

# Early introduction of major morphological innovations

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The origin of major morphological innovations poses a major problem for macroevolutionary biologists. Such innovations appear to be overwhelmingly concentrated early in the history of major clades: subsequent evolution involves elaboration and variation on these early themes. Although confirmation of this pattern requires morphometric techniques only now being developed, it seems too firmly established to be an illusion. A variety of explanations have been advanced for the extensive morphologic innovation during the Cambrian radiation, including the ecospace hypothesis which relies on more extensive ecospace, and a variety of genomic hypotheses ranging from a more rapid rate of real or apparent mutation, to novel types of genetic change, or novel effects within a more plastic developmental system. Recently some theorists have suggested the inherent properties of complex dynamic systems are a sufficient explanation. However, most discussions have emphasized the ecosystem and genomic hypotheses. These have proven difficult to disentangle because no unique predictions about expected patterns have been proposed, but I suggest here phylogenetic tests which do discriminate between these possibilities.

There is a curious distinction between the empty ecospace hypothesis and one variant of the developmental hypothesis: Under the former, extensive morphologic innovation should be possible whenever extensive ecospace becomes available. The constraints on innovation are atemporal and extrinsic. In contrast, under the second scenario the formation of developmental systems itself constrains further innovation. Thus the concentration of innovation early in the history of clades may stem from irreversible changes associated with the origin, rather than subsequent modification, of development.

**Key words:** innovation, metazoan radiation, evolutionary theory, evolutionary radiations.

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## Introduction

Macroevolutionary problems were a major concern of Toni Hoffman throughout his career and his insightful, often provocative questions contributed significantly to the field. The central issues of this paper, the origin of morphologic innovations during the metazoan radiation, was not one which Hoffman specifically addressed, but it is certainly a significant one for evolutionary biologists. Darwin, Simpson and many others have discussed this topic, rephrasing the problem as the field developed. In this paper I hope to address this issue by again rephrasing the questions and expanding on earlier work (Erwin *et al.* 1987; Valentine & Erwin 1987; Erwin 1992). Had Hoffman addressed this topic I have no doubt that his conclusions would have been radically different from those developed below, but he always liked a good argument.

Major morphologic innovations among durably skeletonized marine invertebrates are overwhelmingly concentrated from the Vendian (or Neoproterozoic III) through the Ordovician. This episode established the major morphologic themes of marine invertebrates; although subsequent evolution has endlessly elaborated upon these early themes, there is little evidence for widespread morphologic innovation after this time. These major morphologic innovations include the defining synapomorphies of invertebrate clades. More importantly, the nature of these synapomorphies indicates a profound change in developmental patterns. In many cases these changes are so great that morphologic and developmental characters seem inadequate to recover phylogenetic relationships, compelling reliance on molecular phylogenetics. Why should morphologic innovation be concentrated in the Cambrian? There is no obvious reason why major innovations do not occur sporadically through the history of a clade, or episodically in response to mass extinctions and other events. Yet empirical observation indicates that the pattern of innovation is asymmetric.

Although there are substantial problems with using Linnean ranks as an index of morphologic innovation, in the absence of any quantitative index of morphologic complexity they provide a useful guide. Thus the Vendian-Ordovician radiation produced all 11 skeletonized marine phyla, 54 of the 56 recognized classes and 152 of the 235 orders, with the bulk of the appearances during the Cambrian (Erwin *et al.* 1987; see also Valentine 1977; Campbell & Marshall 1987). Valentine *et al.* (1991) tabulated the appearance of 155 ordinal-level taxa from the Vendian through the Early Cambrian, of which 90% are extinct and at least 40% do not appear to belong to living phyla (see also Valentine 1977, 1991; Jablonski & Bottjer 1990; Conway Morris 1993; Campbell & Marshall 1987; Lipps & Signor 1992; Sirnonetta & Conway Morris 1991). Yet as Muller & Wagner (1991) emphasize, the primary problem is the generation of the novel morphologies accorded high rank, not higher taxa *per se*. The problem would exist even if systematists eliminated ranks entirely, as some cladists have suggested (e.g. de Queiro & Gauthier 1990). Furthermore, the coin-

Tab. 1. Proposed explanations for asymmetric morphological innovation

Hypothesis	Mechanism	Uniformitarian
Mutation-driven	Higher mutation rates; lower fidelity of DNA repair.	yes
Empty-ecospace	Possible only with large amounts of 'empty' ecospace.	yes
Genome	Novel genetic mechanisms, including transposons or genetic instability.	yes/no
Development	Less canalized systems produce more extensive morphologic change.	no
Complexity	Inherent property of complex systems.	?

vidence of morphologic innovations with increased bioturbation, diversity of trace fossils (Droser & Bottjer 1988, 1993; Crimes & Droser 1992), protists (Lipps 1992), and soft-bodied metazoa (Conway Morris 1989, 1992, 1993) clearly indicates the breadth of this evolutionary event (Erwin 1992).

What drives this asymmetric pattern of morphologic innovation? The major competing hypotheses (Tab. 1) involve relatively empty or unfilled ecospace, or some form of genetic change. Several genetic/developmental mechanisms have been suggested, including novel mechanisms of genetic change [genetic instability, transposition or the macromutations of Goldschmidt (1940)], higher effective mutation rates, or unusual effects of genetic mutations on the less canalized developmental systems of early Metazoa.

Finally, several recent theorists have suggested that the problem is intrinsic to the dynamics of complex systems and the behavior is an expected event in the history of life. Several technological examples make the point: personal computers and high-definition television each had their highest diversity of 'body plans' early in their history. In the last example the winnowing process occurred during hearings before the US Federal Communications Commission – a form of selection not entirely anticipated by Charles Darwin!

This paper discusses each of these proposals, focusing particularly on the empty ecospace hypothesis and the genome/development hypothesis. Here I am not concerned with such related issues as why a spate of innovation occurred at a particular time rather than earlier or later. Nor am I concerned with topological imperatives forcing major clades to diverge early (Raup 1983). Neither issue is germane to the problem of why the distribution of morphological innovation appears to be so asymmetric during the Phanerozoic.

Paleontologists have raised three objections to discussions of major morphologic innovation, each dealing with the Cambrian metazoan radiation. Critics charge that higher taxonomic units (phyla, classes) are established retrospectively and for a variety of reasons (Smith 1988), are frequently polyphyletic or paraphyletic (Smith & Patterson 1988), and suffer from other defects (Doyle & Donoghue 1993) which renders the

approach invalid (see also Conway Morris 1989; Erwin 1992). Clearly the ideal situation is to analyze character evolution of monophyletic clades with a well-corroborated tree (i.e., 'tree-thinking' of Doyle & Donoghue 1993) but paleobiologists are generally not yet in a position to do so. Moreover, despite the claims of Briggs & Fortey (1989; Briggs *et al.* 1992) robust techniques to analyze morphologic disparity are not yet available. The argument advanced here depends only upon asymmetric morphologic innovation, a robust observation (Jablonski & Bottjer 1990; Campbell & Marshall 1987) and not upon the 'reality' of higher taxa nor their monophyletic status. The latter issue is a nominalistic one: what names and ranks are applied to groups; the former is a substantive claim based on empirical data. The asymmetric pattern of morphologic innovation would be with us even if systematists eliminated ranks entirely.

The third objection raised is that morphologic disparity was no greater in the Cambrian than it is today (Conway Morns 1989; Briggs & Fortey 1989). This argument, largely triggered by Gould's (1989) claims of greater morphologic disparity among arthropods in the Middle Cambrian Burgess Shale, is far from resolution (Briggset *al.* 1992; Foote & Gould 1992; Gould 1991) but the disputants apparently agree that morphologic disparity was at least as great among Cambrian arthropods as it is today, after a further 530 million years of evolution.

The various hypotheses shown in Tab. 1 have different implications for patterns of evolutionary change. For example, the mutation hypothesis requires that effective mutation rates must have been higher earlier in the Paleozoic, and declined toward the present. Thus the asymmetric pattern of morphologic innovation reflects an asymmetric change in the environment and is essentially uniformitarian. If mutation rates suddenly increased, perhaps through a nearby supernova (Schindewolf's favorite explanation for innovation, see below), innovation should increase as well, and may increase again in response to another burst of cosmic radiation. Most of the remaining hypotheses have this same property. In contrast the genome and genome/development hypotheses may be either partly reversible or largely non-reversible. If the former, they are basically similar to the first and second hypotheses. However, the non-reversible changes in developmental systems involve a temporally asymmetric change in the intrinsic nature of the organisms - thus a fundamental change in the nature of the evolutionary process. This is a point to which we will return in the discussion.

## Proposed explanations

### Empty ecospace hypothesis

Valentine (1980; Valentine & Walker 1986; Valentine & Erwin 1987; Erwin *et al.* 1987) has long championed the view that radiations may begin in an unfilled 'ecospace', with the spaces on a chess board analogous to different

ecological roles. Occupation of the ecospace will expand as taxa diversify, with most new taxa moving into space, or tesseræ (Valentine 1980) adjacent to the parent. Initially, jumps to distant portions of ecospace are possible. These long jumps are viewed as involving the establishment of new morphotypes. As the ecospace fills the success of jumps will begin to drop: the principle of competitive exclusion allows only unoccupied tesseræ to be invaded, and adjacent taxa are more likely to succeed in filling a particular tesseræ than are taxa 'jumping' across large sections of ecospace.

This model contains several assumptions. First, only unoccupied tesseræ can be invaded; competitive exclusion will prevent (or at least inhibit) invasion of occupied tesseræ. Thus the first clade to invade a region of ecospace should pre-empt further occupation of that space. Second, the pattern of occupation will be clumped, with most diversification based on the morphological novelties. Third, although genetic models are not excluded from operating in conjunction with this model, it is viewed as necessary and sufficient to explain the pattern of morphologic innovation. As Jablonski & Bottjer (1990) note, an important implication of this model is that innovation occurs at relatively constant rates but the success of the innovations depends on available ecological opportunities at different points in time. Under this model the incidence of innovation should increase during recoveries from mass extinctions, since at least the largest mass extinctions should clear out large regions of ecospace, allowing extensive subsequent diversification.

The initial versions of this model unfortunately assumed the dimensions of the ecospace are predetermined (Erwin 1992). A more plausible model would focus on the creation of the ecospace as part and parcel of the ongoing radiation. Consider an economic analogy. As an economy expands new markets are constantly opening up. Some are due to replacement of an older technology with a more advanced technology, as telephones replaced the telegraph; others reflect the creation of consumer demand for a new good, for example automobiles or personal computers. But many markets do not exist until the economy is sufficiently advanced (both technologically and in terms of available capital) to permit their development. Similarly, during the Cambrian radiation ecospace was created as the radiation progressed. This expansion occurred not by niche partitioning of existing space, although that may have happened as well, but by expansion of the total ecospace, which in turn allowed further expansion. Thus at least the early phases of the radiation were characterized by positive feedback rather than negative feedback. The expansion of terrestrial ecosystems from their origin in the Silurian through the radiation of terrestrial plants and insects during the Devonian and Carboniferous followed a similar pattern.

The appearance of positive feedback differentiates the Cambrian radiation from later expansions of ecospace. For example, the classic study of the evolution of phytophagy by Mitter *et al.* (1988) employed a cladistic analysis to determine whether the invasion of this empty niche triggered

diversification in the invading clade compared with its sister clade. In 11 of 13 cases taxonomic diversification did occur, yet this result may be specific to phytophagy. It may not be shifts in feeding zone that trigger diversification *per se*, but the invasion of this particular feeding zone. Coddington (personal communication 1993) has emphasized that a true test of the hypothesis requires consideration of a random sample of the universe of all pairwise adaptive shifts, not simply those involving phytophagy by insects.

The recovery of decimated ecosystems following the end-Permian mass extinction seems to provide the best opportunity to test the ecospace hypothesis (Erwin *et al.* 1987). Over 95% of marine invertebrate species disappeared at the close of the Permian (Erwin 1993), and Early Triassic ecosystems were as depauperate as those of the Early Cambrian. Yet if higher taxa are any index of innovation, far more innovation occurred during the Early Paleozoic than during the Mesozoic, a comparable interval of time. No new phyla or classes appear during the Mesozoic, although the distribution of new families is similar. One critical difference between these two intervals lay in the structure of the ecospace: 15 of the 20 ecological guilds identified by Bambach (1983) occur in the Triassic, a situation quite unlike the limited ecological diversity at the start of the Cambrian radiation. Another critical difference is the 300 million years of evolution between the Cambrian and the Permian. The developmental and genetic systems of Cambrian organisms were far closer to the origin of metazoa than those of the Triassic. Further development of this model will require detailed comparison of Cambrian and post-Cambrian ecosystems, and comparative phylogenetic studies as described below.

## Genetic hypotheses

Although Jablonski & Bottjer (1990) distinguished only a single genome hypothesis, there are several distinct proposals relating genomic change to rapid morphologic innovation. These include an increased mutation rate, the activity of novel genetic mechanisms (which, conveniently, are no longer operative today) and have greater morphologic effect, and a less canalized genome in Cambrian metazoans. The latter hypothesis is most usefully compared with the empty ecospace hypothesis, but for heuristic purposes I will begin by considering some of the earlier suggestions first.

**Mutation rates.** — Otto Schindewolf (1950, 1954) emphasized increased mutation rates caused by bursts of cosmic radiation as a trigger for morphologic innovation. Unlike Goldschmidt (1940), Schindewolf was not invoking a particular type of genetic change (systemic mutations in Goldschmidt's case), but simply more mutations. Schindewolf applied this theory to both the Cambrian and post-Permian radiations. In the latter case he located the Permo-Triassic boundary within a monofacial sequence in the Salt Range of Pakistan and argued that both the end-Permian mass extinction and the subsequent burst of morphologic innovation

during the Triassic were caused by cosmic radiation. However the pattern of extinction is wholly inconsistent with an increase in cosmic radiation (Erwin 1993). More generally, morphologic innovation occurred across a variety of both benthic and planktic clades during the Cambrian, yet cosmic radiation is rapidly attenuated by water so benthic clades would have received lower doses of radiation. In addition, cosmic radiation will cause an increase in point mutations and chromosomal rearrangements whereas the cause of the innovation during the Cambrian appears to largely involve developmental repatterning (Erwin in press; Valentine & Erwin 1987). Thus there is little evidence for the mutation-driven evolution suggested by Schindewolf (see also Newell 1952).

Schindewolf's theory depends on sufficient cosmic radiation and thus lacks any temporal asymmetry. This is not so for a related mechanism. The apparent rate of mutation would decline with an increased rate of fidelity in DNA repair enzymes. If repair mechanisms were sloppy during the Cambrian and gradually improved during the Phanerozoic this temporal trend might have allowed greater morphologic innovation during the Cambrian in a manner analogous to Schindewolf's, although over a longer period. However this would be apparent as variation in the DNA repair enzymes of metazoa. The structure of DNA repair systems is highly conserved across all eukaryotes and is very ancient.

**Novel genetic mechanisms.**— Most 'macromutationist' hypotheses are descended from Hugo de Vries' mutation theory (1910) but received their strongest impetus from Goldschmidt's *Material Basis of Evolution* (1940). Goldschmidt invoked genomic repatterning (systemic mutations) as a source of many evolutionary events (see Dietrich 1992, for a history of macromutationist views). There is substantial difference between large-scale rearrangements of the genetic material, as invoked by Goldschmidt, mutations (of any topology) with a large phenotypic expression, and the temporal variation in the magnitude of that phenotypic expression. We often assume the null model is little or no temporal bias in the phenotypic effect of a mutation; in essence that the nature and effect of evolutionary mechanisms has not changed with time. Is this uniformitarian assumption the correct null model, or is it simply the most reasonable assumption in the absence of any evidence to the contrary?

A variety of novel genetic mechanisms have been proposed. For example, Erwin & Valentine (1984; see also Valentine & Erwin 1987) invoked site-specific insertion of retrotransposons as a source of genetic and developmental instability during the Cambrian radiation, although experimental evidence for site-specific reintegration was not developed until several years later. Other mechanisms that have been related to innovation include chromosomal rearrangements and a variety of regulatory mutations (e.g. Valentine & Campbell 1975; Jacobs 1990). For example, recent genetic linkage studies of colon cancer have uncovered evidence of genetic instability manifested as widespread and apparently random mutations through the genome, evidently caused by a single gene

(Thibodeau *et al.* 1993; Aaltonen *et al.* 1993; Peltomaki *et al.* 1993; Marx 1993). One could suggest that the effect of such a gene within the poorly canalized genomes of Cambrian organisms might have been far-reaching. Similarly, genes that caused distorted segregation during meiosis (meiotic drive) could have ensured the rapid spread of a gene through a population (Dover 1986; Lyttle 1991). It is difficult to determine the effects of such mechanisms on less rigidly canalized genetic/developmental systems however. Granted, they could have been operating, but because such hypotheses are so difficult to test, they should be invoked only when all other possibilities have been excluded.

**Development hypothesis.**— Valentine (1986) and Valentine & Erwin (1987) suggested that the breadth of morphologic innovation in the Early Paleozoic reflected the limited canalization of development in early Metazoa, which Jablonski & Bottjer (1990) termed the genomic hypothesis. The role of development in the generation of morphologic novelties has been discussed extensively (e.g. Arthur 1984, 1988; Bonner 1982, 1988; Hall 1992; John & Miklos 1988; Lauder & Liem 1989; Liem 1990; Raff & Kaufman 1983; Raff & Raff 1987; Thompson 1988) but generally in the context of the modification of existing developmental programs rather than their formation (Erwin *in press*). For example, Müller & Wagner's (1991) description of evolutionary novelties focuses entirely on the alternation of existing developmental programs.

Unlike later events, the most significant developmental events of the Cambrian radiation involved the proliferation of cell types, developmental hierarchies and epigenetic cascades that form a necessary part of metazoan development (Bonner 1988; Valentine, personal communication 1992; Erwin 1990, *in press*). A phylogenetic perspective on the evolution of development establishes that while the major building blocks of development, including pattern formation, induction, differentiation of cell types and hierarchical regulatory control, are widespread throughout higher eukaryotes, a series of developmental synapomorphies differentiate metazoan development from fungi, plants and other higher eukaryotes, including homeobox sequences, specialization of the nervous system, and the extracellular matrix (Erwin *in press*; Møms 1993).

The crucial difference between the developmental events of the Cambrian and subsequent events is that the former involve the establishment of these developmental patterns, not their modification. Thus the early phases of the Cambrian radiation feature Metazoa exploring the available possibilities as various functional thresholds are crossed. For example, different metazoan architectures require different numbers of cell types, with eucoelomates requiring more cell types than diploblasts. Thus one aspect of the development of increasingly complex metazoan architectures during the Cambrian was the elaboration of new cell types. One might expect a proliferation of eucoelomates with a variety of morphologies as this threshold is breached. Significant changes in development are required by any model for the Cambrian radiation. However this model



suggests that such changes were a primary forcing mechanism driving the extensive morphologic innovation.

Under this model subsequent increase in the complexity of development and the extent of epigenetic interactions would have necessarily limited the range of possible developmental repatterning. Thus the burst of morphologic innovation is constrained by later intrinsic modifications, rather than a change in the rate of success, as in the ecosystem hypothesis.

## Complexity

As anyone who remembers the early days of personal computing can readily attest, technological innovation often follows a pattern of rampant experimentation, introduction of many competing products and eventual concentration on a few designs which dominant the market (in contrast to the more common pattern of trial and error driving continuous modification). Thus early computers included those from Apple, Northgate, IBM, Tandy, Osborne and a host of others. Most required different operating systems (system software), had unique system architectures and required different user software. The introduction of the original IBM personal computer with the Microsoft Disk Operating System (DOS) and an open architecture signaled the end of most competing designs. Only Apple survived with its unique, graphical operating system, but with a far smaller market share than DOS machines. As the market switched to an IBM/DOS design the open architecture allowed the proliferation of a multitude of clones: a move from innovation and diversity to imitation and conformity. Clearly the past 13 years have witnessed considerable innovation within the computer market (high-resolution monitors, laptop computers, faster chips, et~.) but it has **all** occurred within the framework established by the market success of the original IBM PC.

Are these patterns of early innovation followed by subsequent standardization an inherent property of complex systems? If so, there may be nothing unique about innovative biological radiations: they are an expected consequence of complex systems. Living organisms, national economies, social systems are all examples of such complex dynamic systems – systems characterized by nonlinear behavior including self-organization and positive feedback loops. Models developed to explore the behavior of the economy (Holland 1988; Arthur 1988) have been extended to analysis of a variety of aspects of evolutionary biology (Mittenthal & Baskin 1992; Green 1991).

Kauffman (1989a–b, 1992, 1993; see also Wimsatt & Schank 1988) has been a leading proponent of this point of view, arguing that asymmetric morphologic innovation is a general property of adaptive evolution on what he terms 'rugged fitness landscapes' (Kauffman 1989a). According to this hypothesis a rapid exploration of the realm of possible basic morphologies will rapidly establish the major morphologic variants while subsequent evolution is characterized by more constrained variation. Kauffman rejects both the empty ecospace model and the developmental model, arguing that

fitter genetic variants become progressively more difficult to find and that the universe of allowable early developmental types is smaller than that of later developmental types. In truth however, Kauffman's model appears to combine aspects of both the empty ecospace and developmental model within an interesting conceptual framework that is even more difficult to test than either of the original models.

Economic models have long been a fruitful source of inspiration for evolutionary biologists. Darwin's reliance upon Malthus is well known, but during the 1850's many other British biologists drew inspiration from the economic miracle around them as well. Today, models of complex systems are inspired by developments in physics, economics and other disciplines. There is little doubt that many conceptual ideas being developed by complexity theorists are quite intriguing. It is far more difficult, at present, to figure out how to relate them to actual evolutionary problems. The difficulty, as often happens, lies not with developing models of how evolution could operate, but with learning how evolution actually operates. Complexity models will only contribute to our understanding of the evolutionary process as they move beyond similarity of pattern to a discussion of common process. Inherent in the complexity approach is the assumption that all complex dynamic systems are subject to similar constraints. Specifying these similarities and constraints is the hard part.

## Discussion

Although the ecospace and genomic hypotheses have been presented as alternatives, they are clearly nonexclusive and may even be complementary. They are quite different hypotheses however, both in structure and implications. The ecospace hypothesis seeks to explain the differential success of morphologic innovations, but not their origin. Thus it requires that extensive morphologic innovation be frequent through the Phanerozoic. The ecological circumstances of the time will determine the success of individual innovations. In contrast, the genomic hypothesis of Valentine and Erwin explicitly restricts such innovations to the establishment of new developmental patterns.

Jablonski & Bottjer (1990) argue that discriminating between these hypotheses is difficult because of the lack of predictions unique to a single hypothesis, although they strongly favor ecological control of diversification. In fact comparative tests employing a phylogenetic framework, and additional ecological and functional information provide a way of testing these hypotheses. For example, the ecospace hypothesis requires that many pairs of sister taxa will exhibit high morphologic divergence associated with high ecologic divergence (the latter can be assessed through functional criteria). The Onychophora provide one possible example. Recent molecular results (Ballard *et al.* 1992) suggest that living onychophorans may be highly unusual arthropods rather than intermediates between arthropods and annelids. Thus a rigorously constrained phylo-

genetic analysis of Cambrian taxa (admittedly not yet in prospect), combined with ecological and functional information does offer the possibility of corroborating or rejecting this hypothesis.

Conversely, the genomic hypothesis makes specific predictions about the distribution of genetic and developmental characters among major groups. In this case developmental information is mapped on a cladogram and the pattern of developmental character states is analyzed. (Obviously only living clades can be analyzed in this fashion, but they are sufficient to determine whether the hypothesis has merit.) If this hypothesis is correct, two conditions should be met. First, morphologically distinctive clades, often recognized as higher taxa, should have distinctive developmental synapomorphies. Secondly, unique patterns of constraint, such as increased epigenetic interactions and developmental canalization, should occur within each distinctive clade; this is the sort of historical contingency discussed by Hoffman (1989). Additionally, one might expect that patterns of morphological integration (Olson & Miller 1958; Hughes 1991) would increase rapidly through the Cambrian. This can be examined within fossil groups by studying morphometric covariance matrices (e.g. Foote 1991, 1992, 1993). Since tests for the ecospace and genomic hypotheses are independent, the relative contribution (if any!) of each model can be assessed for a particular clade.

Although neither test can be conducted with much confidence today because of uncertainties in metazoan phylogeny, rapid advances in this area and increasing knowledge of developmental processes, particularly in arthropods and echinoderms, holds the promise that such tests will soon be possible.

The implications of each model bears further consideration as well. The nature of the ecospace hypothesis is little different from most evolutionary mechanisms but this is not true of the developmental hypothesis. The genomic hypothesis calls into question the implicit assumption of many evolutionary biologists that while many evolutionary patterns may be unique this is a simple expectation of history. We assume that the mechanisms operating today are those which have operated in the past; this assumption may well be true. Certainly no contradictory evidence has been advanced (although it is difficult to imagine what evidence could be developed to test the assumption). The effect of mechanisms may change through time however, as the developmental systems themselves evolve, fueling the asymmetric patterns of morphologic innovation. If so, the fossil record may provide not only a broader understanding of the patterns and diversity of life than living organisms would indicate, but a richer view of the evolutionary process as well.

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