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Evolution

Paleozoic record of morphological diversity in blastozoan echinoderms

(evolutionary radiation/macroevolution/clade shape)

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ABSTRACT **There has been extensive debate about the magnitude and implications of morphological diversity in early Paleozoic animals, with some workers using apparently rapid initial diversification to infer unusual evolutionary processes. Analysis of discrete morphological characters shows that initial morphological diversification in the echinoderm subphylum Blastozoa was so pronounced that morphological diversity relative to taxonomic diversity was greatest in the Cambrian, whereas morphological diversity itself was greatest in the Middle and Upper Ordovician. Thus, a small number of Cambrian taxa sparsely occupied a large range in morphological space, whereas subsequent diversification involved expansion and filling of morphospace. A measure of clade-shape asymmetry and a method for statistical testing of clade shape are used to show that morphological diversity is significantly concentrated early in the history of the Blastozoa. The subphylum represents the highest biologic level at which temporal patterns of morphological diversity have been analyzed. Because this study is based on explicit morphological analysis, not taxonomic proxies for morphological diversity, the results are not artifacts of taxonomic practice.**

The early Paleozoic represents an extraordinary phase of life's history, involving extensive radiation of basic body plans, macroevolutionary response to vast ecological opportunities, and, arguably, substantial genomic evolution (1–14). Patterns of morphological diversity are central to our understanding of such large-scale evolutionary processes in early metazoans, but very little of our knowledge is based on direct analysis of morphology. Taxonomic diversity is often used to study the radiation of form but provides only an imperfect proxy for morphological diversity (2, 4, 15–17). In fact, it is discrepancies between morphological and taxonomic diversity that may most clearly illuminate the early metazoan radiations (2–5, 15, 16).

Echinoderms are a major component of the early Paleozoic radiation. Previous studies have emphasized the pace of morphological evolution in echinoderms based on the temporal occurrence of novelties (8, 18). Such an approach is inadequate for assessing diversity. Each organism consists of primitive and derived characters; therefore, exclusive focus on novelties would mean that different characters were studied for each species, largely defeating the purpose of considering all species simultaneously. Moreover, taxonomic turnover plays an important role in patterns of diversity. For example, a clade that contains lineages with the primitive and derived states of a character represents greater morphological diversity than a similar clade in which lineages with the primitive state have become extinct, leaving only lineages with the derived state. Study of novelties alone would overlook this important distinction. For these reasons, analyses presented here are based on quantification of primitive and derived aspects of morphology.

Because it is difficult to quantify organismic morphology in a way that allows comparisons among species in different orders, classes, or phyla, morphometric analyses of diversity patterns have been at relatively small scales and have involved a limited number of taxa (15, 16, 19–22). Clade-shape statistics have been used to describe and interpret structure in the history of taxonomic diversity (23–26), but their application to morphological diversity patterns has been very limited (16). In this paper, quantitative analysis of discrete-character data is used to study the entire history of morphological diversity in the extinct echinoderm subphylum Blastozoa. Morphological diversity is measured as the mean pairwise dissimilarity among species. Clade-shape statistics, including a skewness measure, are analyzed with a bootstrap resampling method to test for asymmetry in the history of morphological diversity and for differential asymmetry in morphological versus taxonomic diversity. The approach presented here is applicable to other higher taxa and may provide a general procedure for analyzing temporal patterns of diversity.

Blastozoan Morphology

Sprinkle (27) recognized the subphylum Blastozoa as a monophyletic group of Lower Cambrian to Permian echinoderms that generally bear brachioles, rather than arms, as feeding appendages. In addition to the taxa considered by Sprinkle as blastozoans, diploporans and coronates (28) are now generally regarded as blastozoans, whereas the status of paracrinoids and cryptocrinoids remains uncertain (27, 29, 30). The subphylum rank *per se* is not relevant to the data presented here, but it is noteworthy that Blastozoa includes what are generally recognized as an enormous variety of forms. This variety reflects differences in fundamental design among the classes and orders, such as the arrangement and number of thecal plates, as well as differences that may seem less striking, such as the form of covering plates on the food-gathering brachioles (27). Given the great variety of blastozoan forms, establishing a continuous morphospace seems unlikely at this point, and analysis must therefore be based on discrete characters. Though quantitative analysis of discrete characters has long been an essential component of systematic biology (31, 32) and macroevolution (7, 8, 18), previous emphasis has been on classification, genealogy, and evolutionary rates rather than on secular patterns of morphological diversity. Analysis of blastozoans has focused mainly on descriptive and diagnostic characters at lower taxonomic levels (27, 33–35), although the class Blastoidea has been studied by cladistic (36) and morphometric (16) methods, and the entire subphylum has been analyzed cladistically (30).

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Abbreviation: ma, million year(s).

Characters were selected to give broad coverage to the principal aspects of blastozoan form and to emphasize aspects of form that vary among species. Characters were not limited to those known or presumed to be of taxonomic utility, as this might bias results. Nevertheless, as most characters are taxonomically useful *at some level*, there is much overlap between the set of characters used to quantify morphological diversity and the set of characters one might design to erect a classification or infer phylogenetic relationships.

Sixty-five discrete characters were defined, reflecting arrangement and number of thecal plates; shape and symmetry of theca; presence, number, arrangement, and plating of ambulacra; presence, arrangement, form, and plating of brachioles; presence, form, and plating of (putative) attachment structure; presence and nature of (putative) respiratory structures; and position and plating of mouth and anus. To decompose complex suites of characters into what are deemed "unit characters," characters were generally defined as binary. For example, ambulacral cover plates may be absent, there may be a single pair per ambulacrum, or there may be a series of plates per ambulacrum. Rather than coding this as a three-state character, it was coded as two binary characters: (*i*) the presence of ambulacral cover plates and (*ii*) the nature of cover plates if present. Multistate characters were retained when division into several unit characters would give undue weight to single components of morphology. Multistate characters were ordered if they could be logically aligned as a morphological series (for example, number of basal plates: 1, 2, 3, etc.). Ordering in this sense is not meant to imply whether a character state is primitive or derived. Forty-nine binary, 11 ordered multistate, and 5 unordered multistate characters were used. In practice, alternative coding schemes do not substantially change the results (see example below).

Homology of character states is not always clear; therefore, character-state definition was based partly on positional equivalence. For example, a stacked series of plates forming a distinct structure and attached to the aboral end of the theca was considered a column, but it was not assumed that the column evolved only once. Likewise, when paracrinoids were included as blastozoans, their "recumbent arms" were coded as "recumbent ambulacra" and their "pinnules" were coded as "brachioles." Phylogenetic analysis might suggest that a particular structure evolved convergently, but the focus of this study is on levels of morphological diversity not the fine details of particular evolutionary sequences. In a very narrow sense, two independent acquisitions of a column would imply more morphological diversity than a single acquisition. But at the scale of analysis of this study, two such convergent forms would represent approximately the same locus in morphological space (with regard to the single character). Related to this argument is the contention that branching order alone, without some assessment of morphological difference, provides inadequate means for studying morphological diversity (19).

Coding of morphological characters was based on published species descriptions, with supplementary study of museum specimens (data available from author). Species were chosen with the goal of not leaving major gaps in stratigraphic coverage. Generally only one species per genus was coded. Over half of all described blastozoan genera are represented, suggesting that a reliable picture of morphological diversity is produced. Moreover, the number of species coded per stratigraphic interval is roughly proportional to the number of genera known from that interval (Table 1, Fig. 1). Because of incomplete material or description, not all characters could be coded for all species. Missing data could often be reliably inferred (e.g., the presence of a column from a column scar). In cases where such inference was not possible, it was considered preferable to code missing data as questionable rather than to assume that the character states are those typical of the higher taxon to which the species belongs. Six characters showed no variation among species; these were omitted from analysis.

For binary and unordered multistate characters the character difference between two species is zero for matches and unity for mismatches. To give equal weight to all characters, ordered multistate characters were scaled so that the maximum character difference is unity. Morphological dissimilarity between two species is the total character difference divided by the number of characters compared. This metric, rather than its square root (see ref. 31), is an appropriate measure of morphological distance, because total character difference increases linearly with the number of characters. Any character that was logically inapplicable for either of two species being compared (e.g., nature of column if none is present) was omitted from that pairwise comparison (31).

There are numerous definitions and measures of morphological diversity (37). An intuitively appealing notion is the volume of morphospace occupied by a clade. Because it depends on sampled extremes, however, amount of morphospace occupied is biased, increasing with sample size (37). Empirically, amount of morphospace occupied tends to show similar temporal patterns as average dissimilarity (15, 37). Moreover, average dissimilarity itself bears important information on diversity structure and is not strongly biased by sample size (37). For these reasons, morphological diversity was measured as the mean pairwise dissimilarity among all species in each stratigraphic interval.

Time scale (38) and sample sizes are presented in Table 1. Stratigraphic intervals were defined to be of roughly equal length, to allow comparable amounts of time-averaging. Mean duration of intervals is 32.5 million years (ma), with a standard deviation of 7.2 ma.

Temporal Patterns of Diversity

For comparison with morphological diversity, generic richness was estimated from published stratigraphic ranges (sources available from author). Morphological diversity and taxonomic diversity are maximal in the Mid-Upper Ordovician (Fig. 1), but morphological diversification in the Cambrian is more pronounced than taxonomic diversification. The ratio of morphological to taxonomic diversity is maximal in the Cambrian, suggesting a sparsely occupied morphospace. The overall difference between morphological and taxonomic diversity is so striking that it is unlikely to reflect taxonomic artifact or incomplete sampling. Moderate levels of morphological diversity are maintained into the Silurian, despite a substantial decline in taxonomic diversity. This agrees with the pattern seen within the blastozoan class Blastoidea (16) and suggests a decline in taxonomic diversity that does not selectively eliminate morphologically extreme

Table 1. Time scale and number of species coded (*N*)

Stratigraphic interval	Age at base,* ma	*N*
Lower Cambrian (C1)	570	4
Middle and Upper Cambrian (C2)	536	8
Lower Ordovician (O1)	510	10
Middle and Upper Ordovician (O2)	476	50
Silurian (S)	439	22
Lower Devonian (D1)	408.5	9
Middle and Upper Devonian (D2)	386	8
Lower Carboniferous (LC)	362.5	21
Upper Carboniferous (UC)	323	3
Permian (P)	290†	12

*From Harland *et al.* (38).
†End of Permian at 245 ma.

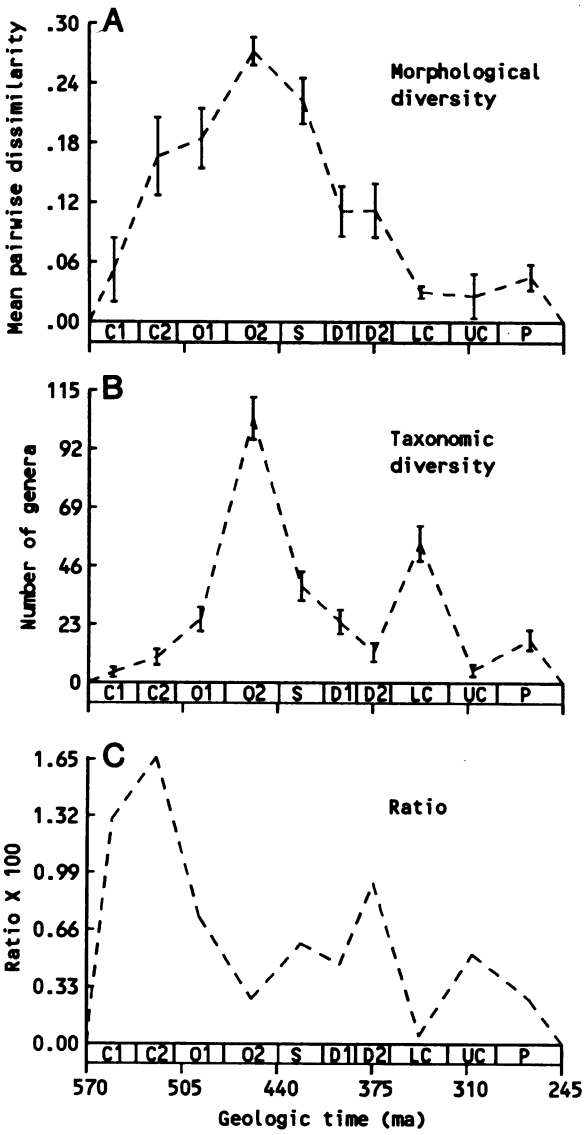

FIG. 1. Morphological (*A*) and taxonomic (*B*) diversity histories for Blastozoa. Abbreviations on time axis refer to stratigraphic intervals in Table 1. Error bars show one standard error on either side of mean bootstrap estimate, based on 1000 bootstrap samples. Note the high ratio (*C*) of morphological to taxonomic diversity in the Cambrian and the maintenance of morphological diversity in the Silurian despite decline in taxonomic diversity. Because some bootstrap samples contain intervals with zero diversity, ratios are sometimes undefined. Therefore, standard error for ratio cannot be rigorously estimated, and the curve in *C* is given by the ratio of mean bootstrap estimates for the two aspects of diversity.

forms (16, 37). The post-Devonian drop in morphological diversity reflects extinction of all forms except blastoids; with respect to the broad range of body plans exhibited by the Blastozoa, blastoids are rather stereotyped. The Lower Carboniferous discordance between morphological and taxonomic diversity in blastoids reflects taxonomic diversification that emphasized numerous minor variations on a few morphological themes (16).

Analysis of Clade Shape

The center-of-gravity (*CG*) statistic (23, 24) and the median (*M*) (16) measure the locus in time at which diversity is concentrated. Asymmetry (*A*) of the diversity history is defined here as the analogue of skewness in a frequency distribution (ref. 39, p. 114). If diversity is very high early in a clade's history and steadily declines, this clade's shape is "bottom-heavy" (23, 24)—i.e., asymmetric toward earlier times. If d_i and t_i are the diversity and temporal midpoint of the ith stratigraphic interval, let

$$c_0 = \Sigma d_i$$

$$c_1 = \Sigma d_i t_i$$

$$c_2 = \Sigma d_i t_i^2$$

and

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

Then *CG* and *A* are given by

$$CG = c_1/c_0$$

and

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

The equation for *A* is a standard formula for skewness. *M* is defined as the point in time at which the cumulative diversity is equal to $c_0/2$.

To test for structure in diversity trajectories, observed clade-shape statistics were compared to those that a clade with uniform diversity would have. The latter are referred to as the shape statistics inherent in the time scale, for they vary with the details of the time scale. For example, if all stratigraphic intervals were of equal length, then *CG* and *M* for a clade with uniform diversity would both fall at the midpoint of that clade's duration, whereas *A* would equal zero. In contrast, if interval lengths increased systematically through time, a uniform clade would have *CG* and *M* below its temporal midpoint and a negative value of *A*.

To compare observed clade-shape statistics to those inherent in the time scale, the sampling distribution of observed statistics was estimated nonparametrically by a bootstrap resampling procedure (40) with 1000 iterations. Given *N*, the number of species on which the morphological diversity curve was based, bootstrap samples of *N* species were drawn with replacement from the total sample. These were assigned to their proper stratigraphic intervals, and the morphological diversity trajectory and all clade-shape statistics were recalculated. A similar procedure was applied to generic diversity. Given *G*, the number of occurrences of genera, bootstrap samples of *G* occurrences were drawn with replacement and assigned to stratigraphic intervals, and generic richness was calculated.

To test for asymmetry in observed clade-shape statistics, the number of bootstrap samples yielding statistics higher than and lower than the inherent value were each tabulated. The smaller of these two numbers was doubled, then divided by the number of bootstrap values to yield the two-tailed probability that the clade-shape statistic inherent in the time scale could have been drawn from the sampling distribution of clade-shape statistics corresponding to the observed diversity data (Table 2). To compare morphological and taxonomic statistics, tabulations were made of the number of bootstrap samples with the morphological statistic greater than and less than the taxonomic statistic. The smaller of these two tabulated sums was doubled and divided by the number of bootstrap values to yield the two-tailed probability that the two clade-shape statistics could have been drawn from the same sampling distribution. Nonparametric statistical testing yields results consistent with tests (not pre-

Table 2. Statistical testing of clade shape

Data	Difference								
	$CG_m - CG_i$	$CG_t - CG_i$	$CG_m - CG_t$	$M_m - M_i$	$M_t - M_i$	$M_m - M_t$	$A_m - A_i$	$A_t - A_i$	$A_m - A_t$
Initial	−0.094§	−0.010	−0.084§	−0.124§	−0.085§	−0.039*	−0.619§	−0.515§	−0.104
Variation 1	−0.102§		−0.092§	−0.134§		−0.092†	−0.679§		−0.164
Variation 2	−0.090§	−0.002	−0.088§	−0.120§	−0.066‡	−0.054§	−0.630§	−0.418§	−0.212†
Variation 3	−0.094§		−0.084§	−0.124§		−0.039*	−0.624§		−0.109
Variation 4		−0.011	−0.083§		−0.086§	−0.038*		−0.625§	0.006
Variation 5		−0.018*	−0.076‡		−0.071§	−0.053†		−0.447§	−0.172
Variation 6	−0.076§	0.016	−0.092‡	−0.074§	−0.014	−0.060†	−0.575§	−0.348§	−0.227
Variation 7	−0.101§	−0.014	−0.087§	−0.110§	−0.060§	−0.050*	−0.598§	−0.456§	−0.142

Subscripts: m, morphological diversity; t, taxonomic diversity; i, value inherent in time scale. Each entry is the difference between two statistics. Negative entries mean that the first statistic is more bottom-heavy. Blank entries indicate initial data. Superscripts indicate two-tailed probabilities that two statistics are drawn from the same sampling distribution (*, $P < 0.1$; †, $P < 0.05$; ‡, $P < 0.01$; §, $P < 0.001$). Data variations are described in the text. Following the original procedure (23, 24), the time scale is adjusted so that CG and M vary from zero to unity.

sented) based on the assumption that the bootstrapped distributions of clade-shape statistics are normal.

By any measure of clade shape, morphological diversity is significantly bottom-heavy (Table 2). Taxonomic diversity is not top-heavy, but whether it is bottom-heavy depends on the statistic used (Table 2). The comparison of morphological and taxonomic diversity is ambiguous; morphological diversity is more bottom-heavy but the apparent significance of this depends on the statistic used. At this point it is most conservative to conclude that the two aspects of diversity, though they clearly show different temporal patterns, differ in ways that are not fully accounted for by these generalized clade-shape descriptors.

Several variations in the data were explored to determine to what extent the observed patterns could reflect subjective choices regarding taxa included in the analysis, coding of characters, time scale employed, and other factors.

Variation 1. To assess the effect of uncertainty in the character data, 15 characters that are unknown in half or more of all species were omitted.

Variation 2. There is debate whether paracrinoids and cryptocrinoids are blastozoans. Initial analysis included these forms, but data were reanalyzed without them.

Variation 3. Several forms, notably sphaeronitid diploporans and some rhombiferans, have facets for the attachment of appendages, but these appendages themselves are unknown. These were initially coded as brachioles of uncertain morphology, but it has been suggested (33, 34) that they may have been erect ambulacra, possibly bearing brachioles. Of 147 species studied, 22 were recoded as having erect ambulacra of unknown morphology.

Variation 4. To judge the robustness of temporal pattern in generic diversity, a new taxonomic data set was made by omitting from the initial data all genera not recognized in ref. 41.

Variation 5. To compensate for differences in time-averaging, a separate analysis measured taxonomic diversity as genera per ma rather than raw number of genera.

Variation 6. Clade-shape statistics were calculated based on a 12-interval Harland scale (like the 10-interval scale used above, but with the Middle and Upper Cambrian and Middle and Upper Ordovician no longer combined).

Variation 7. Analyses were also performed using a 10-interval Odin time scale (42), which differs from the Harland scale mainly in the young age for the base of the Cambrian and the consequently shorter durations of early Paleozoic intervals.

Although variations in the data yield subtle differences in clade-shape statistics, the patterns are largely consistent with those obtained with the initial data (Table 2). Differences in results may be productively interpreted—for example, how do paracrinoids contribute to our perception of blastozoan diversity?—but the emphasis here is on the sensitivity of results to conventions adopted for data analysis. The broad concordance of results suggests that documented diversity patterns and associated clade-shape statistics provide robust reflections of the underlying diversity histories.

Discussion and Conclusions

Morphological diversity in blastozoan echinoderms increases greatly in the Cambrian and is maximal in the Mid-Upper Ordovician, whereas the ratio of morphological to taxonomic diversity is greatest in the Cambrian. Previous authors have advocated similar results for echinoderms as a whole (12) and arthropods (1, 5), although without reference to quantitative morphologic analysis. The high ratio of morphological to taxonomic diversity in Cambrian blastozoans is consistent with a broad but sparse occupation of morphospace. Ordination analysis of species based on the matrix of pairwise dissimilarities (not presented here) supports this inference. Because morphological diversity is based on explicit analysis of forms, not a proxy such as number of higher taxa, documented patterns of morphological diversity are not artifacts of taxonomic practice such as the recognition of many small taxa of high rank.

In a simple, time-homogeneous branching model, morphological diversity in a randomly evolving clade should be more top-heavy than taxonomic diversity (16). Blastozoans clearly violate this generalization, thus suggesting a nonrandom component to their history, one possible example of which would be a secular decrease in the average morphological step associated with evolutionary transitions. This study does not address the cause(s) of early morphological diversification. Pronounced early diversity is consistent with rapid colonization of "empty" ecological space (12, 23), low levels of selection and competition that would permit a broad range of forms (12, 23), and genomic structure that might facilitate evolution of new forms (2, 3).

Unlike previous studies (7, 8, 18), character analysis in this study is aimed at morphological diversity, not evolutionary rates or phylogenetic inference, both of which would often place little emphasis on primitive characters. It bears repeating that the rate of acquisition of novelties is only part of the diversity picture; the maintenance of primitive and derived states and the distribution of character states must also be considered.

Although it is often argued that taxonomic rank is largely a human construct, the fact remains that as taxonomic rank increases it becomes progressively more difficult to quantify the form of all included species with the same set of morphological variables (19). The approach developed here is potentially useful for analyzing morphological diversity in other taxa and at higher taxonomic levels. Macroevolutionary questions that have been difficult to study may be tractable if approached in the manner outlined here.

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