

Development, Ecology, and Environment in the Cambrian Metazoan Radiation

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The Cambrian radiation of animal life is one of the most profound episodes of evolutionary innovation in the history of life. Understanding the causes of this event requires deciphering the relative contributions of environmental triggers, developmental novelties, and changes in ecosystem structure. At present, ecology appears to have been largely responsible for the breadth and structure of this event, but we lack adequate, process-based models to understand these ecological dynamics.

The rates and causes of many episodes of evolutionary innovation remain poorly understood, in large part because we lack adequate process-based models to understand these events. Developing such models is particularly difficult because several of the most interesting episodes of evolutionary creativity involve changes in the physical environment, the establishment of new ecological dynamics and often changes in genetic and developmental information processing. Integrating the three components of this evolutionary triad is demanding, and developing process-based models to understand the range of potential contributions of each leg of this triad is even more challenging.

In this contribution, I want to explore how we can develop greater understanding of evolutionary innovation, using as my example the Cambrian metazoan radiation, which is the explosion of animal life beginning about 575 million years ago that resulted in the appearance of most of the major groups of metazoans. The question I want to address is the role of environmental, ecological, and developmental forces in producing this incredible increase in biodiversity in a relatively short amount of time, at least by geological standards, if not ecological standards. Although there has been a remarkable increase in our understanding of the conservation of developmental mechanisms across metazoans, it looks like the primary factors driving this diversification are ecological. However, I will argue they are ecological in a way that we do not really understand. We do not yet have models allowing us to appreciate the dynamics of this process. A real understanding of events in the Cambrian radiation will require the generation of such models, testing them against fossil and other data and progressively refining them.

EVENTS OF THE NEOPROTEROZOIC-CAMBRIAN TRANSITION

There is a diverse fossil record that precedes the events of the Cambrian explosion. Prior to about 575 million years ago there was a very diverse fossil record of a variety of microfossils and algal groups (for reviews, see Knoll and Carroll 1999; Valentine et al. 1999; Valentine 2002). These include testate amoebae, red and green algae and a variety of spiny, organic-walled microfossils of

uncertain affinities known as acritarchs (Javaux et al. 2003). The very earliest impressions that have been interpreted as possible animals are the *Twitya* disks from the McKenzie Mountains in northern Canada. These enigmatic discoidal fossils appear somewhere between 610-600 million years ago, during a period of glaciation in the late Neoproterozoic. More convincing animal fossils are found in the Doushantuo Formation of southern China. Dating to 590-570 million years ago these include a suite of demonstrably metazoan early embryos, along with a variety of algae and acritarchs (Fig. 1). The exciting thing about this phosphorite deposit is the exquisite preservation of fine cellular detail (Xiao et al. 1998; Xiao et al. 2000; Chen et al. 2002).

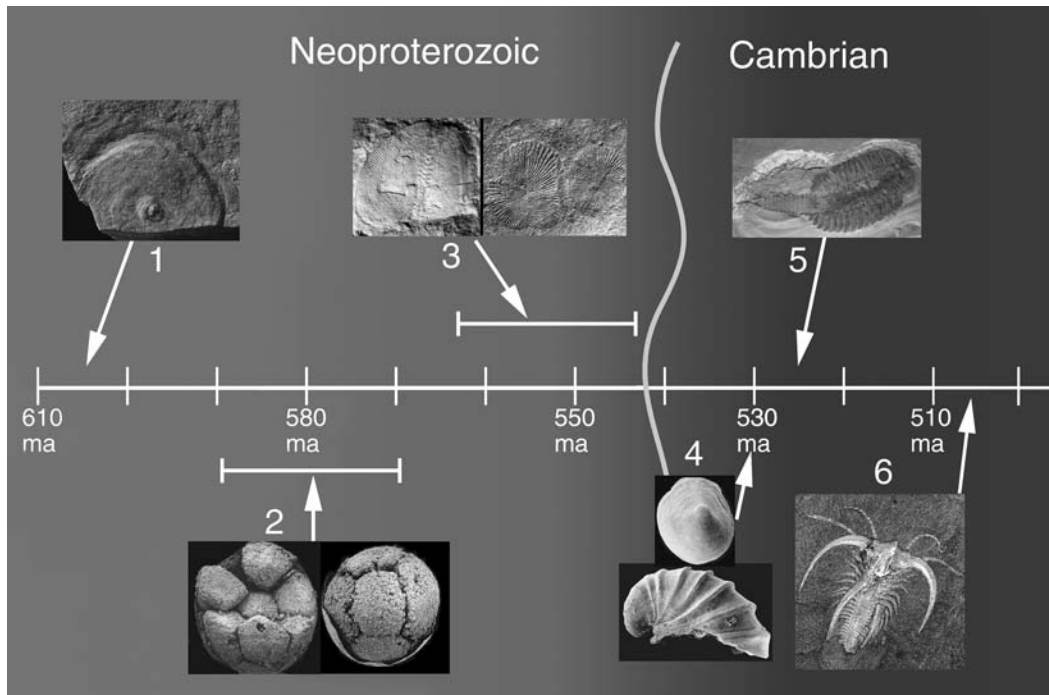


FIGURE 1. The pattern of evolutionary events across the late Neoproterozoic-Cambrian boundary, with some of the distinctive fossils of this interval. (1) Earliest putative metazoans, the *Twitya* discs of the McKenzie Mountains, Canada. (2) Early embryos of the Doushantuo Formation, China. (3) The Ediacaran fossils of the latest Neoproterozoic. (4) Small shelly fossils of the Tommotian Stage of the Early Cambrian. (5) *Fuxianhuia* from the Lower Cambrian Chengjiang Fauna, Yunnan Province, China. (6) The primitive arthropod *Marella* from the Burgess Shale, Canada. Photos of the Doushantuo fossils from Shuhai Xiao, with permission.

Soon after the appearance of the Doushantuo fossils the Ediacaran fauna appears. First discovered in southern Namibia, but most strongly identified with the Ediacaran Hills of South Australia, elements of this assemblage of disks, fronds and other radially and bilaterally symmetrical fossils has since been recovered from many different parts of the world, including the White Sea in Russia, eastern Newfoundland, and the Yangtze Gorge in south China (Gehling 1991; Seilacher 1999). Although the taxonomic diversity of this assemblage is increasingly well understood and the taphonomic conditions under which the fossils are preserved have been exhaustively documented, the evolutionary development and phylogenetic affinities of these taxa remain highly contentious. Some paleontologists have suggested the segmented forms such as *Dickinsonia* may have affinities with annelids, other with arthropods, echinoderms and other groups. Such phylogenetic assignments, if correct, suggest that the origin of the Bilateria lay before the Ediacaran assemblage, and

that each of the major bilaterian clades had already diverged as well. The difficulty with this view is that the similarities between Ediacaran fossils and bilaterian phyla are largely superficial with few diagnostic synapomorphies supporting the assignments. Indeed, most Ediacaran fossils appear to be of cnidarian grade, with no evidence for appendages, mouth, eyes, or other advanced morphological features. That the bilaterian Metazoa predate 555 million years ago is fairly certain, given *Kimberella*, a distinctive bilaterian fossil found in the White Sea (Martin et al. 2000). Although molluscan affinities have been suggested for *Kimberella* (Fedonkin and Waggoner 1997) this remains uncertain. The most one can comfortably claim is that it is bilaterian. The phylogenetic affinities of the remaining Ediacaran fossils are more problematic. Thus, it is entirely possible that, whereas, bilaterian groups had appeared in the late Neoproterozoic, none of them belongs to the extant bilaterian clades. The critical issue, as discussed further below, is the age of the last common ancestor of the two great bilaterian clades, the protostomes and deuterostomes.

Finally, after about 550 million years ago, the earliest skeletonized fossils appear as simple tubes and cones in Namibia and elsewhere. Thus begin the events of the real Cambrian radiation, with an increase in the diversity and complexity of benthic trace fossils at the base of the Cambrian, an increase in acritarch diversity and abundance, then near 530 million years ago a fairly dramatic appearance of small skeletal fossils, molluscs and brachiopods, followed by the first trilobites. Also in the Lower Cambrian are found the wonderful soft-bodied fossils of the Chengjiang fauna in China, then the Middle Cambrian Burgess Shale in British Columbia. By the end of the Lower Cambrian, evidence from the Chengjiang suggests that chordates, and possibly even vertebrates had appeared, along with elements of every durably skeletonized phylum except the bryozoans. These latter two deposits provide a unique window into the soft-bodied fossils of the Cambrian radiation, demonstrating that the diversity of poorly preserved animals was as great as the diversity of those groups with skeletons.

These biological events did not occur in a vacuum, but were intimately connected to a number of changes in the physical environment. A number of distinct glaciation events occurred near 600 million years ago, although the correlations between them remain ambiguous and hence the number of glaciations remains unclear. Glacial diamictites, with large boulders and pebbles encased in very fine-grained sediment, are a very distinctive component of these glacial intervals, but they are often accompanied by the diagnostic cap carbonates. These carbonate deposits, with a clotted texture, radiating aragonitic fans and other unusual features, are found immediately overlying many of the glacial deposits. These and other features have perplexed geologists for several decades. The Snowball Earth hypothesis of Harvard's Paul Hoffman and Dan Schrag is the most challenging explanation (Hoffman et al. 1998, Hoffman and Schrag 2002). They argued that the glacial events of the Late Neoproterozoic involved a complete freezing of the Earth from pole to equator covering the planet in a blanket of ice. The ice persisted until volcanoes released enough carbon dioxide to trigger a rapid greenhouse effect, melting the ice and generating a brief period of acidic oceans.

The diversification of animals happened in the aftermath of the last of these glaciations and Hoffman and Schrag have suggested that the environmental events triggered the Cambrian radiation. Whereas the temporal correlation is correct, whether or not the Snowball Earth hypothesis is likewise correct remains highly contentious among geologists (e.g., Ridgwell et al. 2003; Hyde et al. 2000). It does appear to be the case that many of these glacial diamictites were deposited at low latitudes and it is difficult to see how low latitude glaciers could occur close to sea level without completely freezing the oceans. However, some of the glaciations appear to be very short-lived (Thompson and Bowring, 2000). This poses a problem because the build-up of volcanic carbon dioxide in the atmosphere is believed to end the Snowball Earth events. If the glaciations are too

short, insufficient time will have elapsed for sufficient volcanism, and some other cause is required to end them; or they were not Snowball Earth events.

The critical issue is what the effects these environmental changes had on biodiversity. We do have one way of considering this question, which is to look at recoveries after other major mass extinctions. If you do that, for example, if you look at the Early Triassic after the end-of-Permian mass extinction 251 million years ago, we do not see the extent of morphological innovation that we see in the Cambrian. This and other lines of evidence suggest that although these sorts of environmental factors may be temporally coincident, it is highly questionable that they were both necessary and sufficient for the breadth of the Cambrian radiation.

Glaciations were not the only dramatic events during this interval. Although the only means of documenting changing oxygen levels in the atmosphere are indirect, there is at least suggestive evidence that the amount of oxygen may have risen rapidly in the latest Neoproterozoic (Knoll and Holland 1996; Knoll and Carroll 1999). Collagen is a characteristic protein of animals but synthesizing the protein requires higher levels of oxygen than seemed to have been present for much of the Proterozoic. Other changes in ocean chemistry seem to have occurred as well (e.g., Canfield 1998).

Very sharp negative shifts in the carbon cycle occur throughout the late Neoproterozoic, often associated with the glacial events (Kaufman et al. 1997). Using these isotopic shifts as markers of glaciation is perilous, as many other causes can trigger such isotopic excursions. New evidence from Oman suggests that a very dramatic shift at the base of the Cambrian may reflect a catastrophic mass extinction (Amthor et al. 2003), in turn suggesting that the Cambrian radiation may, at least in part, be coincident with a post-extinction biotic rebound.

One of the challenges of understanding the causes of the Cambrian explosion is sorting out the causal connections, if any, between the environmental changes and the pattern of biological innovation. Many of these environmental events have been implicated, largely by non-paleontologists, as the driving factors behind this increase in diversity. Mere correlation is not enough, however. To understand these events we need to unravel the causal connections, if any, between changes in the physical environment and the evolutionary consequences.

A BIOLOGICAL PERSPECTIVE ON THE METAZOAN RADIATION

Modern animals provide another window into the Cambrian radiation in several ways. First, morphological and molecular data have revolutionized views of metazoan phylogeny over the past decade. A series of studies has confirmed the presence of three great bilaterian clades of metazoans: the deuterostomes, encompassing chordates, echinoderms, and several smaller groups; two protostome sister clades, the arthropods, onychophorans, and other groups which shed an exoskeleton as the ecdysozoa; and the lophotrochozoa including the molluscs, brachiopods, annelids, sipunculids, and other groups (Adoutte et al. 2000; Aguinaldo et al. 1997; Peterson and Eernisse 2001). Significantly, all of the non-coelomate groups previously believed to have evolved before the protostome-deuterostome split appear, with this new evidence, to have affinities within the ecdysozoa or the lophotrochozoa. These reassignments make the nature of the last common protostome-deuterostome ancestor (PDA) even more critical to interpreting the nature of the Cambrian radiation.

The age of the PDA is the second critical area of biological insight. Beginning with the Wray et al. (1996) analysis, a host of new molecular sequences, better techniques, and more rigorous analyses has been applied to molecular clock studies of metazoan origins. Wray et al. suggested the PDA could date to 1.2 billion years ago. If this is correct, it suggests much of the metazoan diver-

gence occurred long before the Cambrian radiation, which then becomes the appearance of these groups in the fossil record rather than their origin. Subsequent studies have reported a wide range of results for the age of the PDA, from 1.5 billion years to as young as 650 million years (Aguinaldo et al. 1997; Aris-Brosou and Yang 2003; Gu 1998; Hedges et al. 2004; Lee 1999; Wang et al. 1999). One obvious conclusion from such a wide scatter of results is that the methods have yet to converge (Smith and Peterson 2002).

Kevin Peterson has addressed one of the potential problems. Most published molecular clock studies rely on vertebrates (basically fish) as the necessary calibration point to the fossil record. Peterson has shown that invertebrates produce very different results (and this would come as no surprise to any paleontologist), evidently because of systematically different substitution rates between vertebrates and protostomes (Peterson et al. 2004). Molecular clock studies do have the greatest promise for establishing divergence points of metazoan groups independent of the fossil record, and, thus, allowing more robust testing of the correlations between these divergences and changes in the physical environment.

The most exciting biological insights into the Cambrian radiation have come from another source, however, the remarkable discovery of highly conserved developmental genes (see reviews in de Robertis and Sasai 1996; Erwin and Davidson 2002; Erwin 1999; Carroll et al. 2001). A decade ago, few developmental biologists would have predicted that flies and mice used the same genes, and often very similar regulatory circuitry for producing eyes, segmentation, appendages, heart formation, and a host of other morphological features. The Hox complex, responsible for anterior to posterior growth (e.g., Balvoine et al. 2002) and Pax-6, responsible for eye formation (e.g., Halder et al. 1995; Gehring 1996), are perhaps the best known of these highly conserved elements. Such ubiquitous conservation has suggested to many observers that the PDA must have been a relatively complex animal, with a heart, eyes, appendages, complex central nervous systems segmentation, anterior-posterior and dorsal ventral differentiation, and a complex gut. Such an animal would be hard to disguise from the fossil record if it were benthic and more than a few millimeters long. Even if it were not skeletonized, the trails and other evidence of activity would be preserved. This developmental evidence, thus, appears to be in strong conflict with the molecular clock results.

In 2002 Eric Davidson and I suggested the conflict may be more apparent than real (Erwin and Davidson, 2002). We described an alternative interpretation of many of these developmental genes in which the original role of these conserved genes involved much simpler cell-type specification rather than the current role of complex morphogenetic pathways. Thus Pax-6 may have been involved in producing a photoactive pigment rather than an eye. From this perspective the PDA becomes a much simpler animal. Davidson and I suggested that much of the complex patterns of morphogenesis arose after the PDA, and is thus likely to be specific to individual clades.

BUILDING MODELS

Our expanding understanding of the sequence of events in the fossil record and their connection to changes in the physical environment and of the complexity of developmental innovation has not been matched by a similar conceptual change in understanding the ecological dynamics of the Cambrian radiation. Although there have been many new empirical discoveries about ecological relationships, conceptual advances in the ecological dynamics of macroevolutionary innovation have been missing.

The most conceptually important models of the ecological components of the Cambrian radiation have been those of Valentine (1980; Valentine and Walker 1986) in which niches exist inde-

pendent of the populations that fill them. The model dynamics focus on filling the open ecospace, and the transition between a relatively empty ecospace in which long evolutionary jumps between distant ecologies (and presumably with very different morphologies) are possible, to a fuller ecospace in which competitive exclusion causes a change in the evolutionary dynamics. Whereas such a model may provide useful insights into re-occupation of environments following smaller biotic crises, it is far from clear that it is appropriate to events of evolutionary innovation in which the construction of new niches is an integral part of the event. The issue of niche construction has recently become popular (see Odling-Smee et al. 2003), but there have been few attempts to develop ecological models of the process, or to explore them in a macroevolutionary context (although Ricard Sole and I are currently developing such models). Greater understanding of the ecological dimensions of this triad will require development of such models, exploring their implications for the fossil record so that we can test them, and further refining the models in light of empirical studies.

UNDERSTANDING THE CAMBRIAN RADIATION

Unraveling the causes of the Cambrian radiation requires comparing the relative contributions of the various changes in the physical environment, which, in turn, requires accurate determination of the age of various divergences. The complex changes in ocean chemistry seem most likely to have been associated with the Cambrian radiation, although these chemical changes may well reflect the biological event rather than trigger them. The three other events highlighted here (Snowball Earth, changes in atmospheric oxygen levels and the sharp carbon excursion at the base of the Cambrian), may explain the timing of the radiation, but we have no theoretical basis to suggest that any of the three could produce either the rate or the extent of the innovation.

Establishing the significance of the various developmental innovations in early Metazoa requires placing these innovations in an accurate comparative phylogenetic framework through analyses of a wide range of relevant taxa. Even more important, however, will be greater understanding of the significance of highly conserved genes. Does such conservation, and even conservation of entire regulatory networks imply, as many have suggested, conservation of morphological outcomes or might these conserved genes have been playing a simpler role in the protostome-deuterostome ancestor? In either case, the facts that the developmental toolkit was unequivocally established in the PDA and that the PDA probably lived prior to 555 million years ago strongly suggest that developmental innovation may have been necessary but cannot be a sufficient cause of the main Cambrian radiation after 530 million years ago. The developmental innovations were a precondition to the later events and may explain the extraordinary breadth of the radiation, but not the triggering of the event itself. Indeed one of the most surprising implications of recent comparative developmental studies is the discovery that far-reaching developmental repatterning occurs relatively frequently. As with most other forms of mutation, the rate of production is far greater than can generally be accommodated by ecological and evolutionary demand.

It appears increasingly likely that the causes of the Cambrian radiation lie with the ecological dynamics of positive feedback that facilitated the generation of many new niches. Critical to understanding this event must be the realization that this event did not involve the filling of an empty ecospace, a metaphor that implies the prior existence of a range of niches awaiting inhabitants. Resources certainly existed, but the biological dimensions of how the resources would be divided by new species were not. Generating these new niches was likely a highly contingent process. The positive feedback element of this process involved the formation of new resources, and new niches, as the radiation progressed. Many questions about this process remain unresolved and process models seem required to suggest the course for more empirical studies. These questions include:

How are new niches created rather than filled? What drives the positive feedback component of an evolutionary radiation and what factors eventually limit further rapid increases in diversity? If, as suggested above, developmental innovations are common and ecological potential limits their viability, what dynamic drives this interplay between ecological and developmental innovation? Finally, how do the processes involved in these episodes of evolutionary innovation differ from those associated with other periods of evolutionary change? Changes in developmental innovation seem unlikely to be responsible, suggesting a change in ecological dynamics is responsible? If so, does this imply that one distinction between macroevolution and microevolution may lie in the evolutionary context of the event itself?

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