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Morphological and developmental macroevolution: a paleontological perspective

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ABSTRACT Evidence of the morphological evolution of metazoans has been preserved, in varying degrees of completeness, in the fossil record of the last 600 million years. Although extinction has been incessant at lower taxonomic levels, genomic comparisons among surviving members of higher taxa suggest that much of the developmental systems that pattern their bodyplans has been conserved from early in their history. Comparisons between the origin of morphological disparity in the record and patterns of genomic disparity among living taxa promise to be interesting. For example, *Hox* cluster composition varies among major taxa, and the fossil record suggests that many of the changes in *Hox* clusters may have been associated with late Neoproterozoic evolution among minute benthic vermiform clades, from which crown bilaterian phyla arose just before or during the Cambrian explosion. Study of genomic differences among crown classes and orders whose timing and mode of origin can be inferred from morphological data in the fossil record should throw further light on the timing and mode of origin of genomic disparities.

KEY WORDS: *morphological disparity, taxonomic richness, genomic disparity, Hox cluster evolution*

Introduction

Biological diversity is commonly understood to contain two major components, richness (number of taxa) and disparity (morphological distance between species within and among higher taxa, or in the case of phylogenetic diversity, the accumulated derived characters that define different groups). For several decades, paleontologists have devoted significant effort to study of the factors that are associated with the rise and decline of taxonomic richness in the biosphere (usually measured at the level of genera or families in order to skirt the greater biases of the fossil record at the species level). Rising levels of richness are commonly interpreted in terms of microevolutionary processes that lead to speciation, and the macroevolutionary dynamics that lead to net diversification (Sepkoski, 1998; Jablonski 2000). More recently, increasing attention has been given to patterns of disparity. The origins of disparity lie in the evolution of novel features, which can be interpreted in terms of developmental evolution, presumably of patterning systems at the higher taxonomic levels, to form distinctive clades. (Herein, higher taxa refer to orders and up, while lower taxa refer to families and down). Although extinction may bite deeply into the richnessses within higher taxa, so long as some representatives of the lineages are preserved the richness at the higher taxonomic levels themselves is maintained, and rediversification may reconstitute richnesses at lower levels, during which novelties may arise in turn. This racheting effect tends to promote conservation within the disparate developmental genomes of higher taxa (see below).

In this study, we review the patterns of the origination and extinction of taxa and the morphological disparity commonly found in the fossil record. These data are then compared with information on the pattern of genomic disparity and conservation reported among higher taxa to attempt to understand the relation of the evolution of developmental patterning systems to the stages of morphological evolution indicated by the fossil record, with suggestions for future work.

Patterns of disparity

Morphological disparity and diversification in the fossil record

In the fossil record, as in the living fauna, disparity has usually been evaluated taxonomically. In general, higher taxa tend to diversify during the early history of clades, commonly when their lower taxa are relatively few, so far as can be told. This pattern suggests that the richness of higher taxa is not driven by cladogen-

Abbreviations used in this paper: Ma, million years ago.

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esis among species, but rather is acquired by selective processes within lineages that may even be species-poor. In other words, taxonomic disparity within clades does not seem usually to arise from a simple expansion of the dimensions of occupied morphospace under the pressure of speciation. This pattern is not universal, but is followed by the bulk of the marine clades that are most readily fossilized and on which the best data are consequently available — including the Echinodermata (Campbell and Marshall, 1987), Mollusca (summary in Valentine, in press), Bryozoa (Antsey and Pachut, 1995), and Brachiopoda (Williams *et al.,* 1996). Owing to the unusual preservation of nonmineralized groups such as the Chengjiang and Burgess Shale faunas, we also know of numbers of taxonomically distinctive stem lobopod (Ramsköld and Hou, 1991) and arthropod (Wills *et al.,* 1997) taxa from early in the history of those clades.

Morphometric studies that directly evaluate large-scale trends in morphological disparity are also available for numbers of classes and subclasses of those better-preserved invertebrate clades. These studies generally map the distribution of taxa in a multivariate space (morphospace) where individual axes represent measures of morphology (e.g. Roy and Foote, 1997; Foote, 1997; McGhee, 1999; Wills, 2001; Ciampaglio *et al.,* 2001). Such approaches may employ axes that are defined either theoretically (as in the basic geometric parameters of a coiled shell) or empirically (as in the output of a Principal Components Analysis of a suite of interesting organisms). Such studies avoid potential taxonomic artifacts that might be imposed by the Linnean hierarchy and its requirement that all species be classified in the full array of higher categories (e.g. Raup, 1983). The classes and subclasses show a variety of trends, but the majority display an early achievement of morphological disparity relative to the peak diversification of their lower taxa. These studies include Echinodermata (Foote, 1992 on the subphylum Blastozoa; Foote, 1999 on Crinoidea), Arthropoda (Wills *et al.,* 1994), and Mollusca (Wagner, 1995 on "Archaeogastropoda"; Wagner, 1997 on Rostroconchia). These data corroborate and extend the inference from taxonomic evidence that the growth of disparity and richness can be independent, particularly at times of major diversifications as in the early Phanerozoic. Some post-Paleozoic diversificationa also show rapid bursts of morphospace occupation involving the acquisition of novelties (*e. g.* Jablonski *et al.,* 1997).

Morphological disparity and extinction in the fossil record

Disparity and extinction can be independent as well. Again, this inference seems plausible simply from the taxonomic patterns in the fossil record. Large declines in diversity at lower taxonomic levels, such as occurred during the major mass extinction events and which may each have extirpated between 60 and 90 percent of marine species, were not accompanied by proportional losses at higher levels.

Studies of the behavior of morphological disparity during and following extinction events strongly support this pattern. When an extinction is random or nearly so with respect to taxa, phylogenetic diversity and therefore morphological disparity tends to be conserved, although the occupation density of morphospace is reduced according to the severity of the extinction and the consequent reduction of richness at lower taxonomic levels (Foote, 1996, 1997; Nee and May, 1997). When extinctions are selective or are extremely severe, numbers of higher taxa and large amounts of phylogenetic branch length may be lost (see Purvis *et al.,* 2000). However, so long as the adverse conditions driving an extinction affect but do not fully extirpate many different clades there will be some preservation of phylogenetic diversity and therefore of disparity that is disproportionate to the loss of species.

Studies of extinction in the fossil record indicate that extinctions that have a noticeable effect on the richness of the marine fauna affect an array of higher taxa, though to be sure some fare better than others. Mass extinction events that have been closely studied seem to be less selective (when entire faunas or at least large clades are surveyed) than "background" extinctions (Jablonski, 1995; Jablonski and Raup, 1995; McKinney, 1997). The selectivities during background times are chiefly recorded at lower taxonomic levels. Whether or not such disparity losses within affected clades are ordinarily compensated by originations of novel morphologies in others is unclear, but at times, combined richnesses at lower taxonomic levels have held fairly steady over tens to hundreds of millions of year despite continuous turnovers (see for example Sepkoski, 1981, 1993). The lower taxa lost to the incessant background extinctions far exceed (perhaps by an order of magnitude) those lost during the five mass extinction events that are scattered over the Phanerozoic Era (Raup, 1986). In contrast, of the approximately 115 well-preserved marine invertebrate orders that became extinct during the Phanerozoic, more than half were lost during or immediately after mass extinctions.

Genomic disparity

There have evidently been no explicit measures of genomic disparity, and thus no comparisons of morphological and genomic disparities can yet been made. An index of genomic disparity, which might position organisms within a genome hyperspace, could include such numerical parameters as the genes in common and their similarities, genes not in common, numbers of gene expression events, and so on. Parameters relating to gene organization would be particularly critical in assessing disparities at higher taxonomic levels, where patterning and other regulatory genes, though tending to be similar in sequence, function in different developmental roles in different taxa. And there are elements of the genome, such as enhancer sites and modules, that cannot yet be routinely studied in a comparative fashion, but which must be fundamental to achieving the distinctive gene organizations in which differences in body plans and subplans are rooted.

What can be done at this time is to inspect qualitative information on the differences in genomes, especially in regulatory genes, among the higher metazoan taxa for which we have data, with an eye to determining whether there is any relationship between historical patterns of morphological and genomic disparity in those taxa. The classic *Hox* gene clusters, which mediate the development of anteroposterior morphologies throughout Eumetazoa, clearly function to produce different and distinctive morphologies in each phylum. Comparative data on the types of effects encountered in *Hox* genes and their regulatory cascades have been reviewed by Gellon and McGinnis (1998), who found a hierarchy of change in the contribution of *Hox* genes to bodyplan evolution.

At the level of phyla, *Hox* genes not only mediate development of entirely different morphological features, but their clusters have unique gene combinations, evidently with the single exception of Onychophora and Arthropoda (e.g. de Rosa *et al.,* 1999), which however do show dramatic differences in the anteroposteror

deployment of *Hox* gene expression (Grenier *et al.,* 1997). When the phyla are grouped into the three major metazoan clades recognized by molecular phylogenetic analyses, the Deuterostomia, Ecdysozoa and Lophotrochozoa, some *Hox* genes are uniquely shared among at least some members of each clade (De Rosa *et al.,* 1999).

Within phyla, some taxa ranked as classes also have distinctive gene combinations in their *Hox* clusters (e.g. Polychaeta and Hirudinea within Annelida; de Rosa *et al.,* 1999 and suppl.). Indeed, the four clusters within mammals (see Krumlauf, 1994) and the clusters known in teleosts (Amores *et al.,* 1998, Aparicio, 2000) are also unique, all evidently descending by differential loss of homologues from the 14-gene cluster known in cephalochordates (Ferrier *et al.,* 2000). Within other phyla, classes commonly show regional differences in *Hox* gene expression even when their *Hox* clusters are identical (the sort of difference in deployment described between Onychophora and Arthropoda), as for example among arthropod groups with different patterns of limbs and/or tagmosis (e.g. Averof and Patel, 1997; Mouchel-Vielh *et al.,*1998; Abzhanov *et al.,* 1999).

Within classes, some orders also show differences in the deployment of *Hox* gene domains (e.g. Averof and Patel, 1997; Abzhanov *et al.,* 1999). In other orders, different features may develop within the same *Hox* domain, some perhaps from evolution in *Hox* target enhancers, others from changes in the targets of genes that are farther downstream, with consequent changes in the regulatory cascade. The types of *Hox* cluster changes recognized by Gellon and McGinnis (1998) thus produce a hierarchy of morphological differences among higher taxa, not precisely parallel to the genetic differences but trending similarly within the Linnean taxonomic hierarchy, which reflects degrees of morphological disparity.

Comparative data are also accumulating on other regulatory genes, which, like *Hox* genes, tend to retain high sequence similarities in binding sites across major taxa, while frequently having different functions in different groups, a common finding that is no longer surprising. Examples include the changing developmental roles of *distal-less*, *engrailed* and *orthodenticle* among phyla and among echinoderm classes (Lowe and Wray, 1997) and of *Brachyury* among phyla and among vertebrate classes (Peterson *et al.,* 1999; Technau, 2001).

Metazoan history and genome evolution

Neoproterozoic and early Cambrian fossils

Fig. 1 depicts major features of the early fossil record of metazoans. The earliest fossils date from the late Neoproterozoic, near 600 Ma (million years ago) (Barfod *et al.,* 2002). These are phosphatized tissues and embryos, preserved with such fidelity that individual cells can easily be discriminated (Xiao *et al.,* 1998, Li *et al.,* 1998). Possibly these early forms are sponges. The first undoubted, well-dated traces of probable vermiform bilaterians are trails and shallow burrows dating from about 555 Ma (Droser *et al.,* 2002) or perhaps slightly earlier, though significantly older rocks have yielded possible traces. The early traces are quite small, chiefly up to 1 mm in width, though a few are as wide as 5 mm, and they continue in this small size range until the beginning of Cambrian time near 543 Ma. Trace widths then increase into the cm range and traces become more varied in form. Body fossils known during the Neoproterozoic are chiefly enigmatic forms (some quite large) that may be at the diploblastic grade, with a few possible bilaterians that are difficult to relate to crown groups (review in Valentine, 2002). Bodyplans of crown bilaterian phyla finally appear during the Cambrian explosion, from about 530 Ma to 520 Ma or perhaps later; these phyla are chiefly represented by stem groups. It is consistent with the phylogenetic tree and with the early records of phyla that bodyplans of all of the living crown phyla evolved in the very late Neoproterozoic or Early Cambrian (reviews in Valentine *et al.,*1999; Knoll and Carroll, 1999; Budd and Jensen, 2000).

Unfortunately there is thus no direct fossil evidence of the morphological features of the earliest members of the bilaterian clades; the

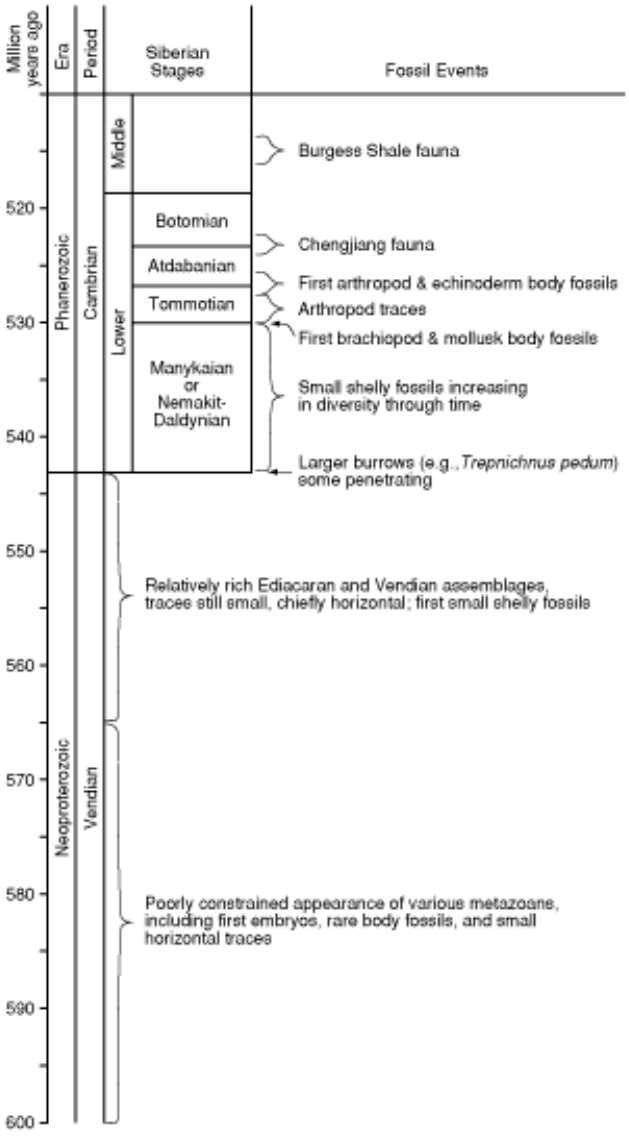

Fig. 1. Major events during the early history of Metazoa that are registered in the fossil record. *The Siberian section is commonly used as an informal standard for the Lower Cambrian succession.* Treptichnus pedum *is a type of burrow that defines the base of the Cambrian System in its stratotype region.*

bodyplans of the phyla come to us ready-made. Presumably Neoproterozoic diversification and extinction dynamics were similar to those of the Phanerozoic, but they cannot be evaluated from the available record. Therefore the largest changes in developmental genomes, including important changes in the composition of *Hox* gene clusters, occurred before we have a fossil record of the associated morphologies or of macroevolutionary dynamics. The finding from molecular sequence comparisons that acoelomorph flatworms are likely to be basal crown bilaterians (Ruiz-Trillo *et al.,* 1999, 2002; Jondelius *et al.,* 2002) provides a marvelous opportunity to study living examples of one of the sorts of small-bodied worms that left us traces from the Neoproterozoic, but as yet we have no molecular developmental information on those forms.

Clues to genome evolution from the fossil record

For better understanding of the relations between the origins of genome disparity and the origin and extinction of higher taxa we must turn to the fossil record of the best-preserved groups following the Cambrian explosion. The events of chief interest are the first appearances of crown classes and orders, which are concentrated in earlier portions of the Phanerozoic, and their contrast with the dynamics of lower taxa, which show incessant turnovers to the present. Immediately we are faced with a problem, for essentially all classes of marine invertebrates are cryptogenetic — they cannot be connected to their ancestors via intermediate forms — as are many orders. In this respect the taxa in these categories are like phyla, which, as described above, are also cryptogenetic. Most phyla originated from small- and soft-bodied, poorly fossilizable groups, however, and their lack of ancestral fossil forms is easily understood. On the other hand, the classes and orders of well-preserved crown groups originated chiefly after the evolution of durable skeletons, and their abrupt appearances are likely to reflect a relatively rapid mode of origin of their novel architectures, for otherwise their ancestral lineages would be expected to appear in the record.

There are two obvious, contrasting hypotheses for the tempo of genomic change associated with those novel morphologies. Either genomic change was gradual, accumulating in stem groups that we don't have or don't recognize, and leading from one higher taxon to another as divergence occurred, or genomic change was essentially as abrupt as the overt morphological record, with periods of relatively rapid genomic reorganization in response to whatever selective factors were in play to create new architectural norms. The supporters of a gradualistic view can invoke the arguments in favor of gradual change associated with microevolutionary processes. However, the understanding that much genome evolution associated with the origin of novelties "simply" represents the reorganization of genes, already present in ancestral forms, into new expression patterns through *cis*-regulatory evolution, much of which is conserved, provides a basis for accepting the possibility of more rapid change. Rapid, in this context, still may involve durations of, say, a few to a few tens of millions of years, representing many millions of generations for the tiny invertebrates of the Neoproterozoic seas.

If the accumulation of disparity among genomes is gradual, then significant variation in gene expression patterns should be present in lower taxa, which presumably would provide stepping stones in the rise of the sort of genomic disparity that is found among higher taxa. We might expect to find "experiments" with novel genomes within lower taxa, which, after all, undergo incessant turnover, so that their genomes are continuously lost, to be replaced by new ones. Granted that taxonomic sampling is far too sparse as yet to provide conclusive evidence, the available data do not support an entirely gradualistic interpretation. The sorts of genome differences associated with phyla, for example — differences in numbers and associations of *Hox* genes — do not seem to be found among the lower taxa of a phylum, and differences in *Hox* expression domains appear to be rare there. The pattern of conservation of major developmental regulatory systems suggests that "experimentation" among lower taxa tends to be restricted to lower reaches of the regulatory cascades, although work on the population genetics of *Hox* gene expression suggests that variation in expression domains does indeed occur even at low taxonomic levels. Taken at face value, however, the major changes in the regulatory genomes appear mostly during the origination of the more novel morphologies, and therefore when we can observe their appearance during the Phanerozoic, they seem to be quite abrupt, geologically speaking.

If it is true that some of the genomic differences at the highest taxonomic levels are not the product of kinds of experiments that are ongoing at lower levels today, but originated before or during the founding of bodyplans of the taxa at those higher levels, then the portion of the metazoan genome subject to selection must have changed since the Neoproterozoic. Why, for example, would the compositions of *Hox* clusters evolve so commonly within Neoproterozoic and Early Cambrian lineages that their differences are characteristic of the higher taxa that originated then, while such evolution must be at least rare today? A plausible answer is that those morphological features whose development was mediated by *Hox* genes were precisely those that were evolving among the minute vermiform metazoans of the late Neoproterozoic, which were probably acoelomate and pseudocoelomate forms. The only crown metazoan phylum for which there are data on *Hox* gene regulation, and which is probably at the same structural grade as the minute Neoproterozoic bilaterians (though perhaps branching later), is Nematoda. The deployment of *Hox* genes in nematodes (see Kenyon and Wang, 1991, Wang *et al.,* 1993) suggests by analogy that it was individual cell types or simple tissues whose anteroposterior positions were mediated by *Hox* cluster expression in those early bilaterians.

A plausible scenario would thus be that as early vermiform bilaterian lineages radiated on the late Proterozoic sea floor, encountering a variety of different habitat conditions within the usual mosaic of marine environments, it was precisely changes of anteroposterior sequences of functions that were adaptive to the disparate ecological requirements. *Hox* genes would be among the genes directly responding to those evolutionary changes, and differences in *Hox* clusters would have arisen within the bilaterian fauna through gene duplications and losses in response to that selection. In time, a rise in body size and complexity preceded and accompanied the Cambrian explosion, and a number of bodyplans of larger crown phyla became established, emerging from among the variety of acoelomate or pseudocoelomate lineages with distinctive modes of life. In this scenario, the *Hox* cluster disparities among phyla noted by Gellon and McGinnis are as likely to have been inherited from their disparate Neoproterozoic or Early Cambrian ancestors as to have evolved during the rise of the crown bodyplans themselves (Valentine, in press).

In combination, the colinearity of the *Hox* genes and their ancestral function in mediating anteroposterior differentiation ensured their involvement in the positioning of new features during evolution of the larger, more complex bodyplans. Among some phyla and certainly among classes within many phyla, continuing expansions and specializations in ecological roles produced radiations within the bodyplans that involved selection for diverse patterns of tagmosis, which were achieved at least in part by altering the expression domains of *Hox* genes relative to body parts. Specialization within modules then involved cis-regulatory evolution downstream of *Hox* expression but under the influence of the *Hox* domains. *Hox* genes had become selector genes for establishing the identity of complex developmental modules and helping to mediate growing cascades of gene activity therein. In general, the *Hox* gene clusters do not seem to have responded directly to evolution within the modules, perhaps with the exception that complete elimination of a module might involve the silencing and eventual loss of a *Hox* gene devoted to mediating its development (e.g. Mouchel-Vielh *et al.,* 1998).

This scenario is consistent with the hypothesis based on morphologic evidence that the abrupt appearances of crown phyla, like the geologically abrupt appearances of crown classes and orders during the Phanerozoic, roughly reflect actual evolutionary events and are not entirely artifacts of a poor fossil record.

Connecting genome evolution to the fossil record

If major changes in the roles of regulatory genes are generally associated with important morphological innovations, we can reasonably hypothesize two outstanding patterns in genome evolution. One pattern is an abruptness and episodicity to the evolution of organization in metazoan genomes, which may proceed by relatively high rates of change during relatively short periods of geologic time. The other pattern is the partial conservation of the results of such change, with earlier changes appearing farther upstream where they are partially sequestered as developmental cascades grow downstream during increases in bodyplan complexity. Of course the early expression patterns are not immutable, and may be subjected to considerable modification, especially during the evolution of early developmental patterns (e. g. Raff, 1992; Lowe *et al.,* 2002). Such modifications, however, go to emphasize the connection between morphological and regulative genomic change.

Extinction has clearly pruned the tree of metazoan life extensively, so that many of the changes in developmental genomes were associated with phylogenetic nodes whose branches have vanished from the living fauna. Given the pattern of extinction, common at lower taxonomic levels and relatively rare at higher, two alternatives can be framed for the loss of information on the evolution of important developmental changes: it was lost because important changes were concentrated in a small number of species that were readily extirpated; or it was lost because of selective extinction against some attribute of the clade in which the changes occurred.

Although the evolution of *Hox* and other key regulatory genes during the rise of the bodyplans of bilaterian phyla cannot now be studied in living genomes, with the likely exception of acoelomorphs, study of the gene regulatory evolution accompanying the rise of crown classes and orders can be approached by comparative methods. In a number of phyla, taxa at those levels have good fossil records and thus provide information on the evolution of their novel morphological features. Most information on the evolution of development among phyla has come from studies of organisms chosen for developmental rather than evolutionary interest, naturally enough. To increase the depth of understanding of the evolution of metazoan genomes, however, it would be most useful to increase the density of genome sampling and particularly to perform comparative studies of molecular development systems in the more basal members of higher taxa for which the timing and tempo of origination can be inferred from the fossil record.

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