

Evolving Form and Function: Fossils and Development

*Proceedings of a symposium honoring
Adolf Seilacher for his contributions to paleontology,
in celebration of his 80th birthday*

Derek E. G. Briggs, Editor

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The Origin of Animal Body Plans

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ABSTRACT

Economic historians make a useful distinction between inventions and innovations (inventions that succeed within an economy). Applying this distinction to the evolutionary novelties of the Cambrian metazoan radiation suggests many developmental inventions were necessary but insufficient as causes for the breadth of the diversification. Comparative developmental studies of modern animals are providing a detailed window into these developmental inventions, with the protostome–deuterostome ancestor, or urbilaterian, occupying a critical node at the origin of the bilaterian clades. Highly conserved developmental elements between vertebrates and arthropods indicate that there was considerable developmental complexity at this node, but the level of morphological complexity remains disputed. Such inventions do not, however, seem sufficient to generate the morphological breadth of the radiation of body plans. Here the primary factor was likely the construction of new ecospace through positive ecological feedback.

KEYWORDS

Cambrian, metazoan radiation, Urbilateria, evolution and development, innovation, niche construction, ecology.

Introduction

Attempting to understand the origins and establishment of morphological novelties often seems an exercise in fruitless speculation and storytelling occasionally enlivened by the discovery of such new fossils as the late Neoproterozoic embryos of the Duoshantuo Formation of China, or by such new sources of data as the wealth of comparative developmental studies of metazoans. All too often, however, the griots envelop these advances and the storytelling resumes.

This is not to argue that significant advances in understanding the origins of body plans have not occurred over the past several decades. Molecular data, initially from 18S ribosomal RNA (rRNA), but now including many other sequences, have revolutionized our views of relationships among various metazoan clades and eliminated such old phylogenetic favorites as the pseudo-coelomates. Comparative developmental studies, when placed in this new phylogenetic frame-

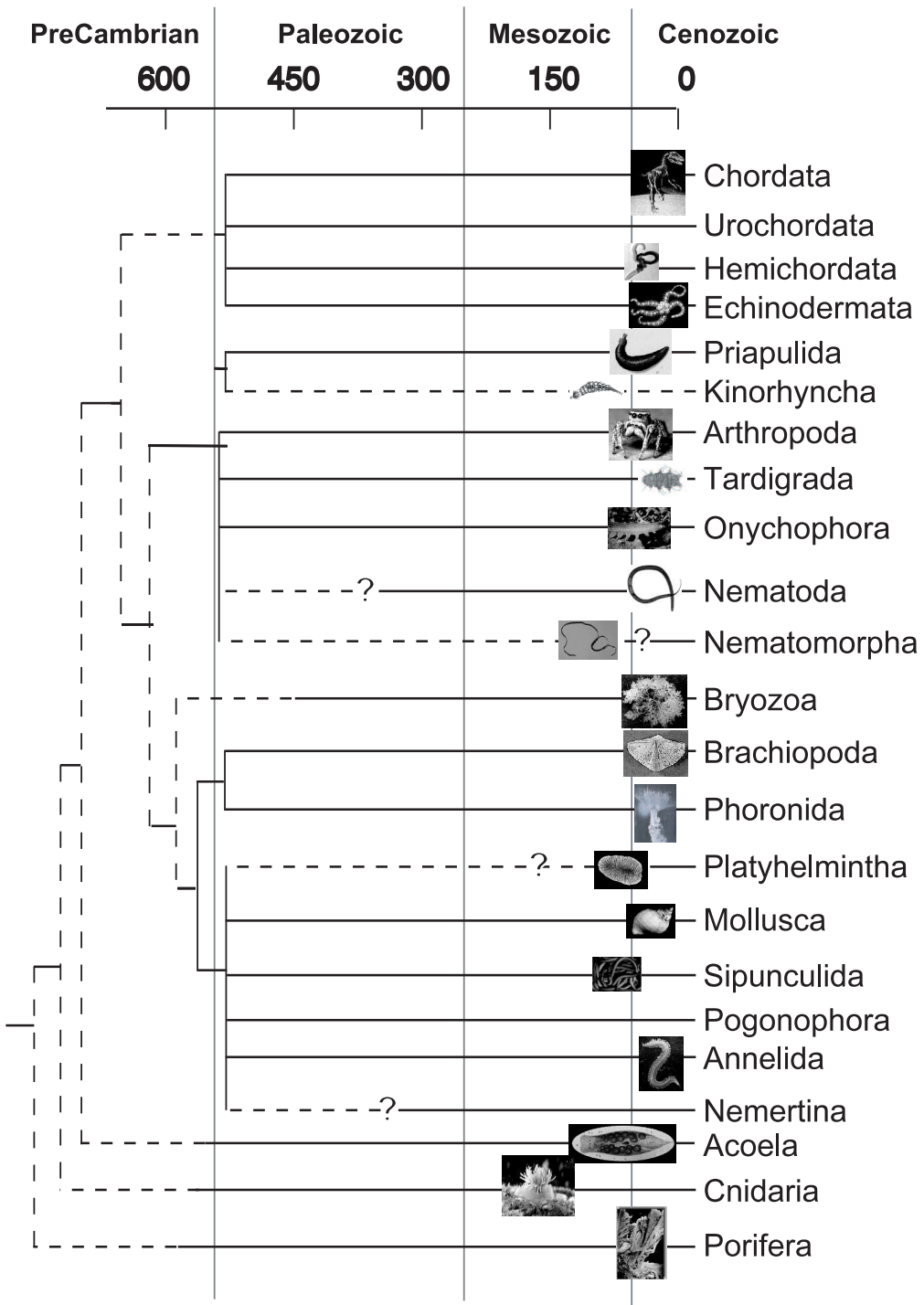


FIGURE 1. Phylogenetic relationships of the major metazoan phyla, scaled against the time of origin in the fossil record.

work, have challenged our views of the origin of limbs, segmentation and eyes, and revealed much deeper regulatory conservation than most developmental biologists had ever imagined. Advances in high-resolution geochronology have provided the first useful temporal framework for the geological and paleontological events of the Ediacaran and the Cambrian periods. Finally, a tight integration of carbon isotope geochemistry and other geological information has provided fascinating new insights into the environmental events of this era, from the provocative but controversial idea of a “snowball earth” to changes in ocean chemistry.

Integrating such disparate data has been a great challenge and assessing the causal relationships among the wealth of developmental, environmental and genetic data has been particularly difficult. Many commentators have focused on single factor causes as the triggering agent for the Cambrian metazoan radiation, whether the advent of skeletonization (Stanley 1976; Vermeij 1989), the origin of eyes (Parker 1998) or the aftermath of the late Neoproterozoic glaciations (Hoffman and others 1998). Others have been more conscious of the complexities of history and have eschewed the beguiling attractions of key innovations in favor of a more nuanced view (Knoll and Carroll 1999). Jim Valentine has recently taken an encyclopedic view of the origin of body plans (Valentine 2004) that I clearly cannot emulate here.

Rather, in this contribution I follow the lead of historians of technology and distinguish between inventions, the creation and establishment of something new, and innovations, the impact that inventions have on ecology and evolution. The economist Joseph Schumpeter (1883–1950) argued for the importance of innovation in economic growth, and distinguished invention from innovation in his first classic work, *Theory of Economic Development* (Schumpeter 1912 [1926]; see also Erwin and Krakauer 2004). Many historians of technology have adopted this useful distinction in addressing cases of technological innovation. Although biologists have long distinguished between the causes of variability in organisms and the fixation of these variants within a population, I think Schumpeter’s is a useful, indeed critical, distinction for biological innovation. Here I contrast invention and innovation in exploring three aspects of the late Neoproterozoic–Cambrian radiation: the possibilities created by the physical environment, the potentials of genetic and developmental inventions, and the opportunities constructed by ecological interactions. My thesis is that the environmental, genetic and developmental changes were necessary but not sufficient to explain the rate and morphological magnitude of this event, in which the construction of new ecosystems played a vital role. The most interesting issue is the dynamic among environment, development and ecology in the origin and establishment of animal body plans.

Dating the Radiation

To establish the relationship among environmental, genetic, developmental and ecological changes requires a firm temporal framework and an assessment of how well the first occurrences of lineages in the fossil record are likely to reflect their times of origin. Accurately placing paleontological and geological events in time and correlating temporal events around the globe are critical to establishing the sequence of changes, inferring possible causal connections, and evaluating rates of evolutionary change. Until the recent development of just such a high resolution timescale based on radiometric ages, it has been very difficult to determine, for example, how many glacial events occurred between about 635 and 575 Ma. The Guab glaciation in Namibia has now been dated to 635 Ma \pm 1.2 Ma (Hoffman and others 2004); the Gaskers glaciation in North America to 580 \pm 1.0 Ma (Thompson and Bowring 2000); the Ediacaran assemblage to 575 to 542 Ma, with the earliest generally accepted bilaterian, *Kimberella*, at 555 Ma (Martin and others 2000); and the Ediacaran–Cambrian boundary to 542 Ma (Amthor and others 2003). The fascinating early metazoan embryos of the Duoshantuo Formation in South China (Xiao and others 1998; Xiao and Knoll 2000), including possible bilaterians (Chen and others 2004), remain poorly constrained by geochronology, although some dates have been published (Barfod and others 2002; Zhou and others 2004). Correlation between sections using carbon isotope chemostratigraphy has also greatly improved the temporal framework (Bartley and others 2001).

Molecular clock analyses, initially based on 18S rRNA but now expanded to include a broader array of genes, suggested that the origin of metazoans and the last common ancestor of proto-stomes and deuterostomes considerably predated the radiation documented by the fossil record. These estimates ranged between 1,500 and 800 million years ago (Runnegar 1982; Wray and others 1996; Bromham and others 1998; Gu 1998; Wang and others 1999), suggesting a long “phylogenetic fuse” before the appearance of novel body plans (Cooper and Fortey 1998). However, more recent analyses have identified several methodological problems related to the earlier molecular clock studies (Ayala and Rzhetsky 1998; Cutler 2000). Significant rate heterogeneity has been identified through the use of a more comprehensive suite of calibration points (Peterson and others 2004) and a Bayesian approach to data analysis (Aris-Brosou and Yang 2003; Douzery and others 2004). These studies yielded considerably younger dates for the PDA: 582 Ma (Aris-Brosou and Yang 2003); 642 to 761 Ma (Douzery and others 2004); and 573 to 656 Ma (Peterson and others 2004). The Aris-Brosou and Yang (2003) dates still suggest a gap between the PDA divergence and the appearance of demonstrable bilaterian fossils (582 Ma to the earliest generally accepted bilaterians at 555 Ma), but all the dates are generally compatible with the fossil record. Some have wondered whether the disjunction between the fossil data and inferences from molecular clock studies could reflect a rapid increase in the rate of sequence evolution during adaptive radiations. Bromham and Woolfit (2004) found no evidence for such an increase in their analysis of a suite of island adaptive radiations. Whether this reflects the fundamentally different nature of events during the Cambrian and other adaptive radiations is unclear. Nonetheless, while the most recent molecular clock dates still suggest a somewhat older divergence than does the evidence of the fossil record, the gap is relatively small.

Environmental Possibility

The late Neoproterozoic witnessed significant changes in climate, and in ocean and atmospheric chemistry, and the close association between these events and the biological transformations has fueled considerable speculation about the extent to which environmental changes facilitated or even drove the evolutionary innovations.

The presence of late Neoproterozoic glacial debris has been known for several decades and geologists studying these rocks had long debated the nature of the unusual “cap carbonates” that sit immediately atop them. The discovery that many of these glacials were deposited near sea level and in low latitudes led to the proposal by Hoffman and others (1998; Hoffman and Schrag 2002) that there was an interval of “snowball earth” with near complete ice coverage of the planet. This was derived from an earlier proposal by Joe Kirschvink for some Paleoproterozoic glaciations (Kirschvink 1992). This remains a highly controversial hypothesis that need not be rehearsed here, but Hoffman and others (1998) noted that the expansion of animals began soon after the Marinoan glaciation and suggested that this might represent a causal relationship. Others have expanded on these possibilities (Runnegar 2000; Grey and others 2003; Peterson and Butterfield 2005).

Two evolutionary stimuli could have been associated with the Neoproterozoic glaciations. First, the global glaciation could have severely restricted available habitats and likely eliminated the bulk of preglacial biodiversity; in this case, the subsequent diversification could have been a response to the glacially induced extinction. Significantly, if the snowball earth hypothesis has some validity, then the most critical restriction on diversity was likely associated with the strong temperature fluctuations and harsh ocean chemistry (particularly pH) of the deglaciation (Erwin, in preparation). Second, it has been suggested that the environmental conditions themselves increased the rate of evolution, either by increasing the rate of mutation or by releasing “hidden variation” that had not been previously expressed because of such evolutionary capacitors as Hsp 90 (Queitsch and others 2002; True and others 2004). Evolutionary capacitors mask genetic variation by stabilizing the phenotype. Only when the environment is severely disrupted can this variation affect the phenotype.

Both proposals suffer from similar defects. First, the latest late Neoproterozoic glaciation at

580 Ma can only plausibly explain the appearance of the Ediacaran fauna, and not the explosion of bilaterians near 530 Ma (and this only if the Gaskiers glaciation is actually a snowball earth type of glacial event). Second, while each of these explanations serves to increase the real or apparent rate of mutation and assumes that this will translate into the extensive morphological diversification documented by the fossil record, this ad hoc correlation tells us little about the actual processes behind this macroevolutionary burst. But perhaps the most telling difficulty with these proposals is that there were several late Neoproterozoic glaciations (perhaps as many as four), and this argument provides no explanation why the latest of the four was the only one to induce any burst of evolutionary innovation.

The most intriguing environmental change is associated with the oxygenation of the previously anoxic and euxinic (sulfur-enriched) Proterozoic oceans and increases in atmospheric oxygen. Increased oxygen levels have long been invoked as a cause of the Cambrian metazoan radiation (Berkner and Marshall 1964). Recent geochemical studies have significantly modified early suggestions and seem to have made some such change more plausible. Carbon (Logan and others 1995) and sulfur (Canfield 1998) isotopes strongly suggest an increase in oxygen levels and a conversion from Proterozoic oceans with anoxic and euxinic deep water and oxygenated surface water (Anbar and Knoll 2002; Knoll 2003a, 2003b) to more oxygen-rich oceans. The difficulty here is timing. As even the advocates of this perspective admit (Knoll 2003b) the constraints on the timing of an increase in oxygen levels remain poor, and it is uncertain whether any such increase was merely permissive of later evolutionary novelty or played a more fundamental causal role.

Evidence for a pronounced shift in carbon isotopes and plausible arguments for a mass extinction at the Ediacaran–Cambrian boundary (Amthor and others 2003) have led to suggestions that the Cambrian radiation was essentially a response to the extinction, akin to other biotic recoveries. As with the earlier glaciations, the breadth and magnitude of the Cambrian radiation is far greater than that following any other mass extinction, even the 95% species-level extinction at the close of the Permian (Erwin and others 1987). Postextinction recoveries may produce large numbers of new species and even families (although it is not apparent that the number of new families is actually greater after mass extinctions). But none of the Phanerozoic mass extinctions show the sort of high-level morphological innovation seen during the Metazoan radiation, and thus provide little support for suggestions that the extraordinary breadth and rapidity of the Metazoan radiation is simply a postextinction biotic recovery. There is a clear temporal link between the origin of body plans and climatic perturbations, increases in available oxygen (particularly in the oceans), and other geochemical changes. What remains uncertain is whether there is a causal link between these events and the biological innovations.

It is difficult to see how any of these environmental changes could be directly responsible for the breadth of evolutionary change. Here the distinction between invention and innovation again becomes useful. These environmental changes can be responsible for creating opportunities, and thus for the timing of these events, but it is the morphological and underlying developmental inventions that explain their breadth. Ultimately resolving the issue of causality requires establishing the age of the PDA and how it is associated with environmental changes. If, as appears likely at the moment, the real pulse of animal bodyplan formation occurred independently during the Early Cambrian in multiple post-PDA lineages, then some external trigger must have played a significant role, either one of the environmental causes discussed above or the ecological events considered below.

Developmental Potential

The critical value of the distinction between invention and innovation is captured in the ongoing controversies about the role of highly conserved regulatory molecules among the bilaterian clades. Developmental biologists have examined organisms belonging to two major and distinct clades of bilaterians: arthropods, principally *Drosophila*, among the Ecdysozoa, and a variety of vertebrates among the deuterostomes. Until relatively recently much less developmental information was avail-

able on the other great protostome clade, the Lophotrochozoa. Placed in a phylogenetic framework, this growing developmental information permits inferences about the last common ancestor of the bilateria, variously termed the urbilaterian or the protostome–deuterostome ancestor (PDA). There is now a decade's worth of ruminations about the complexity of this beast. If it is assumed that the regulatory genes that control the formation of structures in both protostomes and deuterostomes necessarily controlled the formation of a similar structure in the last common ancestor of the two clades, then a great deal can be inferred about the nature of the PDA. Most commentators argued for a relatively complex organism (Shenk and Steele 1994; Slack and others 1993; Scott 1994; Kimmel 1996; Ohno 1996; Knoll and Carroll 1999; Carroll and others 2001).

This has some important implications for interpreting the fossil record, for if the early molecular clock results had been correct in dating the PDA to 850 Ma or older, then it would be difficult to explain how the multiple lineages of such a relatively complex organism had escaped detection in hundreds of millions of years of fossil record (Erwin and others 1997; Valentine and others 1999). The refined molecular clock studies have largely, although not completely, ameliorated this conflict. Comparative developmental studies can still reveal a great deal about the possible complexity of the PDA and greatly inform our views on the origin of animal body plans.

Important elements of body patterning are highly conserved between protostomes and deuterostomes, including duplication of genes within both the *Hox* and *ParaHox* clusters, which suggests that the PDA must have been relatively complex. Genes of the *Hox* cluster are responsible for anterior–posterior patterning along the central body axis of the developing embryo. The number of *hox* genes in the PDA remains unclear, but there were at least eight and possibly as many as 10 (de Rosa and others 1999; Balavoine and others 2002). *Hox* genes have clearly undergone differential duplication and loss within individual lineages, and it was once thought that the PDA may have had relatively few *Hox* genes (Manak and Scott 1994). The work of de Rosa and co-workers now makes it clear that duplications in the lineage leading up to the PDA may have provided it with the full bilaterian suite. The *ParaHox* cluster was derived from the *Hox* cluster early in animal evolution and is responsible for patterning the gut of triploblastic organisms (Brooke and others 1998). Dorsal–ventral patterning involves *sog*, *chordin* (Holley and others 1995) and *twisted gastrulation* (Oelgeschläger and others 2000). Anterior patterning is controlled by *Otx/Otd* (Finkelstein and Boncinelli 1994; Hirth and others 2003), while posterior structures are controlled by *caudal* (a *ParaHox* gene) in *Drosophila*, *C. elegans* and vertebrates, suggesting that both elongation of the central body axis and segmentation are conserved from the PDA (Copf and others 2004).

Different authors have argued that central nervous system development is highly conserved (Nielsen 1999), including the development of neurons and their diversification (Chan and Jan 1999), axon guidance (Chisholm and Tessier-Lavigne 1999) and, most controversially, a tripartite brain structure (see, for example, Ghysen 2003; Hirth and others 2003). All of these attributes suggest that both the central nervous system and its associated elements were relatively highly developed in the PDA. However, this analysis has been highly dependent on analyses of *Drosophila* and vertebrates, both of which have centralized brains, unlike the varieties of nerve nets favored by most invertebrate groups. When Lowe and co-workers (2003) examined the expression patterns of genes associated with a central nervous system in the hemichordate *Saccoglossus* they discovered that most genes were associated with the diffuse nerve net rather than a central nervous system. Consequently, they concluded that ancestral deuterostomes, and likely the urbilaterian, had a diffuse nerve net rather than a brain.

Two of the most controversial aspects of development in the PDA involve segmentation and appendages. While almost no developmental biologists have suggested that appendages were present in the PDA, the possibility of segmentation has been very contentious, favored in some phylogenetic schemes while rejected in others. *Distal-less* is expressed along the proximodistal axis of outgrowths in a variety of protostome and deuterostome phyla, ranging from the tube feet of echinoderms and limb buds of vertebrates to the parapodia of polychaete annelids (Panganiban and others 1997; Panganiban 2000; and especially Panganiban and Rubenstein 2002). There have

long been strong intimations of the conservation of the pathways involved in appendage formation (Shubin and others 1997) despite the near total absence of any morphological indication that appendages were present in the PDA. Segmentation is a more complex case, and those devoted to puzzling out metazoan phylogeny have long battled over the number of times segmentation arose. Expression of *engrailed*, in particular, has been used to support claims that segmentation is a character shared between protostomes and deuterostomes (Holland and others 1997; Davis and Patel 2000; Tautz 2004), but these claims remain contentious, and it is far from clear that the PDA was actually segmented.

The formation of specific tissues is also highly conserved. Gut patterning involves the *ParaHox* cluster, but endoderm formation also involves a sequence of conserved transcription factors from the GATA family and HNF4/fork head (Zaret 1999; Shoichet and others 2000). Conservation of eye formation, as indicated by the genes *Pax-6* and *eyeless*, has made this one of the paradigmatic examples of inferred conservation of both regulatory pathways and their morphological outcome (Quiring and others 1994; Gehring and Ikeo 1999; Arendt and Wittbrodt 2001; Gehring 2004). Even more intriguing, however, is recent work by Arendt and co-workers (2004) identifying both ciliary and rhabdomeric photoreceptor cells in the marine annelid *Platynereis*. Ciliary photoreceptors occur in vertebrates, while rhabdomeric photoreceptors are found in invertebrates, and Arendt and co-workers reasonably interpret the presence of both in *Platynereis* as evidence that the PDA also had them (see also Lacalli 2004). Complex photoreceptors do not necessarily mean complex eyes, however, and there is considerable evidence that morphologically complex eyes developed independently within individual clades (as discussed in Land and Fernald 1992). Heart formation in *Drosophila* and vertebrates is similarly conserved, through the action of *tinman* and several cell adhesion factors (Harvey 1996; Bodmer and Venkatesh 1998; Tanaka and others 1998; Haag and others 1999).

How should we interpret this information? On the face of it, the conserved regulatory data suggests a very complex PDA, with considerable anterior–posterior and dorsal–ventral patterning, differentiation of the head and posterior, appendage formation, and possibly even segmentation. Specialized tissues include a complicated nervous system, a variety of sensory systems (including eyes with both ciliary and rhabdomeric photoreceptors), a heart and a differentiated gut. But before accepting such a sophisticated PDA let us turn to the development of cnidarians for a broader perspective on some of these systems.

Although much attention has focused on the remarkable conservation of developmental and regulatory systems between protostomes and deuterostomes, there is growing evidence that the diploblastic cnidarians already had significant levels of developmental complexity. Elements of all four of the major metazoan developmental signaling pathways (Wnt, TGF- β , Notch and hedgehog) are present in cnidarians although expression data are often lacking, so it is not clear how these elements are used (see Steele and others 2002 for discussion). Mark Martindale, John Finnerty and their colleagues have been studying the sea anemone *Nematostella*, which has a degree of bilateral symmetry. Support for the conservation of bilateral symmetry from the common ancestor of cnidarians and bilaterians comes from the expression of five overlapping *Hox* genes along the oral–aboral axis in *Nematostella* and the asymmetric expression of *dpp*, which controls dorsal–ventral patterning in bilaterians, near the blastopore, defining a secondary body axis (Finnerty and others 2004; although see Ball and others 2004 for a contrary view on whether these are *Hox* or *hox*-like genes). As diploblasts, cnidarians lack mesoderm, but jellyfish do have muscle similar to the striated muscle of triploblasts. Studies of the jellyfish *Podocoryne carnae* have identified expression of *twist*, *Mef2* and *snail* in a similar fashion to endodermal muscle formation in *Drosophila*, indicating that genes that later specify mesodermal development precede the origin of mesoderm (Martindale and others 2004).

The gene *Otx* specifies anterior patterning and head formation in bilaterians. The cnidarian equivalent (*CnOtx*) has been isolated from the hydra, where it is involved in cell movements during formation of the body axis, and may specify general anterior head tissue, although it does not seem to be associated with head formation (Smith and others 1999; but see Galliot and Miller

2000 for a more expansive view of the evidence). In *Podocoryne* the gene is expressed during formation of the medusa bud and then in striated muscle (Müller and others 1999). Other developmental similarities to bilaterians include *Brachyury* and dorsal–ventral patterning genes. The *Pax* genes involved in eye formation in bilaterians are also present in cnidarians, but their role in the development of cnidarian photoreceptors remains unclear (Ball and others 2004).

Many of the basic developmental tools for constructing the dizzying array of modern metazoans were present in cnidarians, but where expression data for cnidarians are available these developmental systems are used in novel ways (from a bilaterian perspective). This could reflect the highly derived nature of the cnidarians studied (the hydra in particular is hardly the optimal cnidarian to study from an evolutionary perspective). However, the role of *Hox* and *dpp* in body axis formation is similar in cnidarians and bilaterians and suggests that it is conserved. The role in cnidarians of genes responsible for mesoderm formation in bilaterians highlights how the role of these regulatory signals evolves. This same process of comparative developmental analysis can be carried back to the Porifera (Müller and others 2004), but that is beyond our concern here.

The role of bilaterian “endodermal genes” in cnidarians, or *Pax-6* in bilaterians, highlights the difficulty of assessing the ancestral role of these regulatory systems. Similarly, despite the apparent conservation of genes responsible for central nervous system formation when comparing flies and mice, Lowe and co-workers’ work (2003) on the hemichordate *Saccoglossus* shows that this inference is incorrect, and that the condition in the PDA was more likely a diffuse nerve net than a centralized, tripartite brain. Eric Davidson and I proposed an alternative view of the PDA in which the ancestral role of many of these regulatory molecules was involved in cell type specification, rather than complex morphogenesis (Erwin and Davidson 2002). We argued that in many cases these genes had been involved in a much simpler regulatory pathway, generating proteins that determined the fate of a particular cell, producing contractile muscles rather than a heart, or simple photoreceptive cells rather than an eye. Other regulatory elements formed essentially a toolkit capable of vectoral patterning. Because of their simple early role, many of these regulatory elements evolved to control more sophisticated morphogenetic pathways, but these pathways often arose independently in individual clades. This is easiest to envisage in the case of eyes, where the morphologic data show clearly that these structures arose independently in many clades.

From this view of these highly conserved regulatory elements, the PDA may have been much simpler: a small organism with a variety of cell types, a through gut and some anterior–posterior differentiation. Many of the genes interpreted as generating complex morphologic structures would have produced simpler cell types within such an organism. Reality probably lies between the extremes, and one challenge for comparative evolutionary developmental biologists is to resolve how best to assess the role of highly conserved elements. For our purposes, however, it is clear that major elements of the developmental machinery required to produce sophisticated animals were already present in the PDA, even if their potential was not yet fully realized.

Ecological Opportunity

The fossil record overwhelmingly shows that there are profound and far-reaching ecological dimensions to the origin of animal body plans and their subsequent diversification during the Early Cambrian. Many workers have argued that predation was a significant force driving diversification, and some even view it as the primary cause (Stanley 1976; Vermeij 1989; Parker 1998, 1999; see also Conway Morris and Bengtson 1994; Nedin 1999). Horizontal and vertical burrowing increased substantially from the Ediacaran into the earliest Cambrian (Seilacher 1956; Droser and others 1999, 2002; Jensen 2003) reflecting an intensified use of the substrate. As Lohrer and co-workers (2004) noted for modern sea bottoms, bioturbation increases primary production through enhanced nutrient flux and the growth of microbes and algae. Butterfield (1997, 2001) documented the expansion of the phytoplankton from the latest Ediacaran into the Early Cambrian as a critical component of the ecological innovations (see also Peterson and Butterfield 2005), although the pattern of causality is likely to be complex.

I am less concerned here with inferring the causal connections among these ecological interactions than with the theoretical framework in which to place them. For over a half a century our conceptual framework for understanding the ecological dimensions of evolutionary innovation has been hampered by an overreliance on models that invoke vacant adaptive zones (Bock 1979) or vacant ecospace (Valentine 1980) largely stemming from the views of G. G. Simpson (1944).

Valentine (1980) developed a theoretical model of the occupation of empty ecospace, which he explored in a series of computer simulations (Valentine and Walker 1986, 1987). But these models assume the prior existence of niches, which are as yet unexploited, and follow the progress of diversification into these niches or empty adaptive zones. Yet niches do not exist independently of the populations of organisms that fill them, and such models largely failed to address how niches are constructed by organisms and their environment. It is this process of niche construction that seems to be fundamental to the process of innovation, whether or not inventions succeed in the evolutionary marketplace. Modeling is a prerequisite to rigorously testing these processes with empirical data (we need to know what to look for).

I have begun exploring such models with Ricard Sole and his students (Sole and others 2002; Sole and others, in preparation). These initial models have addressed two related issues: (1) how interactions between different trophic levels influence the pace of diversification, and (2) how diversification proceeds when speciation depends on interactions between existing species (a positive feedback model). These toy models have captured some interesting dynamics, including sequential diversification up a trophic hierarchy (Sole and others 2002) and long lags followed by rapid expansion (Sole and others, in preparation). We are continuing to develop these models to make them more realistic, but easier to test with empirical data.

Discussion

Understanding the role of evolutionary novelties requires disentangling the fate of inventions from their origin through genetic and developmental systems, to their ultimate success or failure as innovations within an ecological playground. Considering the origin of animal body plans during the Ediacaran–Cambrian interval in this light suggests that environmental changes, particularly the advent of an oxygenated ocean and atmosphere, provided a platform that allowed developmental inventions to have a greater chance of success. But nothing we know suggests that this sort of macroevolutionary change was mutation-driven, other than rarely. Hence, neither the rate nor the magnitude of invention can be charged directly to the environmental account. Environmental changes may have aided the *success* of inventions, and thus have played a critical role in innovation.

The role of developmental innovations is more difficult to untangle because it requires an accurate estimate of the age of the last common bilaterian ancestor, the subject of considerable uncertainty based on molecular clock studies, and of the extent of functional conservation of developmental pathways. One commonly espoused view is that highly conserved developmental pathways necessarily imply functional conservation (Carroll and others 2001; see discussion in Erwin and Davidson 2002). This view requires the PDA to be a relatively complex organism with a heart, eyes, segmentation, appendages, dorsal–ventral and anterior–posterior differentiation, a central nervous system, a variety of sensing systems and other characteristics. The alternative that I favor is that cell-specification and signaling systems have been conserved from a shared genetic toolkit of the PDA (and in many cases precede the origin of the Cnidaria), but that much of the morphological innovation occurred within individual clades that radiated from the PDA. If this latter view is correct, then even though the potential for the Cambrian radiation may have been inherent in these developmental novelties, these did not drive the radiation. In other words, they alone were not sufficient to cause the diversification of many clades, the acquisition of the panoply of morphological complexities within these clades, nor, most importantly, the web of ecological interactions that arose in Early Cambrian communities.

Some would argue that this is true irrespective of the complexity of the PDA; whether it had

the full range of morphological and developmental complexity that some have claimed, or the rather more reduced level of morphogenesis that I have suggested, ecological factors were still of primary significance. I see a critical difference, however, for the simpler PDA implies that the instantiation of the developmental potential in various bilaterian clades would occur in concert with the construction of the ecological space occupied by those clades—a tight link between invention and innovation. In economic studies of innovations this is termed “demand-driven” innovation. The alternative suggested by a more ecologically complex PDA posits that the developmental complexity was already realized; the critical inventions had already occurred, and their realization was simply awaiting some external facilitation. This is analogous to “technology-push” models of technological innovation. The difference is in the locus of the inventions, and their relationship to producing the morphologic breadth of the Cambrian. In evolution as in technology, the reality is that both supply and demand have significant roles to play in the generation and preservation of diversity. This makes it all the more important to carefully distinguish where the controls lie.

It is within this web of interactions that the explanation for the extraordinary nature of the Cambrian radiation must lie. This view is hardly new. Many workers have invoked ecological dynamics as a critical aspect of the Cambrian radiation. But our conceptual framework for understanding this seems curiously dated, relying on empty niches and other arcane concepts. We must now strive to develop an improved conceptual framework for thinking about the network of interactions that drives evolutionary expansion.

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