest. Large-scale patterns in the two aspects of diversity may not differ appreciably, in which case the explicit consideration of both serves to strengthen our conclusions. On the other hand, there are cases, as with Carboniferous versus Permian blastoids, where consideration of both aspects of diversity might lead us to different conclusions than would reliance on a single measure of diversity. Modification of our perception of life's history by incorporation of more complete information can only be considered a step in the right direction.

SUMMARY AND CONCLUSIONS

(1) Conservative arrangement of major thecal plates enables identification of a set of homologous landmarks that encompass important aspects of morphological variation in the blastoid theca.

(2) Blastoids provide a good case study for comparing secular patterns in morphological and taxonomic diversity because they are readily measurable, strictly monophyletic, extinct, stable in their systematic treatment, diverse, and long-lived.

(3) Rarefaction of samples enables comparison of the extent of morphospace occupation relatively independently of sample size.

(4) Although the Silurian and Ordovician represent times of low taxonomic richness and morphological diversity, the correspondence between these two aspects of diversity is not perfect. Most notably, the Lower Carboniferous represents the time of maximal generic richness, whereas morphological diversity is relatively low in Lower Carboniferous blastoids. Conversely, generic richness in the Permian is one third that of the Lower Carboniferous, but the Permian represents the time of maximal morphological diversity in blastoids. Whereas generic richness increases until the Lower Carboniferous and then decreases, morphological diversity seems to increase until the extinction of the Blastoidea.

(5) Descriptors of clade shape can be applied to the history of morphological as well as taxonomic diversity. There appears to be a significant difference in the central tendency of the two aspects of diversity, with morphological diversity more heavily concentrated in the latter half of the blastoids' history than is generic richness.

(6) The biogeographic restriction of Permian blastoids may allow morphological diversity to be better represented than taxonomic diversity. However, artificial degradation of the Devonian, Carboniferous, and Permian records, each to a single geographic region and narrow temporal window, yields diversity patterns that are broadly similar to global patterns.

(7) The use of a null branching model suggests that a large-scale asymmetry in a clade's history–the forward displacement of morphological versus taxonomic diversity–may result from processes that are non-directional and time-homogeneous at a smaller scale. The important factors contributing to the forward displacement of morphological diversity are random diffusion through morphospace and the randomness of extinction with respect to morphology. These factors allow morphological diversity to decrease only slightly, and even to increase, despite substantial decreases in taxonomic richness.

(8) The results of simulations are robust in the face of variation in most biologically significant parameters. Only the duration of a clade and the number of morphological characters have substantial effects. The longer-lived a simulated clade and the more thoroughly documented its morphology, the more likely it is to exhibit forward displacement of morphological diversity relative to taxonomic richness. In other words, the more time a clade has

had to spread through morphospace, and the more directions in which it has been able to spread, the more difficult it is to reduce its morphospace occupation by taxonomic extinction.

(9) The apparent agreement between the histories of blastoids and simulated clades must be interpreted with extreme caution. Although there are suggestions that other real clades may show a pattern similar to the blastoids, much more evidence is needed before we can decide whether the greater asymmetry of morphological versus taxonomic diversity histories represents an empirical generality. Even if this proves to be the case, it would not demonstrate that the null model employed adequately explains the pattern.

ACKNOWLEDGMENTS

I thank F. J. Collier and J. W. M. Thompson for access to blastoids at the US National Museum of Natural History. B. Miljour drafted Figure 1. B. E. Bodenbender and D. C. Fisher gave me technical assistance with measurement; W. A. Ericson (Statistics Department, University of Michigan) provided the solution of Appendix C for the comparison of morphological and taxonomic *CG*s; and J. J. Sepkoski, Jr. first suggested that I use the range-through method for investigating morphological diversity. I thank C. E. Badgley, B. E. Bodenbender, L. S. Collins, T. M. Collins, D. C. Fisher, P. D. Gingerich, N. MacLeod, D. B. Macurda, Jr., D. M. Raup, G. R. Smith, R. E. Tabachnick, and M. L. Zelditch for discussion. D. C. Fisher, N. L. Gilinsky, A. S. Horowitz, and F. K. McKinney made many helpful suggestions on the text. F. L. Bookstein kindly provided a preprint of his forthcoming book. Acknowledgment is made to the Donors of The Petroleum Research Fund, administered by the American Chemical Society, for support of this research.

LITERATURE CITED

ARENDT, Yu. A., A. BREIMER, and D. B. MACURDA, JR. 1968. A new blastoid fauna from the Lower Namurian of North Kazachstan (USSR). Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B, 71: 159-174.

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

BAMBACH, R. K. 1977. Species richness in marine benthic habitats through the Phanerozoic. Paleobiology, 3: 152-167.

BOOKSTEIN, F. L. 1991. Morphometric Tools for Landmark Data. Cambridge University Press, New York (in press).

BREIMER, A. and D. B. MACURDA, JR. 1972. The phylogeny of the fissiculate blastoids. Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afdeling Natuurkunde, Erste Reeks, 26: 1-390.

BRIGGS, D. E. G. and R. A. FORTEY. 1989. The early radiation and relationships of the major arthropod groups. Science, 246: 241-243.

BROADHEAD, T. W. 1984. *Macurdablastus*, a middle Ordovician blastoid from the southern Appalachians. University of Kansas Paleontological Contributions, Paper 110: 1-10.

CAIN, A. J. 1977. Variation in the spire index of some coiled gastropod shells, and its evolutionary significance. Proceedings of the Royal Society of London, B277: 377-428.

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

EFRON, B. 1982. The Jackknife, the Bootstrap, and Other Resampling Plans. Society for Industrial and Applied Mathematics, Philadelphia, 93 pp.

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

FAY, R. O. and J. WANNER. 1967. Systematic Descriptions. Pp. S396-S455, in R. C. Moore (ed.), Treatise on Invertebrate Paleontology, Part S. Echinodermata 1. Geological Society of America and The University of Kansas, Boulder, Colorado and Lawrence, Kansas, 650 pp.

FELLER, W. 1968. An Introduction to Probability Theory and Its Applications (Third edition, revised). John Wiley and Sons, New York, 509 pp.

FISHER, D. C. 1986. Progress in organismal design. Pp. 99-117, in D. M. Raup and D. Jablonski (eds.), Patterns and Processes in the History of Life. Dahlem Konferenzen 1986, Springer-Verlag, Berlin, 447 pp.

FOOTE, M. 1988. Survivorship analysis of Cambrian and Ordovician trilobites. Paleobiology, 14: 258-271.
———. 1990. Nearest-neighbor analysis of trilobite morphospace. Systematic Zoology, 39: 371-382.
———. 1991. Morphologic patterns of diversification: examples from trilobites. Palaeontology, 34 (in press).
———. 1992. Rarefaction analysis of morphological and taxonomic diversity. Paleobiology, 18 (in press).
FORTEY, R. A. and R. M. OWENS. 1990. Trilobites. Pp. 121-142, in K. J. McNamara (ed.), Evolutionary Trends. University of Arizona Press, Tucson, 368 pp.
GINGERICH, P. D. 1983. Rates of evolution: effects of time and temporal scaling. Science, 222: 159-161.
GOULD, S. J. 1988. Trends as changes in variance: a new slant on progress and directionality in evolution. Journal of Paleontology, 62: 319-329.
———. 1989. Wonderful Life: The Burgess Shale and the Nature of History. W. W. Norton and Company, New York, 347 pp.
———, N. L. GILINSKY, and R. Z. GERMAN. 1987. Asymmetry of lineages and the direction of evolutionary time. Science, 236: 1437-1441.
———, D. M. RAUP, J. J. SEPKOSKI, JR., T. J. M. SCHOPF, and D. S. SIMBERLOFF. 1977. The shape of evolution: a comparison of real and random clades. Paleobiology, 3: 23-40.
HALDANE, J. B. S. 1949. Suggestions as to the quantitative measurement of rates of evolution. Evolution, 3: 51-56.
HARLAND, W. B., R. L. ARMSTRONG, A. V. COX, L. E. CRAIG, A. G. SMITH, and D. G. SMITH. 1990. A Geologic Time Scale 1989. Cambridge University Press, New York, 263 pp.
HARRINGTON, H. J. 1959. Classification. Pp. O145-O170, in R. C. Moore (ed.), Treatise on Invertebrate Paleontology, Part O. Arthropoda 1. Geological Society of America and University of Kansas Press, Boulder Colorado and Lawrence, Kansas, 560 pp.
HOROWITZ, A. S., R. F. BLAKELY, and D. B. MACURDA, JR. 1985. Taxonomic survivorship within the Blastoidea (Echinodermata). Journal of Paleontology, 59: 543-550.
HOROWITZ, A. S., D. B. MACURDA, JR., and J. A. WATERS. 1986. Polyphyly in the Pentremitidae (Blastoidea, Echinodermata). Geological Society of America Bulletin, 97: 156-161.
JAANUSSON, V. 1981. Functional thresholds in evolutionary progress. Lethaia, 14: 251-260.
KENDALL, M. G. and A. STUART. 1963. The Advanced Theory of Statistics. Volume I (Second edition). Charles Griffin and Company, London, 433 pp.
KITCHELL, J. A. and N. MACLEOD. 1988. Macroevolutionary interpretations of symmetry and synchroneity in the fossil record. Science, 240: 1190-1193.
MACURDA, D. B., JR. 1966. The ontogeny of the Mississippian blastoid *Orophocrinus*. Journal of Paleontology, 40: 92-124.
———. 1977a. *Arcuoblastus* and *Decemoblastus*, two new Mississippian blastoid genera from the Burlington Limestone, Iowa. Journal of Paleontology, 51: 1201-1214.
———. 1977b. Two Carboniferous blastoids from Scotland. Palaeontology, 20: 225-236.
———. 1978. The Mississippian blastoid genus *Cribroblastus*. Journal of Paleontology, 52: 1288-1293.
———. 1983. Systematics of the fissiculate Blastoidea. Papers on Paleontology, Museum of Paleontology, University of Michigan, no. 22: 1-291.
——— and R. H. MAPES. 1982. The enigma of Pennsylvanian blastoids. Third North American Paleontological Convention, Proceedings, 2: 343-345.
RAUP, D. M. 1966. Geometric analysis of shell coiling: general problems. Journal of Paleontology, 40: 1178-1190.
———. 1967. Geometric analysis of shell coiling: coiling in ammonoids. Journal of Paleontology, 41: 43-65.
———. 1975a. Taxonomic survivorship curves and Van Valen's Law. Paleobiology, 1: 82-96.
———. 1975b. Taxonomic diversity estimation using rarefaction. Paleobiology, 1: 333-342.
———. 1978. Cohort analysis of generic survivorship. Paleobiology, 4: 1-16
———. 1979. Biases in the fossil record of species and genera. Carnegie Museum of Natural History Bulletin, 13: 85-91.
———. 1985. Mathematical models of cladogenesis. Paleobiology, 11: 42-52.
———. 1988. Testing the fossil record for evolutionary progress. Pp. 293-317, in M. H. Nitecki (ed.), Evolutionary Progress. University of Chicago Press, Chicago, 354 pp.
——— and S. J. GOULD. 1974. Stochastic simulation and evolution of morphology—towards a nomothetic paleontology. Systematic Zoology, 23: 305-322.
———, S. J. GOULD, T. J. M SCHOPF, and D. S. SIMBERLOFF. 1973. Stochastic models of phylogeny and the evolution of diversity. Journal of Geology, 81: 525-542.
——— and J. J. SEPKOSKI, JR. 1988. Testing for periodicity of extinction. Science, 241: 94-96.
RUNNEGAR, B. 1987. Rates and modes of evolution in the Mollusca. Pp. 39-60, in K. S. W. Campbell and M. F. Day (eds.), Rates of Evolution. Allen and Unwin, London, 314 pp.
SANDERS, H. L. 1968. Marine benthic diversity: a comparative study. American Naturalist, 102: 243-282.
SAUNDERS, W. B. and A. R. H. SWAN. 1984. Morphology and morphologic diversity of mid-Carboniferous (Namurian) ammonoids in time and space. Paleobiology, 10: 195-228.
SEPKOSKI, J. J., JR. 1984. A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. Paleobiology, 10: 246-267.
———, R. K. BAMBACH, D. M. RAUP, and J. W. VALENTINE. 1981. Phanerozoic marine diversity and the fossil record. Nature, 293: 435-437.
SIMPSON, G. G. 1953. The Major Features of Evolution. Columbia University Press, New York, 434 pp.

SPRINKLE, J. 1973. Morphology and evolution of blastozoan echinoderms. Special Publication, Museum of Comparative Zoology, Harvard University. Cambridge, Massachusetts, 283 pp.
STANLEY, S. M. 1973. An explanation for Cope's Rule. Evolution, 27: 1-26
———. 1979. Macroevolution: Pattern and Process. W. H. Freeman, San Francisco, 332 pp.
———, P. W. SIGNOR III, S. LIDGARD, and A. F. KARR. 1981. Natural clades differ from "random" clades: simulations and analyses. Paleobiology, 7: 115-127.
STIGLER, S. M. and M. J. WAGNER. 1987. A substantial bias in nonparametric tests for periodicity in geophysical data. Science, 238: 940-945.
STRIMPLE, H. L. and R. H. MAPES. 1977. A new Upper Pennsylvanian fissiculate blastoid from Texas. Journal of Paleontology, 51: 357-362.
STUBBLEFIELD, C. J. 1960. Evolution in trilobites. Quarterly Journal of the Geological Society of London, 115: 145-162.
SWAN, A. R. H. and W. B. SAUNDERS. 1987. Function and shape in late Paleozoic (mid-Carboniferous) ammonoids. Paleobiology, 13: 297-311.
TABACHNICK, R. E. and F. L. BOOKSTEIN. 1990. The structure of individual variation in Miocene *Globorotalia*. Evolution, 44: 416-434.
VALENTINE, J. W. 1969. Patterns of taxonomic and ecological structure of the shelf benthos during Phanerozoic time. Palaeontology, 12: 684-709.
———. 1986. Fossil record of the origin of Baupläne and its implications. Pp. 209-222, in D. M. Raup and D. Jablonski (eds.), Patterns and Processes in the History of Life. Springer-Verlag, Berlin, 447 pp.
VAN VALEN, L. M. 1973a. A new evolutionary law. Evolutionary Theory, 1: 1-30.
———. 1973b. Are categories in different phyla comparable? Taxon, 22: 333-373.
———. 1974. Multivariate structural statistics in natural history. Journal of Theoretical Biology, 45: 235-247.
———. 1990. Levels of selection in the early Cenozoic radiation of mammals. Evolutionary Theory, 9: 171-180.
WATERS, J. A. 1988. The evolutionary palaeoecology of the Blastoidea. Pp. 215-233, in C. R. C. Paul and A. B. Smith (eds.), Echinoderm Phylogeny and Evolutionary Biology. Clarendon Press, Oxford, 373 pp.
———, A. S. HOROWITZ, and D. B. MACURDA, JR. 1985. Ontogeny and phylogeny of the Carboniferous blastoid *Pentremites*. Journal of Paleontology, 59: 701-712.
WHITTINGTON, H. B. 1954. Status of Invertebrate Paleontology, 1953. VI. Arthropoda: Trilobita. Bulletin of the Museum of Comparative Zoology, Harvard University, 112: 193-200.
———. 1966. Phylogeny and distribution of Ordovician trilobites. Journal of Paleontology, 40: 696-737.
YOCHELSON, E. L. 1978. An alternative approach to the interpretation of the phylogeny of ancient mollusks. Malacologia, 17: 165-191.
———. 1979. Early radiation of Mollusca and molluscs-like groups. Pp. 323-358, in M. R. House (ed.), The Origin of Major Invertebrate Groups. Academic Press, London, 515 pp.

APPENDIX A. LIST OF SPECIMENS MEASURED

Genus and species	Museum number[1]
Ordovician	
Macurdablastus uniplicatus (Holotype)	USNM 359645
Silurian	
Decaschisma pulchellum	UM 61803
Polydeltoideus enodatus (Holotype)	UM 37805
Polydeltoideus enodatus	UM 47560
Troosticrinus ?reinwardti	USNM 455895
Troosticrinus? concinna (Holotype)	USNM 160573
Devonian	
Caryoblastus bohemicus	UM 66125
Cordyloblastus eifelensis (Plesiotype)	USNM S-5086
Cordyloblastus wachsmuthi	USNM S-6147
Cryptoschisma schultzii	UM 60602
Cryptoschisma schultzii	UM 60605
Cryptoschisma schultzii	UM 60614
Devonoblastus leda	UM 48582
Devonoblastus sp.	UM 47556
Devonoblastus whiteavesi (Topotype)	UM 35036
Elaeacrinus verneuili	USNM 455894
Eleutherocrinus cassedayi	UM 57425
Eleutherocrinus sp.	USNM S-3671
Heteroschisma alatum	UM 62256
Heteroschisma alatum	UM 62257
Heteroschisma alternatum	UM 62264
Heteroschisma canadense	UM 54117
Heteroschisma subtruncatum	UM 62294
Hyperoblastus alveata (Hypotype)	UM 37809
Hyperoblastus filosa	USNM 455889
Hyperoblastus sp.	USNM 455890
Leptoschisma lorae (Plesiotype)	USNM 160709
Nucleocrinus elegans	UM 59997
Nucleocrinus elegans (Hypotype)	UM 66130
Nucleocrinus melloniformis	UM 57840
Nucleocrinus obovatus (Hypotype)	UM 1262
Nucleocrinus sp.	USNM 455893
Pentremitidea archiaci	UM 60625
Pentremitidea archiaci	UM 62252
Pentremitidea pailleti	USNM 455891
Pleuroschisma lycorias (Plesiotype)	USNM 160715
Lower Carboniferous	
Codaster acutus	UM 60646
Codaster acutus	USNM S-6137
Cribroblastus incisus (Holotype)	USNM S-3721
Cryptoblastus melo	USNM S-6154
Cryptoblastus pisum	USNM S-5345
Decemoblastus melonoides (Plesiotype)	USNM S-5358
Diploblastus glaber	UM 57858
Globoblastus norwoodi	UM 59928
Globoblastus norwoodi	UM 66127
Granatocrinus shumardi	USNM 37712
Hadroblastus convexus (Plesiotype)	USNM 248248
Hadroblastus whitei	UM 59712
Hadroblastus whitei	UM 59713
Katoblastus püzos (Plesiotype)	USNM S-3230
Koryschisma parvum (Syntype)	UM 62304
Lophoblastus neglectus	USNM S-6155
Mesoblastus crenulatus (Plesiotype)	USNM S-3775
Metablastus varsoviensis	USNM S-6146
Metablastus wortheni	USNM S-6145
Monadoblastus sp.	UM 66128
Monadoblastus sp.	UM 66129
Monadoblastus sp.	UM 66132
Orbitremites ellipticus	USNM S-6135
Orophocrinus catactus (Plesiotype)	USNM 162411
Orophocrinus conicus	USNM S-6151
Orophocrinus stelliformis (Neotype)	USNM S-4961
Orophocrinus stelliformis	USNM S-6150
Orophocrinus verus (Plesiotype)	USNM S-3237
Pentremites cervinus	USNM S-3290
Pentremites conoideus	USNM S-6143
Pentremites elongatus	USNM S-6142
Pentremites gemmiformis	USNM 455892
Pentremites godoni	UM 54119
Pentremites godoni	UM 56534
Pentremites godoni	UM 66126
Pentremites obesus	USNM S-6139
Pentremites pulchellus	UM 66131
Pentremites pyriformis	USNM S-6141
Pentremites robustus	USNM S-6140
Pentremites sulcatus	USNM S-6144
Pentremites symmetricus	USNM S-3583
Pentremites tulipaeformis	USNM 93626
Phaenoblastus caryophyllatus	USNM S-6148
Phaenoschisma conicum (Plesiotype)	USNM 160757
Phaenoschisma laeviculum	UM 58665
Poroblastus granulosus	USNM S-6149
Schizoblastus moorei (Plesiotype)	USNM 160642
Schizoblastus sayi	USNM S-6152
Tanaoblastus roemeri	USNM S-6153
Tricoelocrinus bipyramidalis	USNM S-6156
Permian	
Angioblastus boliviensis (Holotype)	USNM 160591
Angioblastus variabilis (Plesiotype)	USNM 248354
Angioblastus wanneri	UM 60668
Angioblastus wanneri	UM 60669
Angioblastus wanneri	UM 60673
Calycoblastus tricavatus[2]	UM 58190
Deltoblastus batheri	UM 51213
Deltoblastus permicus	UM 51547
Deltoblastus sp.	UM 66133
Deltoblastus verbeeki	UM 51211
Nannoblastus pyramidatus	UM 62315
Nannoblastus pyramidatus	UM 62331
Nannoblastus pyramidatus	UM 62336
Orbitremites malaianus	UM 58232
Pterotoblastus brevialatus (Plesiotype)	USNM 248367
Pterotoblastus gracilis (Plesiotype)	USNM 248327
Pterotoblastus gracilis (Plesiotype)	USNM 248336
Timoroblastus coronatus	UM 59745
Timoroblastus coronatus	UM 59754
Timoroblastus coronatus	UM 59756
Timoroblastus coronatus	UM 59758
Timoroblastus coronatus	UM 59760
Timoroblastus coronatus	UM 59765
Timoroblastus coronatus	UM 59772B
Timoroblastus coronatus	UM 59775E
Timoroblastus coronatus	UM 60762
Timoroblastus coronatus	USNM S-6138

[1] Abbreviations: UM, University of Michigan Museum of Paleontology; USNM, United States National Museum of Natural History.

[2] The base of this specimen is incomplete. In order to obtain measurements, the base was reconstructed with modelling clay, based on published figures. This procedure does not bias the Permian toward artificially high morphological diversity, since Permian variability remains high when this specimen is omitted from analysis, as in Fig. 10.

APPENDIX B. AVERAGE CARTESIAN COORDINATES FOR SPECIES USED IN THIS STUDY

[Table includes facing page and continues on following pages]

N is number of specimens measured for each species. Coordinates are for landmarks (Fig. 1) in transformed coordinate system. Landmarks 1 and 7 are reference coordinates. See text for explanation.

Genus and species	N	Landmark 2			Landmark 3		
		x	y	z	x	y	z
Ordovician							
Macurdablastus uniplicatus	1	0.2337	-0.2025	0.2211	-0.0196	-0.4270	0.3710
Silurian							
Decaschisma pulchellum	1	0.1106	-0.0876	0.3612	0.0079	-0.1423	0.4310
Polydeltoideus enodatus	2	0.1047	-0.0857	0.5509	0.0302	-0.1507	0.6592
Troosticrinus ?reinwardti	1	0.0932	-0.0582	0.4390	0.0213	-0.1121	0.4842
Troosticrinus? concinna	1	0.1122	-0.0786	0.3674	0.0191	-0.1711	0.4168
Devonian							
Caryoblastus bohemicus	1	0.1770	-0.1443	0.3509	0.0344	-0.2684	0.4145
Cordyloblastus eifelensis	1	0.1496	-0.1042	0.4257	0.0302	-0.1973	0.4688
Cordyloblastus wachsmuthi	1	0.1340	-0.0814	0.2371	0.0251	-0.1746	0.2900
Cryptoschisma schultzii	3	0.1729	-0.1239	0.4950	0.0453	-0.2372	0.5793
Devonoblastus leda	1	0.1386	-0.0663	0.0500	0.0370	-0.2060	0.0735
Devonoblastus sp.	1	0.1209	-0.0639	0.0986	0.0397	-0.2164	0.1533
Devonoblastus whiteavesi	1	0.0998	-0.0523	0.0876	0.0253	-0.1645	0.1230
Elaeacrinus verneuili	1	0.0497	-0.0404	-0.0395	0.0009	-0.1001	-0.0289
Eleutherocrinus cassedayi	1	0.1052	-0.0214	0.0962	0.0888	-0.1291	0.1476
Eleutherocrinus sp.	1	0.0881	-0.0381	0.0550	0.0630	-0.1240	0.0786
Heteroschisma alatum	2	0.1727	-0.0999	0.3846	0.0245	-0.2181	0.4331
Heteroschisma alternatum	1	0.1322	-0.0964	0.2732	0.0372	-0.1960	0.3082
Heteroschisma canadense	1	0.1777	-0.1156	0.3963	0.0366	-0.2084	0.4296
Heteroschisma subtruncatum	1	0.1496	-0.0938	0.3658	0.0365	-0.1863	0.4094
Hyperoblastus alveata	1	0.1133	-0.0717	0.1661	0.0413	-0.1634	0.2032
Hyperoblastus filosa	1	0.1247	-0.0658	0.1398	0.0336	-0.1650	0.1907
Hyperoblastus sp.	1	0.1606	-0.1103	0.2468	0.0274	-0.2260	0.3081
Leptoschisma lorae	1	0.1390	-0.0902	0.4041	0.0364	-0.1534	0.4685
Nucleocrinus elegans	2	0.0594	-0.0369	-0.0109	0.0074	-0.1217	-0.0288
Nucleocrinus melloniformis	1	0.0624	-0.0267	-0.0081	0.0250	-0.0779	-0.0259
Nucleocrinus obovatus	1	0.0306	-0.0211	-0.0036	0.0135	-0.0438	-0.0123
Nucleocrinus sp.	1	0.0612	-0.0228	-0.0430	0.0240	-0.0913	-0.0559
Pentremitidea archiaci	2	0.1231	-0.1037	0.4403	0.0215	-0.1906	0.5350
Pentremitidea pailleti	1	0.1210	-0.0928	0.5207	0.0475	-0.1556	0.6105
Pleuroschisma lycorias	1	0.1035	-0.0670	0.3511	0.0042	-0.1253	0.4090
Lower Carboniferous							
Codaster acutus	2	0.3370	-0.2281	0.2590	0.0716	-0.4598	0.4481
"Cribroblastus" incisus	1	0.0887	-0.0467	-0.0393	0.0147	-0.1491	-0.0524
Cryptoblastus melo	1	0.0529	-0.0333	-0.0170	0.0019	-0.1034	-0.0254
Cryptoblastus pisum	1	0.0975	-0.0381	-0.0209	0.0337	-0.1478	-0.0799
Decemoblastus melonoides	1	0.0655	-0.0266	0.0044	0.0218	-0.1131	0.0182
Diploblastus glaber	1	0.1840	-0.1324	0.1043	0.0470	-0.3239	0.1762
Globoblastus norwoodi	2	0.2190	-0.1009	-0.1215	0.1232	-0.2538	-0.1882
Granatocrinus shumardi	1	0.0471	-0.0241	0.0087	0.0204	-0.1118	-0.0090
Hadroblastus convexus	1	0.3455	-0.2004	0.3322	0.1350	-0.4267	0.4389
Hadroblastus whitei	2	0.2255	-0.1434	0.1453	0.0510	-0.3406	0.2237
Katoblastus püzos	1	0.1671	-0.0790	0.0702	0.0434	-0.2611	0.1766
Koryschisma parvum	1	0.2206	-0.1656	0.3777	-0.0128	-0.3203	0.5039
Lophoblastus neglectus	1	0.1129	-0.0583	0.0170	0.0441	-0.2018	0.0703

APPENDIX B. [Continued]

Landmark 4			Landmark 5			Landmark 6			Landmark 8		
x	y	z	x	y	z	x	y	z	x	y	z
0.4145	0.0000	0.3782	0.0093	-0.1909	1.0661	0.2630	0.0473	1.0538	0.5394	-0.7038	1.1269
0.1663	0.0000	0.4203	0.0062	-0.1136	0.9704	0.1491	0.0077	0.9623	0.1852	-0.1618	0.8060
0.1725	0.0000	0.6600	0.0237	-0.1669	1.0160	0.1839	-0.0159	1.0244	0.1700	-0.1551	0.8864
0.1247	0.0000	0.4790	0.0268	-0.1024	1.0246	0.1232	-0.0027	1.0275	0.1381	-0.0899	0.8882
0.1683	0.0000	0.4184	0.0170	-0.1949	0.9459	0.1899	-0.0336	0.9490	0.1752	-0.1793	0.7781
0.2780	0.0000	0.4007	0.0272	-0.1762	1.1070	0.2346	0.0165	1.0943	0.3238	-0.2922	0.7308
0.2105	0.0000	0.4559	0.0244	-0.1018	1.0191	0.1386	0.0171	1.0161	0.2708	-0.2283	0.7730
0.1810	0.0000	0.2782	0.0222	-0.1098	1.0289	0.1662	0.0389	1.0126	0.2442	-0.2237	0.4227
0.2617	0.0000	0.5682	0.0455	-0.2819	0.9747	0.3131	-0.0189	0.9857	0.2619	-0.2388	0.9010
0.2225	0.0000	0.1126	0.0610	-0.2341	0.8631	0.2445	0.0008	0.9014	0.2813	-0.2372	0.2339
0.1879	0.0000	0.1530	0.0564	-0.1761	0.9633	0.2321	0.0260	0.9471	0.2697	-0.2414	0.2793
0.1504	0.0000	0.1223	0.0384	-0.1732	0.8959	0.2026	0.0055	0.8954	0.1978	-0.1801	0.1854
0.0913	0.0000	-0.0310	-0.0041	-0.2377	0.0962	0.2138	-0.0555	0.0721	0.0882	-0.1170	-0.0391
0.1134	0.0000	0.0994	0.1257	-0.1513	0.9737	0.2195	0.0790	0.9549	0.2419	-0.1049	0.2852
0.1154	0.0000	0.0787	0.0820	-0.1623	0.9604	0.2238	0.0295	0.9538	0.2314	-0.1477	0.1642
0.2154	0.0000	0.4146	0.0336	-0.2023	1.0221	0.2340	0.0008	0.9994	0.2508	-0.2271	0.8282
0.1727	0.0000	0.3038	0.0493	-0.2624	0.9171	0.2889	-0.0039	0.8973	0.2477	-0.2168	0.7808
0.2166	0.0000	0.4267	0.0443	-0.1893	1.0082	0.2267	0.0045	1.0086	0.2468	-0.2023	0.8811
0.2007	0.0000	0.3851	0.0506	-0.1928	1.0118	0.2442	-0.0018	1.0125	0.2392	-0.1916	0.7743
0.1501	0.0000	0.1986	0.0297	-0.1048	1.0583	0.1275	0.0088	1.0450	0.2062	-0.1594	0.2699
0.1695	0.0000	0.1763	0.0368	-0.1418	1.0280	0.1701	0.0049	1.0136	0.2414	-0.2026	0.3143
0.2322	0.0000	0.3045	0.0207	-0.1141	1.0456	0.1438	-0.0119	1.0410	0.2602	-0.2453	0.5026
0.1771	0.0000	0.4514	0.0169	-0.1514	1.0294	0.1608	0.0046	1.0180	0.1938	-0.1814	0.8225
0.1003	0.0000	-0.0124	0.0516	-0.3160	0.1225	0.3154	-0.0387	0.1284	0.2413	-0.2277	0.0529
0.0852	0.0000	-0.0299	0.0616	-0.2342	0.0935	0.2490	0.0050	0.0945	0.1569	-0.1303	-0.0337
0.0409	0.0000	-0.0046	0.0331	-0.1538	0.1123	0.1457	0.0019	0.1100	0.1013	-0.0785	-0.0013
0.0828	0.0000	-0.0604	0.0349	-0.1665	-0.0485	0.1700	-0.0071	-0.0539	0.1657	-0.1401	-0.0720
0.2059	0.0000	0.5239	0.0206	-0.1318	1.0264	0.1601	0.0117	1.0240	0.2289	-0.2128	0.9007
0.1710	0.0000	0.6086	0.0211	-0.0839	1.0202	0.1198	0.0168	1.0182	0.1781	-0.1336	0.9287
0.1531	0.0000	0.3931	0.0073	-0.2054	1.0058	0.2372	-0.0280	0.9988	0.1458	-0.1444	0.7237
0.4736	0.0000	0.4302	0.0688	-0.3751	0.9717	0.4049	-0.0122	0.9837	0.3112	-0.2682	0.9557
0.1421	0.0000	-0.0694	0.0427	-0.2518	1.0031	0.3015	0.0271	0.9948	0.2303	-0.2292	-0.0681
0.0973	0.0000	-0.0138	0.0348	-0.1880	0.9815	0.2320	0.0080	0.9573	0.1267	-0.1162	-0.0402
0.1478	0.0000	-0.0730	0.0882	-0.3937	0.9099	0.4531	0.0023	0.8921	0.2058	-0.1624	-0.1309
0.0969	0.0000	0.0240	0.0855	-0.2772	0.9020	0.2861	-0.0047	0.9269	0.0946	-0.0963	-0.0070
0.3506	0.0000	0.1918	0.0491	-0.3998	0.9282	0.4948	0.0110	0.8795	0.4276	-0.4168	0.3794
0.2764	0.0000	-0.1980	0.0848	-0.2382	1.0243	0.3163	0.1239	1.0059	0.4069	-0.2408	-0.3737
0.1241	0.0000	0.0044	0.0714	-0.2404	0.9169	0.2911	0.0223	0.8977	0.2025	-0.1734	0.0215
0.4684	0.0000	0.4180	0.1260	-0.4209	0.9298	0.4944	0.0325	0.9084	0.3848	-0.2584	0.8939
0.3485	0.0000	0.2208	0.0567	-0.4127	0.7791	0.4443	-0.0167	0.7706	0.3609	-0.3424	0.5035
0.2420	0.0000	0.1653	0.0476	-0.3026	0.9095	0.3366	-0.0038	0.8905	0.3154	-0.2874	0.3877
0.3506	0.0000	0.4558	-0.0347	-0.2042	1.3788	0.3301	0.1107	1.2927	0.3515	-0.3924	0.9896
0.1984	0.0000	0.0613	0.0958	-0.3957	0.5991	0.4231	0.0022	0.5803	0.2576	-0.2089	0.1265

APPENDIX B (continued)

[*Table includes facing page*]

Genus and species	N	Landmark 2 x	Landmark 2 y	Landmark 2 z	Landmark 3 x	Landmark 3 y	Landmark 3 z
Mesoblastus crenulatus	1	0.1887	-0.0860	0.0207	0.0822	-0.3119	0.0500
Metablastus varsoviensis	1	0.0837	-0.0632	0.2546	-0.0131	-0.1310	0.2953
Metablastus wortheni	1	0.0812	-0.0605	0.2150	-0.0059	-0.1314	0.2678
Monadoblastus sp.	3	0.1785	-0.0890	0.0251	0.0557	-0.2928	0.0553
Orbitremites ellipticus	1	0.0659	-0.0420	-0.0088	0.0296	-0.1154	-0.0092
Orophocrinus catactus	1	0.2128	-0.1410	0.2124	0.0604	-0.3148	0.3093
Orophocrinus conicus	1	0.1713	-0.1039	0.3586	0.0424	-0.2236	0.4390
Orophocrinus stelliformis	2	0.1718	-0.1183	0.2293	0.0418	-0.2449	0.2659
Orophocrinus verus	1	0.1846	-0.1128	0.2130	0.0558	-0.2769	0.2719
Pentremites cervinus	1	0.1905	-0.1390	0.2131	0.0726	-0.2873	0.3207
Pentremites conoideus	1	0.1238	-0.0667	0.0459	0.0352	-0.1955	0.0631
Pentremites elongatus	1	0.0842	-0.0498	0.0649	0.0208	-0.1314	0.0934
Pentremites gemmiformis	1	0.1293	-0.0761	0.2095	0.0338	-0.1592	0.2988
Pentremites godoni	3	0.1548	-0.1007	0.1056	0.0556	-0.2567	0.1668
Pentremites obesus	1	0.1905	-0.1164	0.1193	0.0660	-0.2980	0.1766
Pentremites pulchellus	1	0.1623	-0.1001	0.1770	0.0551	-0.2429	0.2449
Pentremites pyriformis	1	0.1404	-0.1051	0.1782	0.0415	-0.2077	0.2502
Pentremites robustus	1	0.1629	-0.0952	0.1438	0.0579	-0.2270	0.1988
Pentremites sulcatus	1	0.1537	-0.1054	0.1185	0.0559	-0.2575	0.1584
Pentremites symmetricus	1	0.1059	-0.0810	0.1251	0.0235	-0.1964	0.1919
Pentremites tulipaeformis	1	0.1658	-0.0945	0.1161	0.0450	-0.2762	0.2220
Phaenoblastus caryophyllatus	1	0.1256	-0.1024	0.2684	0.0107	-0.1865	0.3291
Phaenoschisma conicum	1	0.2128	-0.1211	0.2871	0.0720	-0.2489	0.4059
Phaenoschisma laeviculum	1	0.1197	-0.0918	0.2583	0.0010	-0.1904	0.3337
Poroblastus granulosus	1	0.0658	-0.0567	-0.0028	-0.0133	-0.1199	-0.0115
Schizoblastus moorei	1	0.1299	-0.0574	0.0530	0.0528	-0.2262	0.0878
Schizoblastus sayi	1	0.0626	-0.0338	-0.0071	0.0261	-0.1142	0.0077
Tanaoblastus roemeri	1	0.1743	-0.1013	0.0458	0.0666	-0.2519	0.0857
Tricoelocrinus bipyramidalis	1	0.0905	-0.0723	0.2040	0.0054	-0.1464	0.2633
Permian							
Angioblastus boliviensis	1	0.3392	-0.2157	0.2454	0.0789	-0.3941	0.3985
Angioblastus variabilis	1	0.4484	-0.2524	0.0741	0.1096	-0.5752	0.2852
Angioblastus wanneri	3	0.3747	-0.2363	0.1527	0.1147	-0.4622	0.3417
Calycoblastus tricavatus	1	0.0874	-0.0652	0.1218	0.0107	-0.1436	0.1495
Deltoblastus batheri	1	0.0522	-0.0287	-0.0569	0.0181	-0.0786	-0.0882
Deltoblastus permicus	1	0.0672	-0.0339	-0.0304	0.0228	-0.0644	-0.0315
Deltoblastus sp.	1	0.0658	-0.0294	-0.0238	0.0288	-0.0874	-0.0455
Deltoblastus verbeeki	1	0.0473	-0.0429	-0.0369	0.0247	-0.0743	-0.0313
Nannoblastus pyramidatus	3	0.1753	-0.1227	0.3086	-0.0001	-0.2881	0.4084
Orbitremites malaianus	1	0.1905	-0.1015	0.0144	0.0797	-0.2644	0.0246
Pterotoblastus brevialatus	1	0.2768	-0.2189	0.2164	0.0294	-0.3994	0.3344
Pterotoblastus gracilis	2	0.2715	-0.1603	0.2947	0.0767	-0.3234	0.3788
Timoroblastus coronatus	10	0.4305	-0.2439	-0.0508	0.2546	-0.7944	-0.1804

APPENDIX B (continued)

Landmark 4			Landmark 5			Landmark 6			Landmark 8		
x	y	z	x	y	z	x	y	z	x	y	z
0.3076	0.0000	0.0175	0.0767	-0.2431	1.0623	0.2961	0.0612	1.0374	0.4410	-0.3289	0.0542
0.1206	0.0000	0.2827	-0.0041	-0.0974	0.9857	0.1164	-0.0260	0.9821	0.1106	-0.1431	0.7434
0.1159	0.0000	0.2684	0.0068	-0.1007	0.9961	0.1053	-0.0076	1.0011	0.1211	-0.1355	0.5941
0.3056	0.0000	0.0603	0.0795	-0.4174	0.8541	0.4865	-0.0035	0.8345	0.3610	-0.3279	0.0965
0.1172	0.0000	-0.0216	0.1101	-0.3755	0.5656	0.3897	0.0045	0.5616	0.1730	-0.1418	-0.0205
0.2890	0.0000	0.2953	0.0637	-0.2861	0.9544	0.3424	0.0181	0.9269	0.4284	-0.3376	0.7636
0.2275	0.0000	0.4356	0.0425	-0.2334	0.8640	0.2565	-0.0189	0.8453	0.2342	-0.2128	0.7199
0.2427	0.0000	0.2914	0.0604	-0.3067	0.9028	0.3325	-0.0205	0.8920	0.4247	-0.3832	0.5906
0.2652	0.0000	0.2632	0.0606	-0.2176	0.9779	0.2714	0.0074	0.9514	0.3637	-0.3050	0.6158
0.3037	0.0000	0.2957	0.0571	-0.3278	0.8490	0.3545	-0.0126	0.8471	0.3941	-0.3454	0.5292
0.2269	0.0000	0.0860	0.0401	-0.2735	0.5898	0.3104	-0.0166	0.5858	0.3008	-0.2688	0.1735
0.1296	0.0000	0.0913	0.0596	-0.2603	0.7311	0.2783	-0.0099	0.7225	0.1873	-0.1689	0.1389
0.1870	0.0000	0.2836	0.0351	-0.2261	0.8148	0.2526	-0.0179	0.8227	0.2222	-0.1921	0.4806
0.2626	0.0000	0.1701	0.0827	-0.3566	0.6348	0.3955	-0.0170	0.6376	0.3388	-0.2834	0.2604
0.3304	0.0000	0.1899	0.0936	-0.4095	0.8274	0.4395	0.0064	0.8180	0.4484	-0.3650	0.3075
0.2448	0.0000	0.2506	0.0846	-0.3183	0.7358	0.3427	-0.0111	0.7361	0.3396	-0.2714	0.3847
0.2158	0.0000	0.2528	0.0689	-0.2562	0.8242	0.2863	-0.0018	0.8280	0.2750	-0.2156	0.4975
0.2484	0.0000	0.1913	0.0888	-0.3366	0.7339	0.3665	-0.0163	0.7261	0.3473	-0.2746	0.2827
0.2695	0.0000	0.1682	0.0819	-0.3706	0.7886	0.3921	-0.0246	0.7497	0.3797	-0.3332	0.2811
0.1978	0.0000	0.2085	0.0415	-0.2437	0.7451	0.2683	-0.0204	0.7585	0.2358	-0.2208	0.3516
0.2784	0.0000	0.2015	0.0519	-0.3648	0.7456	0.3935	-0.0198	0.7310	0.3306	-0.2967	0.4236
0.1832	0.0000	0.3239	0.0503	-0.3050	0.9170	0.2968	-0.0127	0.9228	0.2368	-0.2009	0.5730
0.2924	0.0000	0.3835	0.0648	-0.2471	0.9871	0.2888	0.0198	0.9932	0.3107	-0.2587	0.8266
0.1912	0.0000	0.3280	0.0164	-0.2160	0.9204	0.2762	-0.0187	0.9200	0.1984	-0.1981	0.6804
0.1244	0.0000	-0.0148	-0.0425	-0.3973	0.5888	0.4139	-0.1089	0.5840	0.1074	-0.1555	-0.0320
0.2296	0.0000	0.0633	0.0830	-0.4632	0.5609	0.5200	-0.0313	0.5357	0.2982	-0.2491	0.1299
0.1080	0.0000	0.0095	0.0619	-0.2744	0.1959	0.2881	-0.0165	0.1886	0.1337	-0.1101	0.0486
0.2675	0.0000	0.0848	0.0856	-0.3969	0.8124	0.4311	-0.0056	0.7937	0.2985	-0.2452	0.1849
0.1370	0.0000	0.2511	0.0105	-0.0862	0.9876	0.1082	-0.0044	0.9869	0.1451	-0.1519	0.5899
0.3840	0.0000	0.3494	0.0694	-0.2995	0.8955	0.3458	0.0024	0.9053	0.2889	-0.2014	0.9398
0.5860	0.0000	0.2285	0.0964	-0.4648	0.8410	0.5088	-0.0372	0.8022	0.2974	-0.2452	0.9568
0.4951	0.0000	0.3218	0.0798	-0.3280	0.9512	0.3773	-0.0046	0.9521	0.2546	-0.1929	0.9661
0.1207	0.0000	0.1583	0.0257	-0.0761	0.9578	0.1073	0.0027	0.9593	0.1967	-0.1859	0.3483
0.0660	0.0000	-0.0722	0.0992	-0.4562	0.3688	0.5041	0.0058	0.3464	0.2015	-0.1996	-0.2582
0.0811	0.0000	-0.0451	0.1558	-0.4409	0.2945	0.4930	0.0099	0.2446	0.2776	-0.2022	-0.1410
0.0970	0.0000	-0.0472	0.1496	-0.4882	0.4420	0.5348	-0.0121	0.4325	0.2877	-0.2173	-0.1563
0.0660	0.0000	-0.0359	0.1396	-0.4408	0.1860	0.4815	0.0009	0.1575	0.2891	-0.2100	-0.2014
0.3123	0.0000	0.3943	-0.0334	-0.4148	0.8443	0.4846	-0.0640	0.8096	0.2925	-0.3620	0.9846
0.2801	0.0000	0.0047	0.1945	-0.6672	0.5247	0.6985	0.0407	0.4402	0.4781	-0.3673	0.0989
0.4020	0.0000	0.3266	0.0611	-0.3678	0.7732	0.4423	-0.0456	0.7653	0.3534	-0.3138	0.9716
0.3436	0.0000	0.3755	0.0534	-0.3004	1.0070	0.3411	0.0002	1.0095	0.3613	-0.3009	1.1490
0.8088	0.0000	-0.2138	0.1688	-0.5563	1.0706	0.6245	0.0420	1.0618	0.3704	-0.2348	0.9189

APPENDIX C: ESTIMATION OF VARIANCE OF MORPHOLOGICAL *CG*

We begin by noting that the formula for center of gravity, *CG* (Equation 1), is in the form of a ratio. Let $x = \Sigma_i w_i t_i$ and $y = \Sigma_i w_i$ be two random variables. Kendall and Stuart (1963, p. 232, equation 10.17) give the variance of a ratio as

$$V(x/y) = [E(x)/E(y)]^2 \cdot [V(x)/E^2(x) + V(y)/E^2(y) - 2\cdot\mathrm{cov}(x,y)/E(x)E(y)] \quad \text{(A1)}$$

If t_i and w_i are uncorrelated random variables, then

$$\begin{aligned} E(x) &= \Sigma_i t_i E(w_i) \\ E(y) &= \Sigma_i E(w_i) \\ V(x) &= \Sigma_i t_i^2 V(w_i) \\ V(y) &= \Sigma_i V(w_i) \\ \text{and} \quad \mathrm{cov}(x,y) &= \Sigma_i t_i V(w_i) \end{aligned} \quad \text{(A2)}$$

By assumption, w_i is the sum of variances of principal components or other independent variables. If v_{ij} is the variance of the j^{th} variable at time i, then $V(w_i) = \Sigma_j V(v_{ij})$. Substituting into the equations in A2 yields

$$\begin{aligned} E(x) &= \Sigma_i t_i \, \Sigma_j E(v_{ij}) \\ E(y) &= \Sigma_i \, \Sigma_j E(v_{ij}) \\ V(x) &= \Sigma_i t_i^2 \, \Sigma_j V(v_{ij}) \\ V(y) &= \Sigma_i \, \Sigma_j V(v_{ij}) \\ \text{and} \quad \mathrm{cov}(x,y) &= \Sigma_i t_i \, \Sigma_j V(v_{ij}) \end{aligned} \quad \text{(A3)}$$

The variance of a sample variance, i.e., $V(v_{ij})$, is given by Kendall and Stuart (1963, p. 244, exercise 10.13) as

$$V(V) = [(n-1)/n]^2 \cdot [(\mu_4-\mu_2^2)/n] + [2(n-1)/n^3] \cdot \mu_2^2 \quad \text{(A4)}$$

where μ_2 and μ_4 are the population variance and fourth moment, respectively, and n is the sample size. I have used bootstrapping as described above to obtain estimates for μ_2 and μ_4; the results are nearly identical if one uses the observed sample variance and fourth moment instead. Substituting Equation A4 back into A3 and then back into A1 gives an estimate of the sampling variance of the *CG* statistic, i.e., $V(CG_m)$. Assuming that $(CG_i\text{-}CG_m)$ is approximately normal, we can then compute the *z*-value for the difference in means as

$$z = (CG_i\text{-}CG_m) \,/\, \sqrt{[V(CG_i)/\Sigma_i d_i] + V(CG_m)} \quad \text{(A5)}$$

which is compared to the standard normal distribution. As mentioned in the text, the result is similar to that obtained by simply calculating the variance of the morphological diversity trajectory (treating it like a frequency distribution), and using the total number of morphological data points as the "sample size" to convert this variance to the standard error of CG_m.