

# DISPARITY: MORPHOLOGICAL PATTERN AND DEVELOPMENTAL CONTEXT

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**Abstract:** The distribution of organic forms is clumpy at any scale from populations to the highest taxonomic categories, and whether considered within clades or within ecosystems. The fossil record provides little support for expectations that the morphological gaps between species or groups of species have increased through time as it might if the gaps were created by extinction of a more homogeneous distribution of morphologies. As the quantitative assessments of morphology have replaced counts of higher taxa as a metric of morphological disparity, numerous studies have demonstrated the rapid construction of morphospace early in evolutionary radiations, and have emphasized the difference between taxonomic measures of morphological diversity and quantitative assessments of disparity. Other studies have evaluated changing patterns of disparity across mass extinctions, ecomorphological patterns and the patterns of convergence within ecological communities, while

the development of theoretical morphology has greatly aided efforts to understand why some forms do not occur. A parallel, and until recently, largely separate research effort in evolutionary developmental biology has established that the developmental toolkit underlying the remarkable breadth of metazoan form is largely identical among Bilateria, and many components are shared among all metazoa. Underlying this concern with disparity is a question about temporal variation in the production of morphological innovations, a debate over the relative significance of the generation of new morphologies vs. differential probabilities of their successful introduction, and the relative importance of constraint, convergence and contingency in the evolution of form.

**Key words:** Morphological disparity, morphospace, evolutionary radiation, ecomorphology, theoretical morphology.

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THE diversity of morphological form has been at the heart of much of organismal biology since the days of Cuvier, who used the discontinuities in shape and form as a basis for grouping animals into clusters. But this clustering itself raises a host of questions: Why is it that the morphology of arthropods is so disparate, but that of priapulids, or flamingoes, so limited? Why do biological forms exist in clumps, at a variety of scales? What can we learn about the evolutionary process by tracking the diversity of organic form (disparity) through time? Understanding the processes and conditions that influence differences in the range of form is critical for understanding the construction of biodiversity. Over the past two centuries, many approaches have been pursued to understand disparity. Considerable impetus to this effort was provided in 1989 by Stephen Jay Gould's 'Wonderful Life', in which he employed the exquisite fossils of the Middle Cambrian Burgess Shale to argue that the morphological disparity of arthropods at that single locality was greater than for all extant arthropods. Such early

disparity was, in Gould's view, inconsistent with the predictions of an evolutionary theory that implied increasing morphological disparity with increasing taxonomic diversity through the history of a clade. Since 1989, new quantitative and phylogenetic approaches have allowed more rigorous analysis of patterns of disparity. We can now address in a meaningful way issues about the distribution of morphologies through time and across phylogenies, construct state spaces depicting such occupation patterns and ask questions about patterns of occupation.

Palaeontologists have long recognized that among animals, the origin of the morphological disparity recognized (however imperfectly) by the Linnean ranks of metazoan phyla, classes and many orders is largely confined to the early Palaeozoic. Although this pattern has been criticized as an artefact (a claim that can now be rejected through quantitative studies of disparity; see below) discussion has largely focused on whether this pattern is time-inhomogeneous, reflecting a decline in the production of the morphological novelties that produce major new forms, or

variation through the Phanerozoic in the success of major new innovations. The first possibility is generally known as the genetic or developmental hypothesis and in essence posits a mutation-driven model of evolutionary change. The second, ecospace, hypothesis suggests that variations in ecological opportunity control the success of major new morphologies and has produced a pattern that mimics differential introduction on innovations. I must emphasize that although these two models are often seen as competing explanations, they are not logically opposed and it is indeed quite possible that both operated. So the real question may be the relative contribution of the production of developmental potential and the available ecological opportunity. As an aside, these two alternatives find direct corollaries in work by economists of technological change who discuss 'supply-driven' innovation (akin to the developmental hypothesis) and 'demand-driven' innovation (the equivalent to the ecospace hypothesis).

An interesting complication to the developmental hypothesis has recently emerged. The basic genetic and developmental toolkit underlying all bilaterians is fundamentally the same, and indeed is broadly shared among all metazoans. To the annoyance of a few population geneticists, it has been conclusively established that much of the incredible diversity of form among metazoans rests not on entirely new genes, or even novel regulatory and developmental schemes, but on rewiring the relationships among conserved signalling molecules. Morphological disparity does not seem to reflect an underlying structure of developmental innovations. New comparative developmental studies are providing a mechanistic foundation for understanding the origin and basis of morphology.

This review of morphological disparity in the fossil record begins with a discussion of the variety of approaches used to assess morphological disparity, from the use of taxonomic ranks as proxies for morphological distance, through quantitative analyses and the use of character state from phylogenetic analyses to the parallel growth of theoretical morphology. I next review the range of disparity studies and their application to specific evolutionary questions before turning in the final two sections to the questions raised above about the role of development and ecology in producing the patterns of disparity seen among animals, the likely cause of morphological clumpiness, and implications of these studies for the relative importance of constraint, contingency and convergence, and more broadly for our understanding of the processes of development.

## RECOGNIZING IT WHEN YOU SEE IT: MEASURING DISPARITY

Measuring disparity has been described as an issue of characterizing within-group variance of form, a task that

is much easier in some groups than in others (Foote 1997, a paper that remains an outstanding review of morphological disparity). The null model is that morphological disparity, like taxonomic diversity, should increase during the history of a specific clade. This requires establishing whether patterns of disparity exceed those expected given the age of the clade, or conversely whether disparity is less than expected. A wide range of techniques have been used to characterize disparity, from the use of Linnean ranks and the host of quantitative measurements of form, now increasingly in a phylogenetic context, to ecomorphological measurements of disparity and theoretical morphology, which allows one to address the difference between potential and realized forms and how these have changed through time.

### *Taxonomic disparity*

The earliest approach to disparity used taxonomic ranks as proxies for morphological distinctiveness. By counting families or genera one could simultaneously assess changing patterns of taxonomic diversity and morphological disparity (e.g. Valentine 1980). The underlying assumption was that taxonomic rank was a relatively reliable index of disparity, and that genera and families were a reliable proxy for species diversity.

For example, in 1987 Jim Valentine, Jack Sepkoski and I compared the early Palaeozoic diversification to the post-Permian rebound of the Mesozoic (Erwin *et al.* 1987). Using short-lived families as an index of experimentation, we explored whether there was greater family-level experimentation in the early Palaeozoic accompanying the origination of new phyla, classes and families. We assumed that families (and higher taxa) were a reliable proxy for new forms. Our analysis showed roughly equivalent numbers of short-lived families during each interval, from which we concluded that there was a discontinuity in evolutionary dynamics between the introduction of ordinal and higher taxa on the one hand, and family and lower level taxa on the other. This was but one of many studies at the time which used taxonomic ranks as proxies for morphological disparity.

Famously (or perhaps infamously), Gould (1989) used a similar approach in 'Wonderful Life' to argue for an early flowering of morphologies during the Cambrian radiation of animals, followed by a subsequent winnowing of these forms. Writing at the highpoint of a craze for extinct phyla, Gould accurately captured the prevailing sense that the Burgess shale and other Cambrian deposits documented the widespread proliferation of new forms. The degree of disparity thus played a significant role in arguments over the importance of contingency vs. selection and drift in the history of life.

This approach has been criticized because higher taxa are often viewed as artificial, non-monophyletic and subjective (e.g. Smith and Altaba 1988; Smith and Patterson 1988; Smith 1994; Forey *et al.* 2004), but as Foote (1997) noted, the issue is really whether higher taxa have information content that makes them a useful proxy. Aspects of morphological disparity are captured by taxonomic rank, but this provides but a single variable and accurate comparison is difficult. Nonetheless, some of the insights provided by taxic metrics have been largely confirmed by subsequent quantitative assessments of disparity.

#### *Quantitative measurements of disparity*

While a variety of quantitative measurements of disparity have been proposed, the most common have been average pairwise character dissimilarity and the total variance (sum of univariate variance) (see Foote 1997). Ciampaglio *et al.* (2001) evaluated these and five additional measurements of disparity [total range, mean distance, number of unique pairwise character combinations, principal coordinate analysis (PCO) volume, and participation ratio] for their sensitivity to sample size, number of morphological characters, percentage of missing data and changes in morphospace occupation pattern (see also Foote 1991, 1993*b*, 1999; Wills *et al.* 1994; Villier and Eble 2004). The results show that there is no single best estimate of disparity; different measures capture different aspects of disparity. Thus, the appropriate measures will depend, at least in part, on the questions addressed and the samples available. The results of Ciampaglio *et al.* (2001) parallel those of Foote (1993*b*) in suggesting that average pairwise dissimilarity, which is relatively immune to different sample sizes, is a useful metric for differences between taxa. Unique pairwise character combinations can reveal the amount of space occupied, and a distance metric such as PCO volume or mean pairwise distance can reveal changes in character space occupation. In addition, while some studies have looked at single characters or character suites, the trend has been towards inclusion of a greater range of characters, both because estimates of morphological disparity may vary between characters, and because this allows partitioning of characters with different functional roles (Foote 1994; Wagner 1995; Eble 2000*b*; Ciampaglio 2004). Such a combination of metrics will provide a more informative analysis of changes in morphological disparity than a single measure alone.

Phylogenetic characters provide an alternative approach to analysing disparity, one that is particularly useful in the absence of homologous characters amenable to geometric morphometrics. Wagner (1997) used the average patristic dissimilarity per branch over branch distance as his metric of morphological separation and the median

pairwise phenetic dissimilarity among all pairwise comparisons as his metric of disparity. However, Wagner (2000) showed that at least for the sorts of characters useful for phylogenetic analysis, the number of character state spaces is rapidly exhausted, so that further character change is likely to repeat previously achieved character states. In the case of binary characters, after infinite evolution character exhaustion would produce an average similarity of 0.5 (P. Wagner, pers. comm. 2006). With continuous character states, exhaustion is less of a problem. Thus, the potential morphospace as measured with continuous characters should be larger than that for discrete characters, even for the same clade.

Although character-based studies of disparity evaluate changes in form across taxa, Eble (2003) pointed out that developmental morphospaces can also be constructed which more closely illuminate patterns of developmental variation in form. Theoretical morphospaces, the subject of the next section, are one example of a developmental morphospace as they are inherently generative, although often not in a way that can translate directly into how developmental evolution occurs.

*Morphospaces and theoretical morphology.* Vertebrates with six appendages are a biological impossibility, evidently for developmental reasons. Arthropods clearly lack such inhibitions. (Ironically, either this means that angels are arthropods or it is a biological refutation of the possibility of angels!). But establishing such a 'geography of possible worlds' (MacLaurin 2003, p. 463) requires more consideration in other clades. Studies of disparity have largely been based on exemplars of known taxa, facilitating description of changes in the occupation of a morphospace through evolutionary radiations, across time or in response to mass extinctions. Although the distinction has been disputed, most prominently by Michael Foote, such empirical morphospaces are of limited utility in addressing what forms could have evolved but have not, and why.

Empirical morphospaces are defined on the basis of the forms included in the analysis; addition of new forms will change the morphospace, albeit sometimes very subtly. Only with theoretical morphospaces can we distinguish realized from potential forms and explore issues of constraint, as yet unexplored possibilities and impermissible forms [Lauder *et al.* 1995; McGhee 1999; although see Eble 2000*b* for an interesting discussion of how the distinction between theoretical and empirical morphospaces breaks down with raw (unordinated) morphospaces]. Foote argues that given a skeletal element, for example a long bone, it is possible to map out the range of possible forms and compare these with those that are known (Foote, pers. comm. 2006). I think the difference lies in that theoretical morphospaces require some growth model

to generate the diversity of form, and this is what Foote is also doing, at least implicitly, in his example.

That such theoretical morphospaces are easiest to construct for organisms using accretionary or branching growth accounts for the predominance of studies of molluscs, particularly ammonoids. Raup (1966) first developed the concept of theoretical morphospace for logarithmically coiled shells and demonstrated that bivalves, gastropods, ammonoids and brachiopods are limited to particular portions of the morphospace. For bivalves and brachiopods the requirement that the two valves meet imposes an architectural constraint on the regions of morphospace that can be occupied, and in his 1967 paper on ammonoids Raup discussed in detail the reasons behind correlations between different shell coiling parameters. Schindel (1990) subsequently dissected the non-orthogonal nature of the Raupian morphospace despite how it was depicted (and frequently reproduced, e.g. Lauder *et al.* 1995). Thus, at least part of the pattern of morphospace occupation is an artefact of presentation. Thomas and Reif (1993; see also Thomas *et al.* 2000) developed a more abstract morphospace. Termed the 'skeleton space', this allows classification of skeletal features in terms of various aspects of design and growth. By the more abstract nature of the morphospace, it allows a broader range of skeletal types to be considered within the same context. Thus, Thomas *et al.* (2000) evaluated the occupation of this morphospace by the various organisms of the Middle Cambrian Burgess Shale, concluding that they occupied 80 per cent of the morphospace that has been exploited by all extinct and extant animals.

Patterns of occupation within theoretical morphospaces can reveal much about functional constraints. Viable helically coiled bryozoan colonies are limited to low to medium surface area for functional reasons (McGhee and McKinney 2000). Niklas's theoretical morphospace for plant growth captured plant structure by defining branching and rotation angles around an axis, generated a variety of morphologies, and allowed evaluation of their function in terms of light interception and other variables (Niklas 1986, 2004; see also discussion in McGhee 1999). Theoretical morphospaces have now been explored for a variety of other groups, including corals, a variety of bryozoans, echinoids, graptolites and some fish; McGhee (1999) provides a thorough introduction.

McGhee (1999) argued that it is only within the context of theoretical morphospaces that we can address the issue of forms that could have existed but which have never evolved. Although empirical morphospaces can be useful in this quest, McGhee is largely correct that theoretical morphospaces provide a more useful method. It is thus particularly unfortunate that some groups, particularly arthropods, have so far proved intractable for the construction of morphospaces. Application of fractal

growth models (Prusinkiewicz and Lindenmayer 1990; Kaandorp 1994) may provide one avenue to extend theoretical morphospaces.

Theoretical morphospaces are far from a panacea, and for some questions about morphological innovations they can be a trap. MacLaurin (2003) noted that, as with any model, theoretical morphospaces capture only a component of form, and users must be particularly careful not to claim greater generality for the results than is justified by the model. An additional problem is the bounded nature of theoretical morphospaces, which inhibits (or eliminates) the study of significant innovations. These morphospaces may be particularly valuable to studying heterochronic changes, while downplaying heterotypic and other morphological changes (Eble 2000*b*). Finally, if the dimensionality of the morphospace itself changes during innovation, as may often be the case, then neither empirical nor theoretical morphospaces accurately capture the dynamics of the morphological changes.

*Morphospace in a phylogenetic context.* Morphospaces show the distribution of forms in space but provide no information about whether two closely aligned forms are phylogenetically related or share a locality as the result of convergence. Resolving this requires mapping the phylogeny of the group within the morphospace (Bookstein *et al.* 1985; Wagner 1995, 1997; David and Laurin 1996; Foote 1996*a*; Eble 2000*b*; Stone 2003). Relatively few studies have included a phylogenetic component. Doing so allows at least partial reconstruction of ancestors, permits testing hypotheses of evolutionary transformation and can aid in identifying evolutionary constraints.

When morphospaces are three-dimensional mathematical spaces, mapping phylogenies faces the difficulty of positioning non-terminal nodes. Because these internodes represent successive common ancestors, correct positioning of them is essential for testing hypotheses about the patterns of transformation. In character-based studies of disparity this is relatively easy using maximum-likelihood or similar methods. Stone (2003) proposed use of geometric algorithms for three-dimensional spaces, producing what he termed a 'cladistic morphospace'. This technique assumes that evolutionary transitions will follow the straightest path; thus, the technique may be increasingly likely to produce invalid results as the taxa are exemplars of larger clades, or the sparser the recovered record. In their study of the radiation of iguanid lizards, Harmon *et al.* (2003) developed an alternative approach to the inclusion of phylogenetic information that obviates the need to map nodes into the morphospace, but which does not yet seem to have been applied in palaeontological studies (discussed further below).

*Problems in assessing disparity.* As with any technique there are a variety of potential difficulties in assessing changes in morphological disparity. Distinguishing functional explanations for patterns of morphospace occupation from historical and developmental constraints and contingency is not necessarily straightforward. Issues associated with which statistical techniques best sample within-group variance were discussed above, and Raup (1972, 1987) noted that features not captured by the analysis may influence the results. The issue of character exhaustion when discrete characters are used to analyse disparity was also noted above. When comparing the disparity patterns of two or more clades, differences in clade age can become important. As a clade ages we expect morphological disparity to expand; this requires analyses of disparity to control for clade age and to distinguish random walks through morphospace from patterns that need and require explanation.

Because patterns of morphospace occupation have been interpreted as evidence of particular evolutionary processes, they must be distinguished from random walks (Foote 1996b; Gavrillets 1999; Pie and Weitz 2005). Gavrillets's (1999) simple model of taxonomic diversity and disparity showed that deceleration of morphological disparity during a radiation was an expected consequence of the geometry of morphospace coupled with speciation and extinction. This suggests that changing early maximal disparity may not indicate time-inhomogeneous changes in evolutionary patterns. It is not obvious that this criticism applies to any individual case, however, as it requires a demonstration that the empirical distances between taxa have approached the upper limit (M. Foote, pers. comm. 2006). A different approach was advocated by Pie and Weitz (2005) who used branching random walks as a null model for morphospace occupation, with the goal of stripping out the random component. This approach is derived from the earlier work of Raup and Gould (1974; see also Bookstein 1987). Particularly significant was their observation that on simulated adaptive landscapes, clumping of forms into regions of morphospace occurs even if the landscape is flat and thus requires no special explanation. This irregular occupation of morphospace reflects the likelihood of coupled random walks.

Clade age can be a troubling issue, but has been relatively infrequently addressed by palaeobiologists. One normally expects that the older of two clades will have greater disparity, simply because it has had a longer interval over which to explore possible morphologies. However, simply comparing two sister clades may be insufficient if the crown groups under study are of different ages. For example, Collar *et al.* (2005) compared the increases in morphological diversity between two clades of centrarchid fish (sunfish and black basses). After controlling for different ages of the crown groups, the

possibility of random walks and considering rates of change, they concluded that: '... comparisons of within-group morphological variance can be useful for examination of patterns of diversity at some point in time, [but] variance comparisons may confound two distinctly different causes of trait variance – time and the rate of evolution of the trait' (p. 1790). Because rates of morphological change are independent of phylogeny and time, Collar *et al.* concluded that they are a more useful metric than disparity for comparing morphological diversity. This is unlikely to be true for some of the questions of interest to palaeobiologists and other macroevolutionists, but the concerns raised in these studies should be considered.

Differences in analytical methods and procedures including temporal scale and levels of taxonomic refinement and varying efficacy of corrections for clade age, random walks and other factors make comparisons between the results of different studies of disparity hazardous (some might say foolhardy). Villier and Eble (2004) used Eble's (2000a) data on Cretaceous spatangoid echinoids to evaluate how different sources of data (homologous landmarks, traditional morphometrics and discrete characters) and analytical methods influenced the analysis of disparity, and also investigated the role of time and using species vs. genera as the units of analysis. In this analysis, the pattern of disparity appears relatively robust to differences in data, analysis and temporal scale. In particular, Villier and Eble's results suggest that sampling may be less of an issue than suggested by the simulations of Ciampaglio *et al.* (2001).

It is perhaps worth noting that disparity maps in interesting ways to the morphologies defined by systematists. The first, and probably still the most influential, such study was the work of Tabachnick and Bookstein (1990) on variation in the Miocene foraminifera *Globorotalia*. They showed that the named species bore little relationship to the relatively continuous distribution of forms at one time, and even more interestingly, that the distribution of forms evolved to a more clustered distribution. By contrast, Courville and Crônier (2005) evaluated the disparity among presumed 'species' of the Jurassic ammonoid *Kosmoceras* and found a better relationship to previously described taxa.

*Summary.* This review suggests the following conclusions. First, that a variety of quantitative techniques for the analysis of disparity are now available for both geometric morphometric data and character-based studies. Use of several methods together seems wise, and average pairwise dissimilarity, which is less affected by sample sizes, is a useful metric for differences between taxa; unique pairwise character combinations can reveal the amount of space occupied; and distance metrics such as

PCO volume or mean pairwise distance reveal changes in morphospace occupation. Second, use of discrete characters may create a problem with character exhaustion and could produce underestimates of disparity relative to studies using continuous characters. Third, the use of phylogenetic information in conjunction with disparity studies is the only way to recover step sizes between morphologies and transformation series, although studies without such a framework are useful for many questions. Finally, many of the initial studies of disparity did not consider issues of random walks from an initial condition, differences in clade age, or other confounding difficulties.

### PATTERNS OF MORPHOSPACE OCCUPATION THROUGH TIME

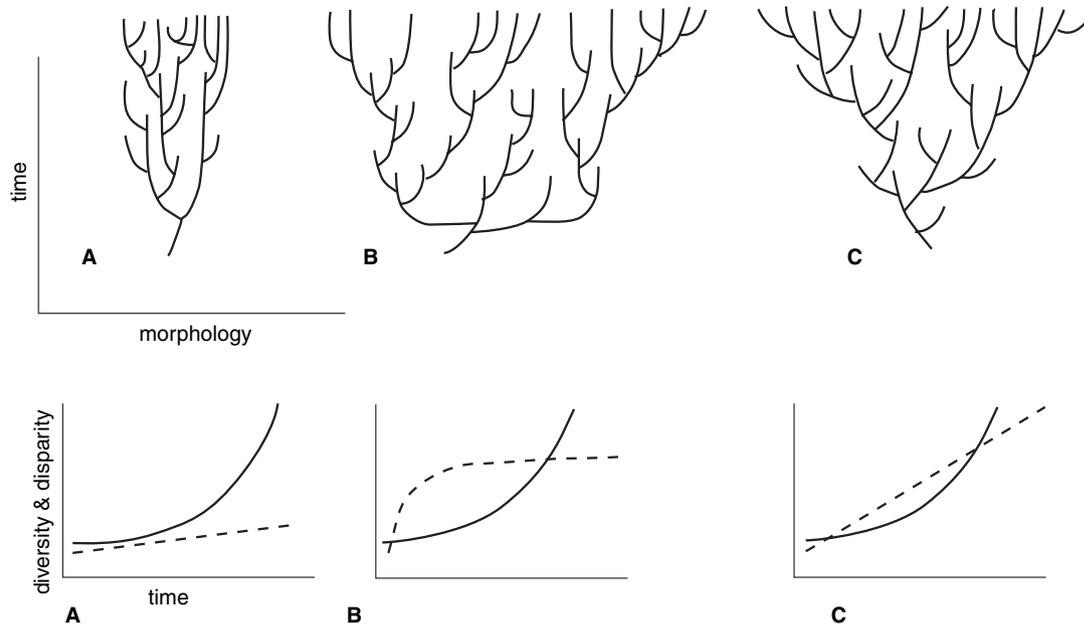
The application of these methods has produced an increasingly detailed picture of the patterns of disparity through much of the Phanerozoic, with particular emphasis on the evolution of disparity through evolutionary radiations, and across mass extinctions and into subsequent biotic recoveries. Most of these studies address patterns among marine invertebrates, reflecting the initial questions about patterns of disparity by Gould, but stud-

ies of plants, terrestrial vertebrates and even acritarchs are now appearing.

#### *Disparity during evolutionary radiations*

Foote (1993*b*, 1996*b*; see also Wesley-Hunt 2005) identified three potential relationships between taxonomic diversity and morphological disparity (Text-fig. 1): constrained morphological disparity with taxonomic diversification unrelated to disparity; a rapid increase in disparity exceeding initial taxonomic diversification, with large early steps in disparity and smaller ones later; and finally concordant increases in disparity and diversity, with no apparent constraints on disparity or changes in step size. The final possibility subsequently turned out to be the least probable when disparity is analysed with discrete characters owing to character exhaustion, as discussed previously.

Gould's publication of 'Wonderful Life' (1989) and his claims about maximal early disparity triggered the early quantitative studies of disparity. Briggs *et al.* (1992*a*) constructed a morphospace based on a principal components analysis of discretely coded morphological characters of 25 arthropods from the Burgess Shale and from representatives of 21 classes and



**TEXT-FIG. 1.** Above, idealized diversity patterns (modified from Foote 1993*a*, Fig. 1, p. 192). Below, predicted diversity and disparity curves over time (solid line, taxonomic diversity; dashed line, morphological disparity). A, constrained morphological evolution with taxonomic exceeding morphological diversification. B, morphological diversification outstrips taxonomic diversification with large morphological steps early in the clade's history; morphological diversity may continue to increase, but steps are smaller. C, morphological diversification is concordant with taxonomic diversification; no constraint on morphological evolution, nor trend in morphological step size (redrafted from Wesley-Hunt 2005).

subclasses of recent arthropods. Their phenetic approach to disparity employed a Euclidian distance matrix, and they concluded that recent arthropods occupied 89–95 per cent of the volume of the Cambrian taxa. That a single sample of Middle Cambrian arthropods occupied a slightly larger volume than a representative sample of all extant arthropods is itself rather remarkable. This study provided the earliest demonstration that maximal disparity was reached early in the history of a clade. Foote and Gould (1992) responded that the sample of recent taxa was biased, and that an unbiased sample would have confirmed that Cambrian disparity exceeded that of recent arthropods (Briggs *et al.* 1992*b*). The debate over Cambrian disparity continued through a series of papers (Gould 1991, 1993, 2002; McShea 1993; Ridley 1993; Wills *et al.* 1994; Fortey *et al.* 1996; Briggs and Fortey 2005) with a portion of the debate focusing on the issue of whether the unusual morphologies of the Burgess fauna represented new ‘bodyplans’ or higher taxa. Unfortunately studies of Cambrian arthropod disparity have not been extended to encompass the Early Cambrian Chengjiang fauna that includes additional arthropod forms not present in the Burgess Shale. Stockmeyer Lofgren *et al.* (2003) did address the pattern of change in arthropod disparity by studying some 100 Carboniferous species distributed across 48 orders, primarily from the Mazon Creek Lagerstätten. Although they

found a shift in the occupation of morphospace there was no evidence of an actual decrease in the volume of occupied morphospace.

Subsequent studies have identified a relatively consistent pattern of maximal disparity early in the history of the clade, during the initial increase in taxonomic diversity (Table 1). Among marine groups such patterns have been established among crinoids (Foote 1994, 1995, 1999), blastozoans (Foote 1992*a*), Palaeozoic gastropods (Wagner 1995), brachiopods (Carlson 1992; McGhee 1995; Smith and Bunje 1999) and Neoproterozoic acritarchs (Huntley *et al.* 2006). Decreases in disparity through time have been reported in rostroconchs (Wagner 1997), Palaeozoic stenolaemate bryozoans (Anstey and Pachut 1995), and within Carboniferous ammonioids (Saunders and Work 1996, 1997). By contrast, Wills’s (1998) character-based comparison of Cambrian and recent priapulids showed an increase in disparity among recent forms, albeit in a different region of morphospace. Mesozoic–Cenozoic aporrhaid gastropods exhibit a pattern of concomitant increase in disparity and diversity during the initial radiation of the group, but both trends continue to increase through the Cenozoic, albeit with differential increase in one of the two major portions of morphospace (Roy 1994).

Studies of disparity among terrestrial groups have lagged the marine realm but are increasing. In his study of pollen during the Cretaceous radiation of angiosperms,

**Table 1.** Patterns of morphological disparity in different groups.

Group studied	Citation
Maximal early disparity	
Proterozoic–Cambrian acritarchs	Huntley <i>et al.</i> (2006)
Palaeozoic gastropods	Wagner (1995 <i>b</i> )
Palaeozoic rostroconchs	Wagner (1997)
Ordovician bryozoans	Anstey and Pachut (1995)
Palaeozoic and post-Palaeozoic crinoids	Foote (1994, 1995, 1996 <i>a</i> , 1999)
Palaeozoic blastozoans	Foote (1992 <i>b</i> ), Wagner (1995 <i>a</i> )
Ordovician trilobites	Miller and Foote (1996)
Marine arthropods	Briggs <i>et al.</i> (1992 <i>a</i> ), Wills <i>et al.</i> (1994)
Insects	Labandeira and Eble (in press)
Angiosperm pollen	Lupia (1999)
‘Ecological carnivores’	Wesley-Hunt (2005)
Concurrent increases in diversity and disparity	
Palaeozoic trilobite clades	Foote (1993 <i>b</i> )
Palaeozoic blastoids	Foote (1993 <i>b</i> )
Mesozoic–Cenozoic aporrhoids	Roy (1994)
North American Cenozoic carnivores	Wesley-Hunt (2005)
Cenozoic ungulates	Jernvall (2000)
Increasing disparity	
Proterozoic–Cambrian acritarchs (probably due to polyphyletic nature)	Huntley <i>et al.</i> (2006)
Priapulids	Wills (1998)

Lupia (1999) established that disparity increased rapidly during the Late Cretaceous before reaching a plateau, and exceeded the increase in taxonomic diversity. Although he could not eliminate constraints as a reason for the change in disparity, he suggested that the pattern was more consistent with a change in the step size of morphological transitions, as described by Foote (1996b). Although Bateman *et al.* (1998) did not perform a quantitative analysis of disparity, they suggested that early, Siluro-Devonian plant radiations also follow a pattern of morphological disparity (which they termed phenotypic diversity) exceeding taxonomic diversity. Knoll *et al.* (1984) reached a similar conclusion.

The number of studies of tetrapods remains limited. New work addresses disparity patterns associated with Palaeozoic tetrapods, and particularly with the transition to land (Ruta *et al.* 2006; Wagner *et al.* 2006), where there is an order of magnitude decline in the rates of morphological change between the Devonian and Permian. The authors favour an intrinsic (developmental) explanation for the increasing constraint on morphological evolution, but could not exclude an ecological component as well. Jernvall *et al.* (1996) examined the disparity of molar teeth during the Cenozoic radiation of ungulates and showed concordant increases in morphological disparity and taxonomic diversity to a peak during the late Eocene, but this concordance breaks down in the post-Eocene. Jernvall *et al.* suggested that this may reflect global cooling and a decline in the quality of available vegetation relative to the Eocene. Wesley-Hunt (2005) also found concordant increases in disparity of tooth morphology and in diversity among North American carnivores, but with an ecological release and a rapid increase in disparity among 'mammalian meat eaters' after an efficient design evolves.

Labandeira and Eble employed an ecomorphological approach to examine the disparity of insects (in press; see also Labandeira 1997), using classes of insect mouthparts, functional feeding groups and dietary diversity as metrics of ecological disparity. This approach allows perhaps a more direct evaluation of how taxonomic diversity is influenced by the differential acquisition of resources than when morphology is employed as an indirect metric of ecological disparity. The results are similar to those for many other groups, with ecological disparity increasing before taxonomic diversity. Furthermore, the taxonomic diversity of insects has increased steadily, aside from occasional crises, while disparity appears to have peaked relatively early in the history of the clade.

Studies of disparity have also become more common on much smaller scales and among ecologists. In a beautiful study of disparity in a phylogenetic context that includes consideration of possible random walks and other confounding factors, Harmon *et al.* (2003) also

found that maximal disparity between subclades of *Anolis* and other iguanid lizards was reached early in their adaptive radiation. Their analysis used a lineage diversity index to assess the extent to which rates of lineage diversification exceeded the expectations of constant rates of diversification per lineage. Each of the four clades studied has a unique pattern of taxonomic and morphological diversification, yet a striking generality emerges as well: taxa that diversify rapidly early in their history partition morphological disparity between subclades, apparently filling the potential ecological space and retarding subsequent increases in disparity. By contrast, more slowly diversifying clades have greater within-subclade disparity.

#### *Changes in disparity across mass extinctions*

Studies of mass extinctions have exhaustively documented changes in taxonomic diversity, biogeographical selectivity and ecological filtering. Changes in morphological disparity have been less frequently analysed, although they promise considerable insight into the patterns of extinction as well as the pattern and processes of subsequent biotic recovery. A further motivation is to explore the issues raised by Erwin *et al.* (1987) about the causes of decreasing disparity through the Phanerozoic. If developmental patterning has become increasingly refractory to major modifications through time, then one could expect to see progressively less innovation after major mass extinctions (the developmental or intrinsic constraint hypothesis). Alternatively, if ecological interactions were inhibiting the success of novel morphologies, and the rate of production of developmental novelties was relatively constant, then the ecological release following mass extinctions might be sufficient to allow the rate of success to increase (the empty ecospace or extrinsic constraints hypothesis). As we pointed out in 1987, the end-Permian mass extinction is the best test of these alternatives because it was so much larger than any of the other great mass extinctions (Erwin *et al.* 1987).

Ciampaglio (2004) studied the disparity of articulate brachiopods (the new subphylum Rhynchonelliformea) from the Ordovician to the present, but concentrated on the impact of the Permo-Triassic mass extinction. He used total range of occupied morphospace, mean distance, number of unique pairwise character combinations and average pairwise dissimilarity, and a variety of different characters (see also Ciampaglio *et al.* 2001). Early Triassic disparity was below Ordovician values, but three of four metrics of disparity (all but range) increased by the Late Triassic. The persistent low values for total range were probably a reflection of the reduced post-Palaeozoic diversity of the clade. Indeed for mean distance and average pairwise dissimilarity, Late Triassic and Cretaceous

values were similar to the late Palaeozoic high for the group as a whole. This is particularly surprising given the extensive extinction of major brachiopod clades at the close of the Permian, but Ciampaglio showed that a finer scale examination revealed that the morphospace occupation of terebratulid and rhynchonellid brachiopods increased after the disappearance of the other groups, suggesting a pattern of ecological release (albeit largely in cryptic habitats). His tests show that in 75 per cent of the cases he considered, post-extinction disparity is equivalent to pre-extinction values, as is the volume of morphospace occupation. This indicates that developmental constraints were not retarding morphological evolution in the post-Palaeozoic articulate brachiopods.

The results of Foote's (1999) analysis of Palaeozoic and post-Palaeozoic crinoids were largely consistent with rapid exploitation of ecological opportunities in each case, but suggested that different regions of morphospace were explored during the two radiations. Significantly, however, the post-Palaeozoic event was not a 'refilling' of morphospace vacated during the end-Permian mass extinction, and there appears to have been a deceleration of morphological diversification among post-Triassic crinoids, although the cause of this remains unclear. Post-Palaeozoic crinoids are ecologically diverse even within their more constrained morphological range, emphasizing that a wide range of ecological strategies are possible even within more restricted morphologies (Foote 1999).

In a study of crinoids and blastozoans through the end-Ordovician, Late Devonian and end-Permian mass extinctions, Ciampaglio (2002) found that disparity rebounded after each event. Unique pairwise comparisons capture character innovation and indicate higher post-extinction disparity after each event for both clades, except for crinoids after the Late Devonian extinction. Considering all the metrics of disparity, 40 per cent of the time post-extinction disparity was *higher* than pre-extinction disparity. As in other clades, disparity does decrease in both groups through the Palaeozoic, and Ciampaglio suggested that this is primarily a function of increased ecological constraints imposed by increasingly narrowly defined ecological roles within guilds. As ecological roles within guilds become more structured with time, the likelihood of success of major new morphologies evidently declines.

Changes in ammonoid disparity through the Permo-Triassic were evaluated by McGowan (2004) and Villier and Korn (2004). Villier and Korn concentrated on the filtering of morphologies by the extinction and used the variety of shell morphologies as an indication of adaptive zones. They compared changes in taxonomic diversity to two measures of morphological disparity and identified three patterns of change in disparity: a long-term loss of disparity through the Permian, evidently a progressive

erosion of morphospace occupation probably reflecting a low rate of successful, new evolutionary novelties; a morphologically selective extinction across during the end-Guadalupian extinction; and finally a morphologically non-selective extinction at the end of the Permian. While diversity increased rapidly during the Early Triassic, disparity is either unchanged or increases slightly (depending on the measure).

In contrast to Foote's findings for crinoids, McGowan's comparison of late Palaeozoic and Triassic ammonoids found that within 10 myr of the end-Permian mass extinction, each of the seven pre-extinction morphotypes had reappeared, and the Triassic forms substantially reoccupied and then expanded the Palaeozoic ammonoid morphospace. There was, however, a significant shift in the relative frequencies of the various morphotypes. What is remarkable about this is that the Triassic radiation of disparity was accomplished in some 10 myr from a single ancestor, and within a single clade, the Ceratitida. While ammonoids may well have reached the limits of the morphospace available to them (Saunders and Swan 1984; McGowan 2004) they clearly possessed the developmental potential to re-explore these limits. Other studies that evaluated disparity through mass extinctions include Lockwood (2004) and Dommergues *et al.* (2002) who found a slight increase in size disparity among Early Jurassic ammonoids after the end-Triassic extinctions. The geometry of ammonoids has made them a favourite for studies of morphological diversity in other contexts as well (e.g. Korn and Klug 2003; Saunders *et al.* 2004).

*Summary.* A persistent feature of many evolutionary radiations is a more rapid increase in morphological disparity than taxonomic diversity. This is generally interpreted as an evolutionary radiation (*sensu* Erwin 1994) in an ecologically undersaturated environment; low competition is often inferred, although on theoretical expectations rather than direct evidence; Foote's exhaustive comparison of Palaeozoic and post-Palaeozoic crinoids (1996c, 1999) was explicitly framed as a test of this hypothesis. None of the studies discussed above found evidence for an increase in developmental constraints and most found evidence consistent with ecological release following mass extinctions. However, Lupia's (1999) analysis of angiosperm pollen disparity suggested a decline in the step size during the diversification of the clade. Although novelties became less likely they did not become impossible. The study of Ruta *et al.* (in press) on early tetrapod evolution through several radiations exhibits both increasing constraint and increasing disparity. Foote (1993a) and Wagner (1997) each made the intriguing observation that clades not exhibiting initial high morphological disparity are often subclades of groups that do show increased early disparity. Thus, trilobites within arthropods and blastoids

within blastozoan echinoderms do not show maximal early disparity but the sister clades of blastozoans and crinoids do show initial high disparity. Wagner (1997) found no pattern of early high disparity among rostroconchs, but did identify reduced disparity among the clade of rostroconchs that survived the end-Ordovician mass extinction relative to the broader clade.

## DISPARITY, DEVELOPMENT AND ECOLOGY

Although there are a number of questions about the evolutionary process to which the study of disparity can help provide answers, from patterns of occupation of morphospace during evolutionary radiations and ecomorphological diversification to the patterns of morphological selectivity during mass extinctions, the focus of this review has been on the extent to which changes in patterns of disparity in fossil clades can reveal underlying processes of change in developmental or ecological constraints. The preceding review of disparity generates four observations, which I will identify here and then discuss in more detail in the remainder of this paper.

First, studies of within-clade disparity have produced little support for the suggestion that internal genetic or developmental constraints have limited the generation of new morphological novelties within clades. Although most studies have confirmed that maximal disparity is reached early in the history of a clade, and often proceeds at a more rapid rate than taxonomic diversification, studies across mass extinctions confirm that substantial increases in disparity and changes in patterns of morphospace do occur through the Phanerozoic. In a sense this is not necessarily surprising because the success of comparative evolutionary developmental biology ('evo-devo') over the past decade or so has established that the basic toolkit for bilaterian morphogenesis is widely shared across Bilateria and did not develop uniquely within individual clades. As discussed further below, the generation of new forms is based on rewiring regulatory networks, some of which originated before the Eumetazoa. I will raise one caveat, however: the elucidation of the gene regulatory networks underlying development suggests the presence of a highly conserved and refractory structure that may constrain developmental trajectories, but at the level of specification of regional patterning mechanisms, aspects of morphology that are often shared at the phylum and class level, or higher than would be revealed by most of the disparity studies that have been conducted.

Second, although the ecospace hypothesis appears to be the better-supported explanation for the documented patterns of disparity, I believe that our conceptual approach to this issue needs to be updated. Palaeontologists have

generally been operating under a model in which evolutionary radiations and post-extinction diversifications occur in conditions of an undersaturated ecological environment with reduced competition. This is often expressed as filling 'empty niches'. Leaving aside our peculiar fascination with competition, I think we have largely failed to address the issue of how organisms are constructing the environments they inhabit: how they build niches and the network of ecological interactions that sustain them. From this perspective identifying the limits to occupied morphospace becomes an even more critical research agenda.

Third, there is another side to morphological disparity, one that is rather less discussed by palaeontologists than the causes of early morphological disparity: Why is the occupation of morphospace so clumpy and why are many regions of morphospace unoccupied? Lewontin (2003, unpaginated) observed: 'The real problem for the evolutionist is not to explain the kinds of organisms that have actually ever existed. The real problem for the evolutionist is how it is that most kinds of potential and seemingly reasonable organisms have never existed.' This is obviously an area where theoretical morphospace studies can be particularly useful. The *structure* of morphospaces and how they have evolved is clearly an area where a great deal more can be learned.

This leads me into the final observation. Having established a rigorous basis for the study of morphological disparity in a wide range of organisms, for incorporating (where available) phylogenetic information, and for addressing such confounding factors as random walks, clade age and character exhaustion, palaeontologists are now well placed to have a significant impact on the dissection of *how* clades occupy morphospace, and, more specifically, the extent to which modularity in development, constrained patterns of variation, and functional and ecological considerations influence the evolution of form.

Having noted each of these general observations I will next discuss each in greater detail.

*The developmental hypothesis revisited.* The lack of evidence for a restriction of morphological disparity after major mass extinctions would seem to suggest a rejection of the developmental hypothesis of increasing genetic or developmental constraints through the Phanerozoic. Recent discoveries in evolutionary developmental biology suggest that the flaws in the developmental hypothesis may be more apparent than real, for there is a fundamental difficulty with the research agenda on disparity. Most of the studies discussed here (Thomas *et al.* 1993, 2000 being a conspicuous exception) address changing patterns of disparity *within* major clades. Less a deficit than a reflection of necessity, geometric morphometrics and, in a

different way, character-based methods require reasonable comparability of form as a basis for comparison. The fewer the homologous points, the less the basis for comparison. But this approach assumes that processes and constraints extrapolate smoothly between various clades and subclades within the hierarchy of life. What if the most interesting developmental and ecological innovations are reflected in changes between clades that lack sufficient homologous points to make the analysis of disparity meaningful? If constraints are hierarchically nested, patterns of change in disparity *within* clades or subclades will reveal little about the constraints that exist *between* them.

Comparative studies of metazoan development ('evo-devo') have established to general satisfaction that the toolkit of developmental machinery was determined quite early in metazoan evolution, indeed before the origin of the Bilateria (as recognized early on by Valentine 1995; see discussions in Knoll and Carroll 1999; Valentine *et al.* 1999; Carroll *et al.* 2001; Erwin and Davidson 2002; Valentine 2004; Carroll 2005; Erwin 2005, in press; Davidson 2006). The incredible diversity of bilaterian form is produced by a highly conserved set of transcription and signalling factors that control specific patterning mechanisms, and by rewiring the regulatory interactions between genes. More complex animals do not have substantially more genes than less complex forms. In fact, it appears evolution can craft an animal of any complexity from roughly 20,000–25,000 genes.

The extent of this conservation was not anticipated when the developmental hypothesis was first established. As I recall, it seemed quite likely that a critical component of the Metazoan radiation was the construction of the mechanisms of pattern formation. No one had any idea in the mid-1980s that similar genes would be found to control eye or appendage formation across the Bilateria. It thus seemed a reasonable presumption at the time that the construction of these regulatory networks could harden them against subsequent major change and, thus, that there was significant evolution of the underlying mechanisms of metazoan development during the diversification of bilaterians. It may have been reasonable, but it was not correct. With increasing evidence that the tools for regional body plan specification evolved quite early, with many in place among cnidarians (Ball *et al.* 2004; Miller *et al.* 2005; Matus *et al.* 2006), followed by clade-specific elaboration of morphogenetic pathways for specific aspects of the bodyplan (in other words, arthropod vs. vertebrate appendages). Consequently I no longer see in our knowledge of development any expectation for the sort of hardening of regulatory networks suggested some two decades ago.

Eric Davidson of Caltech and I recently advanced a proposal that, if correct, may reinvent the develop-

mental hypothesis, in a very different way. Experimental studies of a variety of modal organisms have revealed that not only is the activity of specific regulatory elements highly conserved across bilaterians but also the network of gene interactions may be similarly conserved. Manipulations of these networks in some limited cases have demonstrated a core of genes that do not appear subject to much change: if any of the relevant transcription factors is knocked out, the embryo fails to develop. The set of five or six genes controlling heart specification is conserved across bilaterians, for example. Davidson and I suggested (2006) that a highly refractory gene network, which we termed kernels, lies at the core of all regional specification mechanisms among bilaterians. These regulatory networks can be deduced by reconstructing the *cis*-regulatory interactions among genes (see Davidson 2006 for details). In our view, the formation of these networks was responsible for much of the morphological diversification of the Ediacaran–Cambrian metazoan radiation. We are not suggesting that there is anything unusual about the mechanisms behind the formation of kernels but that once formed they fix modules controlling particular regional patterning mechanisms. This has the effect of forcing subsequent changes to modify either upstream or downstream portions of the regulatory network. The ways in which these modules are used allows the remarkable variety of form in arthropods, echinoderms and other groups, but it also provides constraints, evidently limiting how variation can occur within these modules. Critically, these constraints limit the range of possible variation that can occur subsequent to the formation of the kernels.

We also elaborated a hierarchical view of regulatory changes, with the formation of kernels responsible for the sorts of morphological features that have been recognized by Linnean taxonomy as those between phyla and perhaps classes (Davidson and Erwin 2006). At the opposite extreme, we see changes in allele frequencies and similar mutations as responsible for the differentiation of genera and species. The range of morphological changes of an intermediate level appear to be related to modifications of regulatory control among what we have termed 'plug-ins', regulatory elements which are re-used frequently to achieve particular effects (the transcription factor *Notch* is an obvious example), and input/output (I/O) links that connect different regulatory modules.

What are the implications of this view for morphological disparity? First, the hierarchical structuring of regulatory changes suggests that disparity at different levels may reflect changes at different regulatory levels. Among extant clades this is a testable hypothesis, and one that may open up opportunities for more rigorous analysis of changes among fossil groups. Second, this hypothesis suggests that the *potential* morphological space available

among bilaterians may have been greater in the late Neoproterozoic, as the kernels were forming, than subsequently. Once the kernels formed within a particular clade this may have frozen in the range of potential forms. This may be at least partly responsible for the patterns of clumpiness among clades. Third, the deep similarities in developmental processes may be mechanistic insights into the ubiquity of convergence and parallelism. Convergence is commonly explained as reflecting a similar adaptive response to particular problems, but the structure of development processes may facilitate the formation of variation.

*Disparity and niche construction.* The distribution of forms reflects the abilities and failures of organisms successfully to acquire resources. Thus, in some sense a morphospace, however constructed, reflects the distribution of successful means of adapting to both biotic and abiotic demands, and to acquiring the necessary resources for reproduction and for the clade to persist. The interest of functional morphologists in disparity comes, in part, from their desire to address such issues, although relatively few palaeontologists have used such an approach (Carlson 1992 and McGhee and McKinney 2000 are two notable examples). While the ubiquity of morphological convergence is a testament to the limitations that are placed on possible solutions, the dimensions of the niche constructed by a lineage reflect the sum of the behavioural, morphological, physiological and other adaptations to a way of making a living, and the modifications that the population makes to its environment (Odling-Smee *et al.* 2003). Combining fine-scale (ideally species-level) measurements of disparity with ecomorphological data in a phylogenetic framework provides a potential avenue for understanding how species construct and define these niches. This is conceptually a far different approach from assuming that the niches exist independent of the species that occupy them (see also Herbold and Moyle 1986). One of the more intriguing questions is how the patterns of extrinsic constraints described above can be related to processes of niche construction within individual clades.

*Clumpiness of morphology.* There is another side to morphological disparity, one that is rather less discussed by palaeontologists than the causes of early morphological disparity: why the occupation of morphospace is so clumpy and why many regions of morphospace are unoccupied. Four different, although partially overlapping, views have been offered as explanations. The default assumption has been that it reflects an earlier, more continuous distribution of forms broken up by subsequent extinction. In this case, the fossil record should document increasingly uniform patterns as we move to the early his-

tory of a clade (for which there is no evidence). By contrast, Gould's explanation (1989) was that the current distribution of form was heavily influenced by chance. The contingent elimination of some of the early forms produces later clumpiness, but as Gould famously observed, run the tape of life again and different forms might be preserved. Lewontin (2003) articulated another, also widely held, view that fossil and extant patterns of morphological form represent merely an incompletely explored fraction of a vastly larger space of potential forms. But Lewontin realized that the interesting issue was really the hierarchical clumping of form. Neither the default assumption nor Gould's argument for contingency make explicit claims about whether or not the space of potential form is much larger than what has been explored, although based on other writings Gould probably thought this was the case.

A residue of Sewall Wright's work on fitness landscapes informs the fourth perspective to the extent that clumps of form are viewed, often implicitly, as representing local optima surrounded by less fit alternatives. Such fitness landscapes would be rugged (Kauffman 1989, 1993), producing hierarchical clumping. Rather than representing adaptive optima, morphological clumps could also represent the structure of ecological opportunities created by the network of ecological interactions within communities. This is subtly different from the usual argument because there is no claim of optimality; the clumps of form represent not the supply of morphological novelties but the success of those that survive. This can also be viewed as an argument that the morphological clusters are seeded by ecological innovations (I am explicitly avoiding the misbegotten term 'key innovations', which generally obscures far more than it illuminates; Erwin 1994). Either of the two forms of this argument raises the obvious question of how such 'optima' could persist over hundreds of millions of years through mass extinctions and multiple reorganizations of ecological relationships. If clumpiness does reflect local optima one might expect that quantitative studies of disparity would identify shifts in occupied morphospace across mass extinctions.

Finally, patterns of morphological disparity and clumpiness may represent a deep, highly conserved structuring of developmental innovations. If this is the case, there may be considerable structure in the variation that is available for selection. This approach separates the initial cause of clumpiness, which could well have been ecological optima, contingency or some other cause, from the forces that have subsequently maintained it.

*Future directions for disparity research.* Lewontin's (2003) answer to why so much of morphospace is so empty was simply that the dimensionality of the space is so large, even relative to the history of life, that it is incompletely

explored. This is a fairly common view, but studies of disparity have revealed a structure to the distribution of form, and work by functional and theoretical morphologists and others has begun to establish the causes for some of these patterns. But Lewontin recognized that the hierarchical clumping of organisms (under-dispersion) in space was the real issue, and required other explanations. Having established a variety of tools for understanding disparity, and for ensuring that issues such as random walks and clade age do not unduly confound the results, palaeontologists now have the opportunity to untangle more of the causal factors underlying disparity. Carroll (2005) identified four 'secrets' of evolutionary innovation: (1) working with what is already present, or as François Jacob put it, tinkering; (2) utilizing structures for multiple functions; (3) redundancy, which allows specialization through division of the redundant structures; and finally (4) building forms in a modular fashion, the secret behind the success of the arthropods. Although palaeontologists are unable to plumb the developmental details of these issues in the way that Carroll and his developmental colleagues can, we do have the only access to the detailed record of how morphologies have evolved. The fossil record does contain a history of tinkering, multifunctionality, redundancy and modularity that we can use to understand the processes underlying the formation and occupation of morphological spaces.

## IMPLICATIONS FOR EVOLUTIONARY THEORY

Patterns of evolution of form have been the major impetus for various theories about macroevolution. Darwin and most adherents of the Modern Synthesis adopted an extrapolationist view of the subject, with major differences in form a consequence of gradual divergence followed by extinction of intermediates. Gould's concern with form and development in evolution and the tension he saw with the Modern Synthesis was remarkably perceptive. As the philosopher of biology Ron Amundson (2005) recently noted: '... neo-Darwinism had its origins not in *developmental* genetics but in *transmission* genetics.' (p. 7; italics in original). Population genetics, the core of the Modern Synthesis, requires only transmission genetics, not an understanding of how form is produced through development or how that processes is modified by evolution. Quantitative studies of disparity have rendered this approach untenable. The response of Gould and some other palaeontologists and evolutionary biologists has been to champion a hierarchical view of evolution, with differential sorting (and possibly selection) and a variety of levels above and below the species (see Gould 2002). It is not clear to me how the hierarchical expansion

of evolutionary theory explains many patterns of disparity.

The term macroevolution originally was invoked for large-scale morphological changes before it took on its modern connection with hierarchical views of differential sorting and selection (see discussion in Erwin 2000). More recently there have been a variety of calls for a new modern synthesis. These take a variety of forms, from the previously discussed hierarchical expansion to West-Eberhard's (2003) suggestion that behavioural plasticity enables evolution to use phenotypic plasticity as a foundation for innovation (see also Schlichting and Pigliucci 1998) and Jablonka and Lamb's (2005) discussion of multiple sources of inheritance. Most relevant here, however, are numerous discussions, many based on the recent discoveries from comparative evolutionary developmental biology, that there may be important biases in the introduction of morphological variation. This could skew the processes of evolution in significant ways (see Wagner and Laubichler 2004; Brakefield 2006; Stoltzfus 2006) with substantial implications for understanding the mechanistic basis of morphological disparity, but the implications of this for evolutionary theory remain uncertain.

## CONCLUSIONS

Studies of morphological disparity and its relationship to taxonomic diversification have now encompassed a wide variety of marine invertebrates as well as insect mouthparts, basal plant and angiosperm radiations, and both basal tetrapod and some aspects of Cenozoic radiations. Several groups have been studied through mass extinction intervals and we have excellent longitudinal studies of changes in disparity among groups as diverse as Palaeozoic ammonoids, Cretaceous spatangoid echinods and Proterozoic acritarchs. Many of these studies, particularly of more inclusive clades within the Metazoa, do exhibit patterns of early maximal morphological disparity, and there are indications that step sizes between taxa were also larger early in clade history. Increases in disparity after mass extinctions provide little support to suggestions that developmental or other intrinsic constraints limited potential innovations *with clades* during their later history. Direct support for ecological or extrinsic constraints as a control on patterns of disparity is often equivocal, but this may reflect the way that hypotheses have been structured. Equally importantly, the analysis of both geometric morphometric and character-based disparity is well advanced. Although fewer studies have made use of a phylogenetic framework, allowing analysis of changing step sizes, or compared results against a random walk of the data, the methods of doing so are now well worked out.

Studies of disparity have to some extent been overtaken by advances in comparative developmental biology, which have demonstrated that the patterning machinery underlying all bilaterians is far more common than ever anticipated two decades ago. Indeed our entire conception of developmental constraints has been revolutionized by the discoveries of deep homologies in many aspects of metazoan development.

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