

# THE EVOLUTION OF MORPHOLOGICAL DIVERSITY

*Mike Foote*

Geophysical Sciences Department, University of Chicago, Chicago, Illinois 60637

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## ABSTRACT

The diversity of organismic form has evolved nonuniformly during the history of life. Quantitative morphological studies reveal profound changes in evolutionary rates corresponding with the generation of morphological disparity at low taxonomic diversity during the early radiation of many clades. These studies have also given insight into the relative importance of genomic and ecological factors in macroevolution, the selectivity of extinction, and other issues. Important progress has been made in the development of morphological spaces that can accommodate highly disparate forms, although this area still needs more attention. Other future directions include the relationship between morphological and ecological diversification, geographic patterns in morphological diversity, and the role of morphological disparity as a causal factor in macroevolution.

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## MORPHOLOGICAL DIVERSITY IN SYSTEMATIC BIOLOGY

How has the diversity of organic form, living and extinct, come to be? This question, perennially at the heart of systematic biology, has been addressed in paleobiology with a focus on quantitative approaches and large-scale evolutionary questions. The goals of this review are to discuss some recent developments, mainly paleobiological, in the study of morphological diversity [disparity (55, 56, 57, 112, 172)] as opposed to taxonomic richness, and to outline some promising future directions in disparity studies. Many of the pressing questions, such as the pattern of divergence early in clade history and the filling of morphological space, have a long pedigree (54, 108, 116, 122). Although

some macroevolutionary studies mainly provide documentation of evolutionary patterns and mechanisms that have been proposed without quantitative approaches, nevertheless a unique perspective exists that reflects an interest in how distributions of form evolve over the fullness of geologic time (58) and at different hierarchical levels. This discussion also entails some consideration of methodological problems, such as the measurement of disparity, the comparison of results from different approaches, the use of evolutionary models in understanding disparity, and the effect of paleontological incompleteness on perceived evolutionary patterns.

## APPROACHES TO STUDYING DISPARITY

Although taxonomic richness is the most common measure of biological diversity (81), the distinction between variety and numbers of species is essential (11, 29, 30, 31, 35–38, 40, 41, 43). For descriptive purposes, it may not be necessary to assess form quantitatively (64, 65), but many substantive issues in disparity studies involve comparing levels of morphological diversity among taxa (12, 16, 18, 32, 39, 109, 110, 164, 165) or among different periods in the history of a single clade. Therefore, some quantification of disparity is necessary. In this brief survey of disparity measures, I do not consider advantages and disadvantages exhaustively (partly because this has been done elsewhere, e.g. 155, 162–165, 172, and partly because the relative strengths and weaknesses for various questions are not yet fully understood). Instead, I comment on some of the more salient features of each approach.

### *Indirect Measures*

The extent of morphological divergence among taxa generally increases with taxonomic rank (e.g. 16–18, 36, 42, 44, 59, 173, 175), so secular changes in the number of higher taxa (generally, phyla, classes, and orders) provide an obvious index of disparity (3, 28, 142–144). Using higher taxonomic richness to assess disparity has a number of advantages. The pertinent data are relatively easy to compile, the common currency of taxa can be summed across disparate biological groups, and a reasonable concordance with more direct measures may be obtained (45). Although taxonomic proxies may be criticized on the grounds that taxa are artificial, subjective, nonmonophyletic, or erected on the basis of criteria other than morphological distinctiveness (124–127), these criticisms miss the point somewhat. The relevant issue is not the biological meaning, but rather the information content, of higher taxa. Simply, is there a reasonable empirical concordance between taxonomic richness and more direct measures of disparity? If so, the heterogeneity and comparability of higher taxa, while still interesting questions (153), may be of secondary importance. Moreover, even

direct measures of disparity are not free of subjectivity, because they rely upon the choice of a finite number of organismic traits. In a limited analysis of three major clades of Paleozoic marine invertebrates (trilobites, crinoids, and blastozoans), the number of higher taxa (orders and suborders) captured many, but not all, features of the history of morphological disparity revealed by more direct measures (45). Some discrepancies are substantial enough to recommend direct morphological analysis. Nevertheless, higher taxonomic data have suggested a number of important evolutionary patterns that have later been corroborated (see below); thus, ignoring this rich source of information would be shortsighted.

Morphotypes, which are recognized sometimes by eye and sometimes biometrically (23, 26, 53, 66, 72, 113, 114), present many of the same advantages and disadvantages as taxonomic proxies. However, morphotypes are generally quite deliberately conceived in a way that cuts across phylogenetic lines. Thus, compared to simple taxonomic proxies, they facilitate the study of iterative and convergent evolution. For example, Fortey & Owens's study (53) of trilobite morphotype and family diversity suggests the rise and fall of blind trilobites as one component of the rise and fall of morphological diversity through the early Paleozoic.

### *Morphological Measures*

The study of ecomorphology has focused on the expansion of the concept of diversity to include morphological similarity (31), the relationship between morphological and ecological differences within species (152a) and among species (104, 166), and the extent to which greater morphological (ecological) packing and expansion of morphological (ecological) variance among species result from an increase in the number of species in a community (104–106, 157, 158, 160). Although paleontological studies of secular patterns in disparity have had somewhat different goals, many of the methods of measuring morphological diversity are similar to those used in ecomorphology. Starting with a sample of species represented in a morphological space of discrete or continuous variables, disparity can be measured as the variance, range, average pairwise distance between species, number of discrete character states in the sample, number of character-state combinations, as well as related measures and multivariate extensions (2, 35–38, 40, 111, 117, 132, 136, 140, 154, 155, 164, 165). Several studies have been concerned with the effect of sampling on measures such as the range and volume, which increase monotonically with sample size (38, 172). This problem is especially relevant in paleontological studies; the incompleteness of the fossil record implies that substantial changes in range can result simply from changes in the quality of preservation or sampling (38, 172). When volume is measured as the product of variances or standard deviations (e.g. 106), the sampling issue is not as relevant.

A point of contention has been whether morphological distances between species should be measured along the branches of an estimated genealogy (patriistic dissimilarity) or not (phenetic dissimilarity) (43, 45, 126, 162, 165). There is no single, correct approach. Nonphylogenetic measures have the advantage of not relying on an estimate of genealogy that may be inaccurate. On the other hand, phylogenetic measures may allow a more direct assessment of transition magnitudes, something that is often of interest in inferring mechanisms in the evolution of disparity. It should always be kept in mind that morphological differences among species include autapomorphies and symplesiomorphies. Even though such traits are not informative for cladistic branching sequence, they are informative for other aspects of genealogy, such as ancestor-descendant relationships (163), and are essential for assessing disparity (56, 57). The crucial question is whether one is interested in net evolutionary change (how dissimilar two species end up, regardless of the evolutionary pathways) or total evolutionary change (how long the evolutionary pathways are, regardless of where they end up) (43, 45). Of course, in the absence of homoplasy, the two measures are identical. It is worth considering both approaches, since in some cases they corroborate each other, and in some cases the disagreement between them is evolutionarily informative (162, 164, 165). This is discussed in more detail below.

### *“Predicted” Character Diversity*

A curious hybrid between direct and indirect approaches stems from the incorporation of phylogenetic analysis into studies of diversity, especially in the context of conservation biology. Since we can consider only a small, potentially biased sample of the indefinitely large number of organismic traits, the measurement of patriistic dissimilarity based on observed traits may provide an inadequate proxy for total character diversity (the same, of course, is true of any measure of disparity). A number of authors have advocated predicting (estimating) character diversity based on an estimate of genealogy (or, in the absence of a genealogy, taxonomic structure) and a presumed model of character evolution (29, 30, 171). This raises the obvious questions of how sensitive estimated character diversity is to the presumed model and to the accuracy of the genealogy, and whether a genealogy estimated from a biased subset of characters could yield an unbiased estimate of character diversity. Although some models of character evolution have been advocated over others (30), a more thorough analysis of the robustness of this approach, based on extensive simulation or on jackknifing of observed characters, for example, is essential.

### *Choice of Traits*

It should go without saying that a limited set of traits allows measurement not of “overall” disparity (30, 78), but rather of the diversity of form in the chosen

traits. Most studies have attempted to include a broad range of anatomical features, or, when necessary, those features that are sufficiently well preserved to be measured. A complementary approach is to select those traits of particular importance for the question at hand, for example functional morphology (12, 65) or ecology (166). In this vein, some authors have advocated a greater consideration of the developmental and architectural significance of characters as a prerequisite for understanding the Cambrian explosion of animal disparity at a deeper level than permitted by a tabulation of the number and size of evolutionary transitions (56, 57, 88, 107). Although his interpretation of characters may be controversial, Wagner (163) has made a step in this direction by categorizing gastropod shell traits as related to trophic demands versus fundamental architecture.

### *Factors of Uncertain Relation to Disparity*

Morphological diversity is commonly discussed in connection with the complexity and “bizarreness” of organisms. If we think of complexity as a property of individual organisms, there need be no correspondence with disparity, which is a property of distributions of organisms. We may observe a wide spectrum of simple forms or a limited array of complex forms (90). Schemes such as the Skeleton Space (139–141), the quantification of tagmosis in arthropods (20), the number of cell types (150), or the differentiation among serial elements such as vertebrae (87, 89) assess complexity in terms of the disparity among parts within the same organism, thereby allowing the evolution of average complexity and variance in complexity to be studied together. Unlike complexity (20, 87, 89, 90, 114, 150), the notion of bizarreness has not been properly operationalized; currently, the concept is highly subjective. Most workers seem to regard bizarre forms as those that are morphologically extreme (e.g. 73, 93), but at least one author (63) has suggested that flatness is a key element of bizarreness! It is also common to regard forms of uncertain genealogical relationship as “weird” (161), but taxa whose phylogenetic relationships are understood can nevertheless be quite disparate morphologically; disparity and branching sequence are logically distinct (8–10, 56, 96, 147, 161).

## PROGRESS IN DISPARITY STUDIES

A primary contribution of disparity studies has been the simple description of evolutionary history, the “kinetics” of biological diversity (119). Documenting the morphological exuberance of clades through their history, and the ways that different taxa contribute to overall morphological diversity (12, 39), helps hone specific evolutionary questions and hypotheses. For example, I initiated a largely exploratory study of crinoid disparity through the Paleozoic with no

intention of testing for constraints on form. Yet the striking pattern that maximal disparity (measured as mean pairwise phenetic distance) was attained early, and that the morphological extremes reached early in the group's history were scarcely exceeded over the next 200 My, despite the proliferation of hundreds of new genera, together suggested some severe limits on the evolution of crinoid form (41–44). (See 113 and 137 for a similar assessment in Carboniferous ammonoids, and 8, 9, 49, and 77 for a discussion of this issue in arthropods.) Here I outline some of the principal substantive issues that have been addressed in the paleobiological analysis of disparity.

### *Testing for Adaptive Radiations*

The common conception of adaptive radiations concerns both a proliferation in numbers of taxa and a diversification of form (122). For example, in an influential treatment of macroevolution in the fossil record, Stanley (131) cited the case of Cambrian trilobites (among other groups), partly using the increase in number of families as evidence for adaptive radiation. However, morphometric data show that the diversification of trilobite form (increase in morphological range and variance) was actually rather limited in the Cambrian, and that the greater proliferation of morphological diversity followed in the Ordovician, during a decline in family-level taxonomic diversity (34, 36, 40). The point here is not to criticize Stanley's example, but to illustrate the nature of the test. Likewise, Cambrian biomerer (repeated stratigraphic sequences apparently marked by iterative evolutionary patterns in trilobites) have been discussed as examples of adaptive radiation, but most analyses have focused on taxonomic data (60, 133, 134). Sundberg (136) analyzed morphometric data on trilobites through one of these biomerer, verifying that the evolutionary sequence involves a substantial diversification of form. Implicit in these tests is the ecomorphological assumption that a diversification of form is likely to reflect an ecological diversification (see discussion below).

### *Patterning in Morphospace*

Although many disparity studies have focused on the extent of morphospace occupation and variance among species, other aspects of pattern in morphospace have also provided insight. For example, Cambrian trilobites seem to exhibit pronounced homeomorphy, and they have been notoriously difficult to group into higher taxa (families and superfamilies) (135, 169), a pattern that may be related to developmental flexibility in the Cambrian (67, 68, 86; but see 128). In contrast, Ordovician trilobites are, for the most part, easier to sort into morphologically distinct groups (135, 169). Morphometric analysis suggests that higher taxa in the Ordovician occupy a greater range of morphological space, but with less overlap (36). Ignoring higher taxa altogether, the analysis of morphological

nearest-neighbor distances has supported the pattern of greater clustering in the Ordovician (34). Tabachnick & Bookstein (138) suggested that, at a smaller scale, specimens of the Miocene planktonic foraminiferan *Globorotalia* are spread continuously through morphospace, so that named taxa and morphotypes do not correspond to clusters or modes in the distribution. Moreover, this pattern itself has evolved; some periods in foraminiferan history are apparently marked by greater clustering (RE Tabachnick, personal communication). Although some preliminary simulations (34; see 103) suggest that an increase in morphological clustering could result from simple diffusive evolution and extinction of intermediates, the evolutionary processes responsible for changes in the clustering of morphological distributions need to be explored in greater depth.

### *Ecomorphology*

Determining the extent of community convergence is a principal question in ecomorphological studies. Do ecologically similar communities in different places show similar patterns of morphological similarity and morphological diversity among species (104)? Van Valkenburgh has explored this issue in a temporal context and found that a number of mammalian paleocommunities show similar guild structure (based on extent of morphospace occupation and nearest-neighbor distances), despite the passing of tens of millions of years and substantial taxonomic turnover (157–160). This suggests that ecological interactions may be strong enough to outweigh historical influences on community structure (157, 158). Another study noted similarities in Pleistocene and Recent community structure in vultures (61), based on the relationship between body size and feeding strategy. The difficulty of ecomorphological analysis of fossil taxa is discussed briefly below.

### *Responses to Extinction*

Because variance in form is generally unbiased by sample size, a morphologically random culling of taxa should, on average, leave variance unchanged. Thus, the question whether morphological variance among species changes as taxonomic diversity declines has been used as a test for extinction selectivity (19, 35, 40, 43, 46, 84, 109–111, 158; cf. 152). Because many of these studies compare disparity before an extinction event to disparity at some period of time afterwards, they confound the change in the morphological distribution attributable to extinction with that attributable to subsequent diversification. However, Churchill (19) overcame this problem by comparing all taxa before the event to the subset of taxa surviving the event. McGhee (84) documented an interesting pattern in articulate brachiopods (specifically, the subset of them having two convex shells). He found that reduction in diversity generally resulted in a reduction of the distribution of forms to a morphological mode

which he interpreted as advantageous in allowing a high ratio of body volume to surface area (82).

An unsolved problem in extinction studies concerns the sensitivity of tests for selectivity. What combinations of intensity of selectivity, pattern of selectivity, and sample size allow departures from random survivorship to be detected? In principle, this is easily addressed with simulation studies, but, to my knowledge, the necessary work has not yet been carried out.

### *Replacements and Successive Diversifications*

Extinction of incumbent taxa commonly opens new opportunities for the diversification of other groups (4, 5, 121, 122). Although studies of replacement have generally focused on taxonomic diversity, morphological analysis has shown that the replacing taxon sometimes occupies vacated morphological space [Ward (167) on Tertiary nautilids versus Mesozoic ammonoids, and Roy (110) on Tertiary strombids versus Cretaceous aporrhoids]. To the extent that species in the two groups in question coexisted spatially and thus were capable of interaction, and to the extent that morphological traits are ecologically significant, the colonization of morphological space provides stronger evidence for the role of ecological interaction (competition) in macroevolution than do data on taxonomic richness alone.

The pattern of morphological diversification during successive intervals of taxonomic diversification provides some evidence bearing on the role of ecological versus genomic and developmental changes in macroevolution. The origin of higher taxa is concentrated early in the history of many groups (e.g. 22, 108, 116, 122, 142, 143, 146–148). Although some might argue that this says more about taxonomic practice than morphological divergence (21, 24, 125, 127), available morphological data support a rapid, early proliferation of morphological diversity (see discussion below). Two leading explanations for this pattern are that ecological opportunities were greater in the early history of many clades, diminishing as the world became ecologically saturated, and that genetic and developmental systems were less canalized early on (27, 28, 88, 142, 143, 146–149, 151). Erwin (27) suggested a test of these alternatives involving the analysis of disparity. If ecological opportunity were responsible, then one would expect later radiations of a clade following extinction events to involve a rapid proliferation of morphological diversity (perhaps to the same high level attained earlier), whereas an increase in genomic and developmental canalization might severely limit morphological diversification later on. In support of the ecospace model, Wagner (164) noted that some subclades of Paleozoic gastropods exhibited accelerated morphological diversification following the Late Ordovician extinction event. Similarly, Foote (46) documented a rapid increase in disparity in early Mesozoic crinoids (the same pattern as seen in the

Paleozoic), following the end-Paleozoic extinction event that had drastically reduced the taxonomic diversity of this group.

### *Rapid Filling of Morphological Space During Evolutionary Radiations*

Perhaps the most common theme in disparity studies so far has been the asymmetric deployment of morphological diversity early in the radiation of major clades. This pattern has long been advocated (e.g. 22, 54, 97, 98, 108, 116, 129, 130, 143, 176), but it has been disputed because it is sometimes discussed in terms of taxonomic proxies (8, 21, 24, 124–127). However, most authors who describe the pattern in terms of higher taxa use this description as a shorthand to express what are perceived as profound morphological differences (e.g. 55, 129, 130).

Although we can always benefit from more examples, it seems safe to say at this point that studies of disparity within class- and higher-level taxa have documented more cases of accelerated morphological diversification early in a clade's history, at relatively low taxonomic diversity, than of a more gradual unfolding of morphological and taxonomic diversity together. Evidence for acceleration of morphological evolution early in history has taken a number of forms: peak disparity early; more rapid proliferation of disparity versus diversity; secular decline in the rate of increase of morphological disparity; secular decline in the dissimilarities between sister taxa (i.e. decline in estimated magnitude of evolutionary transitions); failure of taxa to converge morphologically toward their time of phylogenetic splitting (11); and failure of later-evolving subclades, throughout their entire history, to generate as much morphological diversity as the more inclusive clade did just in its initial phase of diversification (77, 88, 164). Because the pattern in question concerns the magnitude of morphological differences, arguments based purely on cladistic branching order (8–10, 96, 161) are not immediately relevant to the question of early disparity (56, 147).

Examples of pronounced early increase in disparity include Cambrian marine arthropods (9, 49, 77, 172), Paleozoic gastropods (163, 176), Paleozoic rostroconch molluscs (165), Paleozoic stenolaemate bryozoans (1), Paleozoic seeds (123), Cretaceous angiosperms (based on pollen; R Lupia, personal communication), Cenozoic ungulates (72), Carboniferous ammonoids (113, 114, 137), Paleozoic articulate brachiopods (13, 84), Ordovician trilobites (but not Paleozoic trilobites as a whole) (91), early-mid Paleozoic tracheophytes (75), Paleozoic crinoids (41, 42, 43, 44), Mesozoic crinoids (46), Paleozoic blastozoans (37, 47, 162), and Cambrian Metazoa (141). Counterexamples include Early Jurassic ammonites (23), Paleozoic trilobites (40), Paleozoic blastoids (35, 40), Paleozoic cladid and flexible crinoids (43), and, apparently, insects from the

mid-Paleozoic to the Recent (based on number of mouthpart morphotypes; 76). Several of these studies suggest that disparity within large clades may increase rapidly early in history, while disparity within concurrently diversifying constituent subclades increases more gradually. If this pattern proves to be more general, it will provide important support for hierarchical views of evolution that regard patterns at different scales as distinct qualitatively rather than just quantitatively (71, 142). Interestingly, at least one author has considered the pattern of early morphological diversification to be such a robust evolutionary generality that he has assumed, for the sake of phylogenetic analysis, that the groups showing greater disparity in the basal part of the cladogram are more primitive (79)!

At first glance, one might suspect that, since many of the foregoing studies are based on discrete morphological characters, the pattern of early maximal disparity is an artifact of this type of data. There are a number of reasons to think the pattern is not a simple artifact, however. First, not all clades that have been analyzed with discrete character data show this pattern (e.g. 37). In fact, the very same set of discrete characters showed a rapid increase to maximal disparity within crinoids as a whole but not within a major subclade of crinoids (43, 44). Second, in at least one case, the same pattern was found when characters used to differentiate the higher taxa were omitted (41, 42). Third, in the cases I have studied (37, 41–44, 46), no pair of species exhibits a morphological dissimilarity approaching the theoretically maximal value (i.e. the clade is not up against the theoretical limits of the morphospace imposed by the choice of characters). Fourth, different sets of discrete characters sometimes yield different evolutionary patterns in a single taxon (e.g. 41, 42), which we would not expect if the discrete nature of characters were itself responsible for perceived patterns. Finally, at least one study of the same group comparing landmark-based, continuous measures to discrete characters found that both kinds of data show a long-term increase in morphological diversity over time, although the patterns differ in detail (38). Thus, it is more reasonable that the common pattern of maximal early disparity reflects true early divergence to extremely dissimilar forms, such that it is necessary to use discrete characters to quantify them (limited homologies make biometric or landmark approaches problematic).

The combination of disparity data and simple evolutionary models has had limited success in explaining the proximate mechanisms underlying the early diversification of form (40, 47). Although some potential explanations for a rapid, early increase in disparity seem unlikely (e.g. logistic taxonomic diversification—47), many other factors, such as a secular decline in taxonomic turnover rates, a secular decline in the size of morphological transitions, and boundaries in morphological space, can yield this particular evolutionary pattern (47). Nevertheless, the fact that this pattern is soundly grounded in morphological analysis rules out the possibility that it is an artifact of taxonomic

practice, such as the erection of higher taxa that diverge early phylogenetically, but only later morphologically (21, 24). Comparison of results from different approaches to disparity has helped narrow down evolutionary mechanisms in particular cases (see below).

### *Sensitivity of Patterns to Approaches Adopted*

In the foregoing survey of approaches to measuring disparity, I deliberately avoided advocating one method over others. With so many ways to quantify form and measure the differences between forms, it would be pointless to argue that one approach is best in principle, since this depends on the organisms studied and the kinds of evolutionary patterns one hopes to detect, among other factors. The more fruitful approach has been to explore various methods and to test for consistency of evolutionary patterns. When a number of methods of quantifying form and measuring disparity converge on a similar result, we can be more confident in that result. [I should point out that by consistency I do not mean, strictly, the same temporal pattern in two or more disparity metrics, but rather a pattern in the metrics that has the same evolutionary implication. For example, if disparity is measured as patristic dissimilarity between sister-species on the one hand and by mean phenetic distance among all species on the other hand, a pattern of constant patristic dissimilarity would be consistent with a steady increase in phenetic distance, since constant step size in a diversifying clade yields an increase in variance among forms (47, 150).]

Wills et al (172) showed that disparity metrics including range, variance, and distance from basal node on the cladogram all point to comparable disparity in Cambrian and Recent arthropods. Jernvall et al (72) found an early increase in morphological diversity of Cenozoic ungulates, whether based on number of morphotypes or pairwise phenetic distances. Wagner (162) considered the case of blastozoan echinoderms, in which an early increase in disparity at low taxonomic diversity had been used to infer that morphological transitions were larger early on (37). This result had been disputed because the disparity metric was not phylogenetic (126), but Wagner showed that, using patristic dissimilarity per branch on a cladogram to estimate transition magnitudes, the original, indirect, inference was supported. Wagner also found a similar concordance in an analysis of rostroconch molluscs (165). Many other examples could be cited in which different disparity metrics, different morphological traits, different sampling protocols, different estimates of phylogeny, or different methods of character weighting were used to test the robustness of evolutionary patterns (34, 41–44, 46, 74, 165).

Of course, different approaches need not yield the same patterns. Such discordances can be interesting in their own right, rather than suggesting that one approach is right or wrong. It can be very informative to break away from

arguments about phenetic versus phylogenetic metrics (162, 163, 165). For example, in rostroconch molluscs, Wagner (165) found that patristic dissimilarity increased much more than phenetic distance during the Ordovician. This suggests substantial evolutionary transitions with a high degree of homoplasy (165). Likewise, a discordance between abundant character change and limited expansion of the morphological range may suggest either extreme convergence or boundaries in morphospace (43, 49, 77).

Considering what we can learn from the agreements and disagreements among various methods, it would be wise, especially during this expansive phase of the history of disparity studies, to take a lesson from evolutionary radiations by practicing early experimentation. Whether and how we settle into patterns of later standardization is an open question.

### *Effects of Incompleteness on Temporal Patterns of Disparity*

The incompleteness of the fossil record affects various measures of disparity in different ways. Simple average phenetic distance and variance have an advantage relative to measures of extremes such as the range in that the former measures are less sensitive to completeness, provided that sampling is representative (35, 38, 48). Thus, contrary to some suggestions (73), incomplete preservation will not bias average distances unless the species preserved are systematically more or less extreme morphologically than those not preserved (see discussion below). Of course, if a clade is not preserved at all for a substantial part of its early history, then the temporal patterns of morphological and taxonomic diversity will be biased; it remains to be seen how common a problem this is (52).

Sister-species differences generally increase as the record becomes less complete, since there are, on average, more missing intermediates. Wagner (163) has addressed this problem by estimating sampling intensity. He found that a temporal decrease in the morphological distance between gastropod sister-species (or ancestors and descendants) was not matched by an increase in sampling intensity, and that the evolutionary pattern was therefore probably not an artifact of incompleteness. While this is an important first step, it is also worth estimating completeness (proportion of taxa preserved in an interval) in addition to sampling intensity. This is because, if extinction rate is higher (taxonomic durations are shorter), the same intrinsic preservability and the same intensity of sampling will still yield lower completeness (50, 128a), and thus artificially greater dissimilarities between sister species. Therefore, a decline in taxonomic turnover rates, which is sometimes found during the diversification of clades (47, 156), could bias perceived patterns in the magnitude of evolutionary transitions. Wagner (165), estimating the proportion of rostroconch taxa preserved, found that temporal changes in sister-species differences could not be explained

by changes in completeness (165). Since quantitative methods for estimating completeness are not yet fully developed, this problem deserves further consideration (6, 48a, 50, 80, 99, 128a).

## OUTSTANDING PROBLEMS

In contrast with the almost routine documentation of taxonomic diversity in the history of biologic groups, there is still a relatively small (but rapidly growing) number of case studies quantifying secular patterns of disparity. I do not dwell on the obvious need for more data to establish, for example, how common it is for subclades to show qualitatively different evolutionary patterns than their more inclusive clades. Rather, I consider several unanswered but important questions (some of which have already been discussed at length by others).

### *Broadening the Taxonomic Scope of Disparity Studies*

Without suggesting that taxonomic ranks have a consistent meaning, we can note that it is common to be able to accommodate species within the same class with a consistent biometric scheme (e.g. 13, 31, 35, 36, 84, 100, 105). On the other hand, studies that span several classes within a phylum tend to be stymied by difficulties in establishing measurable homologies, and therefore they often must rely upon discrete character data. Generative and architectural models have transcended taxonomic boundaries to some extent. Of these, models of shell coiling (83, 100, 101, 115) and branching growth (14, 15, 51, 85, 94) have been most common in paleobiological studies. Other models, such as those that view organisms as fluid-filled sacks taking on a shape that balances internal and external forces, have been successful as heuristic tools in constructional morphology (102, 118), but there have been only limited attempts to establish model parameters and estimate these parameters on observed organisms (25, 102). A general advantage of theoretical models of growth and form over simple empirical descriptions is that the former allow a comparison between the observed spectrum of form and the theoretically conceivable spectrum (65, 83). This is important in assessing the fullness of morphological space.

Perhaps the most significant development in broadening the taxonomic scope of morphological diversity studies is the application of a combinatorial system for describing some of the principal features of skeletal structures—the Skeleton Space of Thomas & Reif (139–141). This is a bold attempt to distill the skeletal elements of animals to their most salient constructional features: for example, location (internal or external), number of parts, mechanical properties, mode of growth, and nature of contact or articulation. The Skeleton Space is of greatest utility in assessing the morphological diversity of very high-level taxa such as phyla or kingdoms, since taxa below this level tend to be relatively invariant

in their skeletal structures (e.g. the common skeletal formula for gastropods is a single, external, tube-like, accreted, rigid, self-produced shell; but then, of course, there are opercula, slugs, and the occasional bivalved snail). Thomas & Reif stated that there are over 1500 possible combinations of features in their space, but, to keep their analysis tractable, they considered pairwise combinations of traits (e.g. skeletal elements that are internal and accreted, external and accreted, internal and remodeled, external and remodeled, and so on). With this approach, nearly all pairwise combinations have been exploited in living and extinct animals, and thus the space seems quite richly occupied. It would be worth extending this analysis to include the full spectrum of combinations, not just the features taken in pairs.

One complication that must be kept in mind when comparing the Skeleton Space to other approaches is that a single organism can occupy many loci in the Skeleton Space, whereas in nearly all other morphospaces, each organism is considered to occupy a single point. This is not just because features are considered pairwise (e.g. vertebrate long bones occupy the rigid-remodeled locus, the rigid-articulated locus, the internal-rod-shaped locus, and so on), but, more importantly, it is because different parts of an organism may have fundamentally different structures. For example, the long bones and the cranium of vertebrates have different skeletal formulae.

To some extent, the apparent fullness of the space depends on the way features are decomposed (e.g. the number of elements has only three states: one, two, or greater than two). Although one may criticize the space on such grounds, it is the first scheme to allow a quantitative assessment of the morphological diversification of all (skeletonized) animals. Applying the Skeleton Space to the Middle Cambrian Burgess Shale fauna, Thomas & Stewart (141) found that about 90% of designs ultimately used by animals (considered as pairwise combinations of skeletal features) had already been exploited rather early in animal history [or at least early in their preserved history (174)]. Thus, we have direct morphological documentation for a broad diversification of skeletal designs during the Cambrian explosion.

### *Comparing the Fullness of Different Morphospaces*

Do snails, based on parameters of shell coiling, occupy more of the morphospace available to them than do arborescent bryozoans, based on the parameters of branching growth? In morphospaces that lack theoretical maxima and/or minima for at least some parameters (such as the coiling space), this question may be intractable. If we somewhat less ambitiously restrict ourselves to the observed extremes (observed maximal and minimal values of quantitative traits), then average differences between species can be expressed as a proportion of the maximal possible difference (as is commonly done with discrete character

data). Clearly, how fully a morphospace is occupied is potentially very sensitive to the choice of traits (83). A common approach in interpreting secular patterns of morphological diversity is to consider disparity at any time relative to the maximal disparity reached by a group in its history (e.g. 40, 47). Even if this does not allow us to say that diatoms are more diverse morphologically than dinosaurs, it does allow us to address whether morphospace was filled more gradually or abruptly in one group versus another.

### *Sampling and Preservation of Morphological Diversity*

One measure of the robustness of evolutionary patterns concerns their sensitivity to sampling (48, 120, 168, 170). Blackburn & Gaston (7) found that smaller-bodied species in several groups of living animals have been discovered at an increasing rate toward the present day. Thus, apparent geographic and ecological patterns based on body size may not be robust to sampling. On the other hand, a study of several large groups of fossil marine invertebrates showed that, based on multivariate measures of morphology, there is no appreciable preference for morphologically extreme or modal species to be described earlier or later in the history of systematic paleontology (48). This suggests effectively random sampling of preserved forms at the large scale, although certain details of evolutionary patterns of disparity within the studied groups have changed as more material has been discovered and described (48).

Whether a sample of fossil species is biased with respect to morphological disparity (relative to the entire statistical population of preserved species) is a different question than whether those preserved species are a representative sample of all the species that lived in some group. Some organisms are more likely to be preserved than others. For example, all else being equal, thick skeletons are more likely to enter the fossil record than are thin skeletons, and single-element skeletons are more likely to preserve than those consisting of unfused sclerites. But this bias does not imply that disparity itself will be biased; the crucial question is whether the average morphological dissimilarity among preserved species is the same as that among all species that could have been preserved. To my knowledge, this question has not been addressed in detail, but a simple test is possible (similar to that which Valentine performed to assess the completeness of the fossil record of marine molluscs in the Californian province—145). Take a large group of Recent species that can be divided into a number of groups, say taxonomically or geographically. Quantify the form of each species and measure the disparity of the entire group and each subgroup. Now consider only those living species that are known from the fossil record, and measure the disparity of the entire fossil sample and the fossil samples of subgroups. If disparity is unbiased by preservation, then the values of disparity for the entire fossil sample and fossil subsets should be statistically

indistinguishable from the values for the entire living sample and its corresponding subsets. This test requires that disparity be measured in a way that is sensitive not to sample size alone but to the representativeness of the sample; variance of morphology, for example, would be preferable to the range.

### *Ecomorphology*

The success of ecomorphology rests on the ecological or functional significance of measured morphological features (104, 159). In many cases the correlation between form and ecology or function seems sufficiently strong (12, 104), but this may not always be the case. For example, is it reasonable to suppose that the diversification of form as represented by the outline shapes of trilobite heads reflects ecological diversification (36)? Considering the ubiquity of character correlations (95), the diversity of a large array of haphazardly selected morphological features may provide a good proxy for ecological diversity, but this should be tested extensively with living species. For example, we could quantify trophic and functional differences among a large number of species and compare these to the morphological differences among these same species based on traits that are not deliberately selected for their presumed ecological or functional significance. If many comparisons of this kind revealed a general correspondence between morphological and ecological dissimilarities, then the inference of ecological diversification from morphological diversification would be reliable.

### *Geographic Context of Morphological Diversification*

Latitudinal, provincial, and bathymetric patterns of taxonomic diversity have revealed interesting patterns in life's history. For example, Jablonski & Bottjer (71) showed that higher taxa (orders) tend to originate preferentially in near-shore environments, in contrast to lower taxa (genera), and Jablonski (70) documented the preferential origin of higher taxa in the tropics. Miller & Mao (92) found that global patterns of taxonomic diversity in the Ordovician were not matched by patterns within provinces, implying that explanations for global diversification could not simply be extrapolated up from smaller-scale explanations, but might, for example, involve changes in faunal differentiation among provinces. In contrast, geographic patterns of morphological diversity in the fossil record have scarcely been explored (111). Do those areas that generate evolutionary novelties (nearshore environments, tropics) also accumulate greater morphological diversity, or are they simply a source of novelties, with the net disparity accumulating elsewhere? Do areas with higher taxonomic diversity tend to have a greater diversity of form, or do they reflect numerous trivial variations on the same themes? How is global morphological diversity broken down into provincial patterns? In some preliminary analyses, AI Miller & M Foote (unpublished) found that the global increase in morphological diversity of Ordovician trilobites is matched by an increase in disparity of endemic

genera, but that the disparity of cosmopolitan genera scarcely changes through the Ordovician. This suggests that global diversification of form is mainly attributable to endemic radiations.

### *Evolutionary Models and Data Analysis*

I stated earlier that simple branching models of evolution have been of limited success in isolating the mechanisms of morphological diversification, since a range of different parameters can yield very similar patterns of taxonomic and morphological diversity. The range of patterns that could result from stochastic variation about a constant set of parameters has mainly been addressed by simulation (35, 39, 47, 103). The variance in taxonomic diversity trajectories is understood analytically, and it would be worth developing a similar analytic distribution for disparity trajectories. This would give clues as to how different two observed disparity histories need to be before we have some confidence that the difference does not simply reflect sampling error or stochastic variation.

In addition to incorporating phylogenetic information to assess the size of transitions and to understand in more detail how morphological space is filled (33, 62, 65, 126, 163–165), it is also crucial to consider alternative ways of analyzing diversity and disparity data. For example, Wagner has suggested that the comparison of cumulative diversity and cumulative disparity (total number of taxa that have lived up to some point in time and the disparity among them) may help address whether a rapid proliferation of morphological diversity is attributable to many smaller evolutionary transitions or to a few larger transitions (164). (There are certainly difficulties here. For example, a clade may wander around in morphospace with the result that cumulative disparity increases substantially even though standing disparity may change little; such a pattern would be difficult to distinguish from one in which a clade continually expands its diversity of form. But such complications would thwart interpretations only if we relied on just one mode of analysis.) I suggested earlier that using a variety of methods to study disparity is generally more enlightening than attempting to select the single most appropriate approach. Considering the diversity of methods that have been developed, a serious effort to understand the theoretical and empirical relationships among these approaches, and how these relationships depend on particular models of evolution, could result in significant advances.

## CONCLUSION: THE ROLE OF DISPARITY IN MACROEVOLUTION

This review and most of the work discussed here have focused on morphological disparity essentially as a passive response variable. How is disparity affected by extinction events? How do changes in taxonomic and morphological rates of evolution affect disparity? How do new ecological opportunities allow a

clade to diversify morphologically? How do limits of form check the increase in disparity? However, just as higher-level properties of taxa (such as species richness of genera and geographic range of species) may affect the risk of extinction (69), the morphological diversity of a clade may also affect its evolution. For example, Wagner compared the evolutionary histories of two concurrently evolving clades of rostroconch molluscs to determine whether the group that survived the end-Ordovician extinction also showed a more substantial early diversification of form (165). This might be expected, since a wider range of form could represent a greater range of ecological and functional modes, which would enhance the probability that at least some lineages would survive. In this case, a concordance between early diversification of form and later resistance to extinction was not found. In contrast, in a preliminary study (unpublished) of variation in body size among species within families of Late Ordovician trilobites, I found that the families with a greater variance in size preferentially survived the end-Ordovician extinction event, even when the effect of species richness was factored out statistically.

The study of disparity in the fossil record is in some ways still young, yet it has already enhanced our understanding of large-scale heterogeneities in the history of life (such as the early generation of substantial morphological diversity at low taxonomic diversity and the characteristically different pattern of morphological diversification within major clades versus their constituent subclades), the nature of evolutionary radiations and biotic replacements, selectivity of extinction, and the role of ecological interactions in shaping macroevolution and community structure. The future success of disparity studies will continue to rest upon a pluralistic attitude and a willingness to consider morphological diversity, not just as a characteristic of evolving systems, but also as a causative agent in macroevolution.

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