10 Macroevolution, Minimalism, and the Radiation of the Animals

1. MINIMALIST MODELS OF MACROEVOLUTION

Palaeobiology is our main source of direct evidence about the history of life. But while that history is fascinating in itself, palaeobiology's most distinctive contribution to evolutionary theory is the insight it provides on the importance of scale. Palaeobiologists see the results of evolutionary processes summed over huge sweeps of space and time. As a consequence of that window on the effects of deep time and vast space, we have a chance to see whether the palaeobiological record enables us to identify evolutionary mechanisms that are invisible to contemporary microevolutionary studies with their local spatial, temporal, and taxonomic scales. Palaeobiology, in other words, is the discipline of choice for probing the relationship macroevolutionary patterns and microevolutionary processes.

This chapter will be organised around an important framing idea: that of a "minimalist model" of this relationship. I shall discuss minimalism in detail shortly, but as a rough first approximation, according to minimalism, macroevolutionary patterns are direct reflections of microevolutionary change in local populations; they are reflections of changes of the kind we can observe, measure, and manipulate. For example, Michael Benton (forthcoming) discusses models of global species richness that depend on scaling up in space and time equilibrium models of local ecological communities. To the extent that such scaled-up models are adequate, macroevolutionary patterns are nothing but local changes summed over vast sweeps of space and time. This chapter aims to make explicit the

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patterns for which this minimalist model is appropriate; to consider the quite different ways in which that model can be enriched; and to highlight some phenomena that suggest that minimalism does indeed sometimes need to be enriched.[1]

The challenge to minimalism is that *scale matters*: there are aspects of the history of life that are not (solely) the result of population-level processes accessible to neobiological investigation. Because scale matters, palaeobiology tells us something we cannot otherwise know about evolutionary processes. But when is a macroevolutionary pattern just a "mere aggregate" of the results of local processes? As I see it, minimal models are simple, perhaps simplified models of the relationship between microevolutionary process and macroevolutionary pattern. But they are simple in four independent aspects.

i. First: they are individualist. In these models of evolutionary change the fitness values that matter are fitnesses of individual organisms. One move beyond minimalism is to develop evolutionary models in which species themselves are selectable individuals in a population of species. In the recent palaeobiological literature, this idea has been centre stage; a good deal has been written on how to characterise and empirically test species selection models (see for example, Vrba 1989, Gould and Lloyd 1999, Sterelny 2003). But while species selection might be important in explaining, for example, patterns of survival in mass extinction events, the case for its importance remains to be made. In contrast, as we shall see in considering the origins and elaboration of multicellularity, some form of group selection is almost certainly important in driving major transitions in evolution.

ii. Second, extinction and speciation probabilities are effects of individual-organism fitness. The speciation and extinction probabilities of a species stand in a simple, direct relationship to selection on individuals in the populations of which the species is composed. For example, if its extinction probability is high, it is high because individual organisms are not well adapted by comparison to their competitors, not because (say) the species lacks genetic variation or because it lacks metapopulation dynamics in which migration buffers individual populations against local extinction. Minimalist models idealise away from the evolutionary consequences of species-level properties.[2]

iii. Third, novelties, key innovations, and the like, arise as ordinary variations in extraordinary circumstances. Some evolutionary innovations (for example, the invention of sex) expand the space of evolutionary possibility open to a lineage. But there is nothing unusual about the genetic, development, or selective origin of those innovations. Novelties arise and are established as ordinary, small variants from ancestral conditions. Possibility-expanding changes are, in Dennett's helpful phrase, ''retrospective coronations'' (Dennett 1995). Dawkins has argued that the origins of phyla are retrospective coronations: the great branches of animal life began with ordinary speciation events; nothing about those speciations at that time marked those branchings as of especial importance, though it turned out that they were important. Likewise, looking backwards, we can see that (say) the evolution of flowers was a possibility-changing key innovation. It led to an ecological and evolutionary revolution in plant communities. But the importance of this innovation in pollination would not have been identifiable at the time. Key innovations are genuinely important. But their importance can only be recognised retrospectively: a key innovation is one that happens to take place in the right place, time, and taxon. Its origin and establishment in that taxon are not the result of any unusual evolutionary process. We move away from minimalist models if we think that the origin or establishment of novelties (sometimes) requires special explanation.

iv. Fourth, we can idealise away from the changes in the developmental and selective background of genetic variation in phenotypes. We can treat the selective and developmental background of change as a fixed background condition. In microevolutionary studies – for example, models of the response of guppies to sexual and natural selection – we can usually treat the developmental system as a stable background condition of within-population microevolutionary change. We do this when we treat genes as *difference makers*: the substitution of one allele for another makes a selectable phenotypic difference: it (say) makes a male guppy brighter. Genes are difference makers, but only if we hold fixed the causal background in which they act. In such restricted contexts, the concept of a genotype-phenotype map and these associated causal claims makes good sense. Obviously, when our interest turns to macroevolutionary pattern, this assumption becomes much more problematic; models that make these stability assumptions idealise

radically, for selective environment and developmental system are labile on deeper time frames. We cannot extrapolate from constraints on short-term evolutionary responses to similar constraints on long-term evolutionary responses.

Understood this way, minimalism is a model, not a doctrine. Everyone would accept that the four elements of minimalism idealise away from some of the complexities of the biological world. No one supposes that selective and developmental environments are invariant. Almost everyone would concede that selection can act on collectives of individuals or that large-effect mutations might occasionally be important. The idea of minimalism is that it is *typically fruitful* to idealise away from these complications. So instead of thinking of minimalism as a doctrine to be defended or undermined, we should instead focus on identifying the range of cases for which minimal models are appropriate, and those cases in which these models need to be supplemented. As we relax the simple picture of the relationship between population level events and species dynamics, we thus get a space of models. Our problem becomes one of identifying the evolutionary phenomena for which models in differing locations in that space are appropriate.

2.   FOUR VIEWS OF LIFE

To show that minimalism is fruitful, we need to show that we can develop insightful minimal models of major macroevolutionary phenomena; that we can explain the tree of life's most striking features. To show the limits of minimalism, we need to identify those palaeobiological phenomena for which minimal models are not adequate. That is beyond the scope of any single chapter, not least because there is vigorous disagreement about the phenomena to be explained. Given the richness of palaeobiological phenomena, and the vigour of palaeobiological debate,[3] my strategy will be illustrative rather than exhaustive. I shall begin with four representative examples of overall views of life's history, and an initial characterisation of their relationship to minimalist models. Two of them seem to fit minimal models; the other two suggest that we need extensions of those models. I then explore in much more detail one crucial and controversial episode in the history of life, the early radiation of the animals.

View 1: The Spread of Variation

In his (1996), Stephen Jay Gould argued that while there really has been a rise in both the maximum and mean complexity of living agents, this fact of history is best understood as an expansion of variation in complexity. If processes of differentiation, speciation, and extinction act independently of complexity, *variation in complexity* will nonetheless increase over time. If we graph change, with complexity on the horizontal axis and time on the vertical, variation will spread both to the left and to the right from the point of life's origin. However, even if differentiation, speciation, and extinction are independent of complexity, the spread need not be equal in both directions, for life's complexity has a minimum bound (set by the biomechanics of metabolism and replication) but no upper bound. Moreover life originated near this minimum bound. So variation will spread to the right, in the direction of greater complexity, but very slightly if at all to the left. Thus maximum and mean (but not necessarily modal) complexity will drift upwards over time. Given a minimum bound and a point of origin close to that bound, the null expectation is an increase in maximum and mean complexity. So even a biased spread of variation need not challenge minimalism. The local evolutionary processes of adaptation of populations to their specific local circumstances, perhaps significantly modified by drift, and by developmental and genetic constraints, would generate spreading variation.[4]

View 2: Escalation and Arms Races

One divide within biology is between those who emphasise the importance of interactions between biological agents and those who emphasise the importance of abiotic factors for the life of organisms. Many evolutionary biologists have emphasized hostile coevolutionary interactions between lineages: arms races between differing competitors for the same resource; between predators and prey, plants and herbivores, hosts and parasites. For example, Geerat Vermeij has defended an "escalation model" of the history of life, taking as his model interactions between bivalves and their predators. As he reads the long history of bivalve evolution, it is one of the gradual improvement of defence. Bivalves have evolved the

capacity to dig deeper and faster into the substrate, and they have evolved thicker, spikier shells. Predator efficiency too has ramped up over time. Predators have become better at digging up, drilling into, crushing, or breaking open shells. Vermeij thinks of these bivalve histories as indicative of life's history as a whole: organisms become better adapted over time (Vermeij 1987, 1999).

Thinking of the history of life as an escalation of adaptation driven by arms races is to think of that history in a more selectionist way than does Gould. Escalation scenarios presuppose both that selection tends to drive evolutionary dynamics and that there is a systematic bias in the direction of selection. But this idea is compatible with overall trends in evolution and ecology reflecting locally determined events. The causal engine of escalation is ecological interaction in local communities. Escalation is a minimal model of the history of life, though one whose empirical presuppositions may not be met. External events can interrupt the association between lineages, breaking coevolutionary connections. For example, the changing biogeography and climate of Australia might change the suite of insects to which the eucalypt lineage is exposed, thus aborting arms races between eucalypts and phytophagous insect lineages.

View 3: The Increasing Space of Evolutionary Possibility

When we consider life at a particular time, we should see it as having an upper bound as well as a lower bound (Sterelny 1999d, Knoll and Bambach 2000). For example, the evolution of the prokaryotic cell had significant evolutionary preconditions. Until genes were organised into chromosomes, and the fidelity of gene replication improved, prokaryotic cells were not in the space of evolutionary possibility. There is an upper limit on the complexity of quasi-biotic systems that lack a division of labour between metabolism and replication. The same is true of other grades of complexity. For example, Nicole King has pointed out that only the evolution of signalling and cell adhesion mechanisms in protists made possible the evolution of multicellular life (King 2004). At a time (to use Gould's metaphor) there is a wall to the right as well as on the left. Over time, though, that wall shifts, for the preconditions for a new

grade of complexity and of differentiation are assembled. The space of evolutionary possibility for life as a whole expands, because the right wall moves for some lineages. As it expands, some of those possibilities are realised.

The best-known model of this kind is that developed by John Maynard Smith and Ers Szathmary (Maynard Smith and Szathmary 1995, 1999). They see evolutionary history as characterised by a series of major transitions. These include the shift from independently replicating structures to the aggregation of codependent replicators into chromosomes; the shift from RNA as the central replicator to DNA replication; the evolution of the eukaryotic cell; the invention of cellular differentiation and the evolution of plants, animals, and fungi; the evolution of colonial and social organisms from solitary ones; and even the evolution of human language. Many of these transitions have two crucial characteristics: (i) they are revolutions of biological inheritance systems, involving the expansion of the transmission of heritable information across the generations, and (ii) they are revolutions in selection, for they involve the assembly of a new, higher-level agent out of previously independent agents. Minimalist models, trading in the fitness only of individual organisms, do not seem well suited to give an account of such revolutions in selection. Yet, jointly, these revolutions lead to an expansion of the space of biological complexity.

So this view of evolutionary history does raise issues about minimalism, for it suggests that minimalist models cannot give an adequate account of the distinction between two very different kinds of evolutionary change: the *expansion of possibility* versus *the exploration of possibility*. Standard microevolutionary theory seems to be about possibility-exploring change, not possibility-expanding change. This same distinction between possibility-expanding and possibility-exploring innovations seems to be implicit in our next picture of the overall pattern of life's history, too.

View 4: Expanding Ecospace

Andrew Knoll and Richard Bambach (2000) develop a view of evolutionary transitions that focuses on the ecological changes that are consequences of morphological innovations; thus this poses similar challenges in understanding the origin and establishment of

novelty. For Knoll and Bambach, the crucial pattern in the history of life is an expansion of the habitats organisms exploit, an expansion of the range of resources organisms exploit within those habitats, and an expansion of the complexity and variety of the ecosystems that are assembled as a result of transitions in morphological complexity (Knoll and Bambach 2000). In developing their model of the expanding ecospace, Knoll and Bambach identity six ''megatrends'' that map roughly onto the major transitions of Maynard Smith and Szathmary: trends that yoke morphological innovation to ecological revolution. These are (i) the transition from the prebios to life as we know it, (ii) the radiation of the prokaryotes, (iii) the protist radiation, (iv) the evolution of aquatic multicellularity, (v) the multicellular invasion of the land, (vi) the evolution and global dispersal of intelligence.

In their view, these trends all involve ecological revolutions. The radiation of the prokaryotes expanded the range of energy sources into which life could tap. The evolution of the protists, according to Knoll and Bambach, added depth to ecosystems, for it involved the evolution of predation. As prokaryotes mostly extracted energy from abiotic sources, the structure of bacterial ecological communities was fairly simple. Eukaryotes can engulf particles, including living ones, and hence they have added layers to ecological communities, increasing their vertical complexity: grazing, predation, decomposition, are eukaryote specialties.[5] The evolution of marine multicellularity was obviously a very dramatic morphological transition. But, equally, it was an ecological transformation as well. This transition resulted in greatly increased vertical complexity of communities, and greatly increased ecological engineering. For example, with the radiation of marine animals in the Cambrian, the nature of the sea floor changed. Instead of sediments on the floor being stable, they were mixed by animals burrowing through them (this is known as ''bioturbation''). Corals and other shelled forms created substrate and habitat for other organisms, as did kelp forests (and much more recently, sea grasses). Rich coevolutionary interactions (both symbiotic and parasitic) between multicelled and single-celled organisms became possible. The invasion of the land, likewise, was an ecological revolution: a whole array of physical environments became habitats. As a result of that invasion, there are new kinds of communities and new kinds of coevolutionary interactions (most

strikingly, those between flowering plants and insects). The direction of evolution is marked by the establishment of successively more complex ecologies with more and more vertical layers. Eukaryotes were added to the top of a bacterial foundation, and various multicelled layers were eventually added to persisting though doubtless transformed prokaryote-protist systems.

If Geerat Vermeij is right, these increasingly complex communities are also increasingly dominated by energy-greedy organisms: organisms that harvest the available energy at ever higher rates, and as a consequence have increasing impact on their local environments (Vermeij 1999). In his view, both the radiation of the flowering plants at the expense of the gymnosperms and the radiation of mammals and birds at the expense of amphibians and reptiles exemplify this trend (Vermeij 1999). Ecosystems have become increasingly dominated by these high-activity organisms. At times, these act as defectors in a tragedy of the commons. They harvest more resources than others at the same trophic level, thus sucking resources out of the system at increasing rates, for their numbers expand at others' expense. But because they use so much energy, they exert more power over the local environment, increasing the rate at which energy and nutrients cycle through local ecosystems. Their overall effect is to ramp up the pace of life, thereby further selecting for agents with similarly large energy appetites.

In the next section, I link minimalism to a crucial case: the radiation of the animals. In Section 4 I present – I hope – a near-consensus view of the large-scale history of that radiation. In Sections 5 and 6, I discuss evolutionary explanations of that radiation and the relationship between macro and microevolution. I then very briefly conclude.

3.   MAJOR TRANSITIONS: A CHALLENGE TO MINIMALISM?

In the remainder of this chapter, I shall explore minimalism through consideration of major transitions in evolution and, in particular, the radiation of multicelled animal life. I shall suggest that these transitions take us beyond minimalist models of evolution for three reasons. First, as much of the major transitions literature emphasises, a multilevel perspective is essential to understanding the

selective regimes responsible for movements of the right wall. Transitions in complexity have often involved independent agents' coming to share a common evolutionary fate. These transitions involve a trajectory from a population of interacting agents to a more complex collective agent. Perhaps in a few cases (conceivably, the first eukaryote) this transition took just a single step. But in most cases there was (and often still is) a transitional regime in which the fitness of the incipient collective and the fitness of its now semi-independent elements were both important. In understanding such transitional regimes, one crucial problem is to understand the mechanisms that prevent the functional organization of the new collective from being undermined by selection on its components for defection and free-riding. So one theme involves the interaction between levels of selection, and the process through which selection on the collective results in the components of that collective (more or less) ceasing to be Darwinian populations (Buss 1987, Michod 1999).

A second challenge involves the evolution of novelty and the expansion of evolutionary possibility. The possibility space accessible to a lineage depends in part on its current location in morphospace. A lineage in which (say) the arthropod adaptive complex has evolved has evolutionary possibilities open to it that are not open to (say) velvet worms: segmented animals but without the structural complexity and skeletal support of the arthropods. But access to possibility space depends as well on the mechanisms of inheritance and development that characterise a lineage, on the variations from current location that are possible. Developmental mechanisms make some regions of space more accessible from a lineage's current location, and others less accessible (see for example, Arthur 2004, Schlosser and Wagner 2004). As I have noted, minimalist models treat the evolution of novelties as a species of retrospective coronations. Novelties arise and are established in local populations through mechanisms that are indistinguishable from those driving ordinary microevolutionary change. One potential problem for minimalist models of novelty is the role of macromutation (i.e., mutations with dramatic phenotypic effects) in evolution, but in my view, the importance of macromutation for minimalism has been overstated. No one thinks that macromutations are impossible. Even someone as sceptical as Dawkins about

the role in evolution of macromutation allows that they have probably played some role in expanding the space of evolutionary possibility, perhaps in the evolution of segmentation (Dawkins 1996). But even if rare macromutational events have played an important role in expanding the space of possibility (as is quite likely), macromutations are certainly not common enough to be the normal explanation of the origin of novelty.[6] Hence in modelling the evolution of novelty and the expansion of possibility, it may well be reasonable to neglect this complication.

In assessing minimalism, it is important to avoid a false dichotomy. On the minimalist model, a possibility-expanding novelty is an ordinary variant crowned retrospectively. One way of being extraordinary is to be the result of a macromutation. But there are other and more important ways, for evolutionary possibility is multifactorial: it depends on a lineage's current position in phenotype space, the array of potential variations in the heritable developmental resources available in that lineage, and in variations in the ways genetic and other developmental resources are used. And while there are good reasons to think that sudden macromutational shifts in morphospace are indeed very rare, those reasons do not generalise to the other factors on which evolutionary possibility depends. For example, in Sterelny (2004) I argued that the formation of symbiotic alliances often involves major shifts in evolutionary possibility. The acquisition of microbial symbionts has given many Metazoans access to lifeways that would otherwise be closed to them. And while the evolutionary origination of symbiotic alliances is not an everyday feature of the biological world, it is not vanishingly rare, either.

Possibility-expanding innovations may be changes in the control of development, and these need not be minimal variations of prior systems of developmental control. The crucial point here is that the mechanisms of developmental plasticity can cushion the immediate phenotypic effect of significant changes in the developmental system. That is why large changes in the genes themselves – chromosome inversions, duplication, and the like – are not always fatal. Significant developmental changes need not result in large (hence almost certainly catastrophic) jumps in morphospace (West-Eberhard 2003). The power of these mechanisms is illustrated by West-Eberhard's extraordinary example of the goat born without front legs. It adopted a two-legged posture and moved in somewhat

kangarooish fashion. The adjustment was not just behavioural but morphological. The goat developed with changed hind leg and pelvic structures, a curved spine, strong neck, and associated muscular changes.

Possibility-expanding changes in a lineage may often have their origin in *iceberg mutations*: variations that are not radically different in phenotype from their ancestors and contemporaries, but that generate that phenotype from an importantly changed set of developmental resources. One relatively uncontroversial example of a possibility-increasing change in development is one that increases modularity. If some aspects of phenotype are under modular developmental control, they will be relatively more evolutionarily labile (Lewontin 1985, Kauffman 1993). But there are other examples: for example, Mark Ridley argues that morphological complexity is constrained by the fidelity of inheritance. The error rate characteristic of prokaryote replication would be fatal to multicellular animals with their larger genomes; their evolution depended on the evolution of a more accurate system of error correction (Ridley 2000). In Section 6, we will consider in some detail the claim that the evolution of complex animal bodies depends on the evolution of new mechanisms of gene control.

A third challenge is the integration of internal and external factors in explaining transitions. Selection-driven microevolution is often conceived as a hill-climbing process: a population finds itself suboptimally located in an adaptive landscape and responds to that location by optimisation. As Richard Lewontin has pointed out, even when doing microevolutionary studies we often should not think of environments as fixed and organisms as labile (Lewontin 1985, Odling-Smee et al. 2003). In evolutionary transitions, selective environments and developmental possibilities are labile, so such an idealisation is less likely to be appropriate for possibility-expanding transitions, such as the invention and elaboration of multicellularity.

It is to that transition I now turn. There is no single transition to multicellularity; instead, there is a cluster of transitions that took place at different times and to different degrees. Bonner's 1998 review notes, in addition to the obvious multicellular clades of plants, fungi, and animals, the green, red, and brown algae and a variety of other more exotic cases (Bonner 1998). In these more exotic cases, multicellularity has been established without much

differentiation (as in the case of the algae). Indeed, in some of the cases it is not clear whether we should think of these systems as a single multicelled agent or as a social, cooperative population of single-celled agents (as in cellular slime molds and myxobacteria, which aggregate to form stalked structures with spores at the top). I shall focus on just one of these transitions, the Metazoan radiation, for it is an especially important case. So my stalking horse will be the early evolution of complex animal life.

4.   THE METAZOAN REVOLUTION

The "Cambrian Explosion" names the radiation of animal life in the early to mid-Cambrian, from about 543 million years ago (mya) to about 505 mya. The animals of the Cambrian were not the earliest multicelled animals. They were preceded in the fossil record by an enigmatic Ediacaran fauna: an array of discoid and frond-shaped forms whose relations both to one another and to living animals remain controversial (Narbonne 2005). But the Cambrian saw the first appearance of undoubted ancestors of contemporary animals. By then the first bivalves, arthropods, echinoderms, molluscs, and chordates had certainly evolved. There are hints of such animals before the Cambrian, in trace fossils and fossil embryos. But by the mid-Cambrian (about 530 mya), they were richly present. Moreover, this explosion was of enormous consequence. In contrast to (say) the evolution of multicelled red algae and the few multicelled lineages of ciliates and diatoms, the evolution of the metazoa changed the evolutionary and ecological landscape. Arguably, this transition was fast and vast. It resulted in a highly disparate, taxon-rich clade. It was the invention not just of multicellularity but of the control of differentiation and a full division of labour. The metazoa vary widely amongst themselves, yet are characterised by complex though reliable developmental pathways, involving many cell divisions and differentiation into many cell types. All but the earliest (or the most secondarily simplified) Metazoans are vertically complex, with cells organised into tissues, which in turn are organised into organs and organ systems. Many have complex life histories involving radical changes in phenotype over time: many Metazoa, in other words, are adapted not just to a single environment but to different environments at different stages of their life history. In many animal clades

there is a fundamental division of labour between reproduction and interaction with the environment, for in these lineages there is an established soma/germline distinction, with the early sequestration in development of those cells that will be the future gametes.

So the Metazoan radiation is not just a transition to multi-cellularity. It is a transition to structurally and behaviourally complex agents. The evolution of such agents depends on the evolution of the reliable developmental control of large numbers of differentiated cells and the complexes they make. Their diversity depends on the proliferation of a vast number of distinct developmental control systems, and the reliable transmission of those control systems to the next generation. Moreover, the invention and radiation of the animals was the invention of fully treelike evolutionary histories, with limited horizontal gene flow and (comparatively) well-defined species taxa. Notoriously, the systematic vocabulary that has been developed to describe animal lineages fits other radiations less well. Moreover, the Metazoa have been profound agents of ecological change. The radiation of the Metazoa established wholly different kinds of ecological communities based on webs of organisms that live by eating other organisms and their products. These communities profoundly changed the physical environment in which organisms lived. David Bottjer, for example, has written of ''the Cambrian substrate revolution'': Cambrian animals profoundly changed the physical substrate of shallow seafloors. Before this radiation these were stabilised (and hence available as habitat for the Ediacaran biota) by microbial mats. Once burrowing animals radiated, these mats were broken up, and the muds became unstable. The soft seabeds were no longer available to sessile organisms that lacked special stabilising adaptations (holdfasts of some kind) for such seafloors (Bottjer et al. 2000). Likewise, the invention of the turd revolutionised the chemistry of ocean waters: it packed waste chemicals in a form that was heavy enough and compact enough to sink to the seafloor rather than disperse suspended in the water (Logan et al. 1995).

The Metazoan radiation is an especially central case for understanding evolutionary transitions and the limits of minimalist models of evolution. Indeed, if the fossil record is a true record, we go from seas and seafloors with a few simple animals (sponges, jellyfish, perhaps a few wormlike bilaterians) to seas and seafloors

teeming with animal life. The Metazoa appear fairly suddenly and richly in the record. Does this rapid diversification in the fossil record reflect evolutionary history, and if so, does it show that unusual evolutionary mechanisms were responsible for this radiation? Famously, in *Wonderful Life*, Stephen Jay Gould argued for affirmative answers to both these questions, arguing that the extraordinary fossils of the Burgess Shale showed that an unprecedentedly disparate animal fauna evolved extraordinarily rapidly in Cambrian seas, and thereafter the mechanisms that generated such great disparity shut down (or, at least, slowed very dramatically) (Gould 1989).

However, our view of the life in the Cambrian has since been transformed. There is reason to suspect that Gould's estimate of its disparity rests on a taxonomic illusion. Gould thought that the Cambrian fauna was more disparate – more morphologically differentiated – than any subsequent fauna. Many of the Burgess Shale fossils did not match the body plans of any of the extant great clades. For example, many Burgess arthropods did not have the characteristics of trilobites; nor did they have the body plan characteristics of spiders and their allies; nor of insects and their allies, nor of crustaceans. But we should not expect early members of a lineage to fit body plan specifications used to identify the living members of a lineage (for a particularly forceful statement of this argument, see Budd and Jensen 2000). Living crustaceans (for example) have limb and segmentation patterns – one that, for example, includes two paired antennae – that (in all probability) were assembled incrementally and have then been inherited by the living crustaceans. Those taxa with that inherited pattern, living and extinct, are the *crown group crustaceans*. On the assumption that this limb/ segmentation pattern was assembled gradually, there will be *stem group crustaceans*. These are taxa on the lineage that leads to the living crustaceans, taxa that lived after that lineage diverged from the other arthropods and before the definitive crustacean package was assembled. Stem group taxa are bound to look strange. And there must have been stem group Metazoans aplenty in the Cambrian, for that was the period in which the great Metazoan clades were diverging and acquiring their distinctive morphologies. Gould's extreme Cambrian disparity pulse may be nothing but his encounter with this array of stem group Metazoans.[7] To the extent

that the Cambrian challenge to minimalist models was based on the idea that Cambrian animal evolution generated extraordinary amounts of disparity, and then the supply of new disparity dried up, this challenge now looks less pressing.

Even so, if the fossil record is to be trusted, there was a rapid diversification of the Metazoa from the early to the mid-Cambrian. But is that record to be trusted? Over the last ten years or so, molecular methods have served as an independent check on the relationship between the fossil record of early Metazoan evolution and the true pattern of that evolution. A variety of molecular clocks have been used to calibrate the divergence times of the Metazoan phyla. The idea is (a) to compare homologous, slowly evolving genes in different phyla, and calculate the extent to which those gene sequences have diverged one from another; (b) to calibrate the rate of evolution using taxa with a rich, reliable, and well-dated fossil record; (c) to use that rate to calibrate divergence times for other taxa.[8] The earlier results of using these molecular methods were very striking indeed: they pushed the apparent divergence of the basal Metazoans long before the Cambrian. Some of these studies estimated the divergence times between the sponges and other Metazoans (and even the later split between the cnidarians and the lineage leading to the bilaterally symmetrical Metazoa) as over one billion ya (for discussion of these earlier studies, see Bromham et al. 1998, Lee 1999). While the division of a lineage need not imply the simultaneous evolution of their distinct body plans, these dates imply a very long period of cryptic evolution. If they are right, the challenge to evolutionary biology becomes that of explaining why Metazoan animal evolution was invisible for so long, and how and why it suddenly became visible.

However, more recent molecular clock estimates of deep Metazoan splits are more congruent with fossil dates. One deep divide amongst the Metazoa is between the protostome and deuterstome developmental pathways, and Kevin Peterson and his colleagues estimate this divergence in the range 573–656 mya (Peterson et al. 2004). They argue that the very deep divergence times depended on using vertebrate evolution to calibrate the clock; this gave a misleading result because the relevant genes in vertebrates seem to have evolved much more slowly than in other lineages, making the clock run faster than it should.[9] So divergence

times are deeper than the fossil record suggests, though not hundreds of millions of years deeper. For example, Peterson and Nicholas Butterfield estimate Metazoan origins at 664 mya (Peterson and Butterfield 2005, 9549). If those dates are right, Metazoans existed for close on 100 million years before they left an unmistakable record of their presence. If the first animals were tiny, soft-bodied elements of the plankton, that invisibility is no surprise. James Valentine has provided a very helpful table of the first appearance in the fossil record of the various animal phyla (Valentine 2004, 186). The Ediacaran is the final era of the Proterozoic eon; it immediately precedes the Cambrian. Only two phyla (Cnidaria and Porifera) have a first appearance in this Ediacaran era, whereas there is a large cluster of first appearances in the Cambrian. However, twelve phyla have no fossil record at all. These are all small, soft-bodied animals. So there is nothing extraordinary in the suggestion that small animals could have been present in the Ediacaran world without leaving a fossil record.[10]

Moreover, while there is no direct fossil evidence of surviving Metazoan lineages until about 570 mya, perhaps there is indirect evidence. Peterson and Butterfield argue that ancient Metazoans have left an indirect ecological signature. They claim that there is a signal of protists becoming vulnerable to Metazoan predation at the base of the Ediacaran period (i.e., at around 635 mya). Sponge-grade organisms, because of the basic design of their bodies, can capture only bacteria and similar size particles. A nervous system and a gut are needed to capture eukaryotes: these innovations were established by the last common ancestor of the cnidaria and the bilaterians. Peterson and Butterfield think there is a palaeobiological signature of that new vulnerability of protists to predation. Before that period, acritarchs (single-celled organisms of unknown affiliation) had hyperstable evolutionary dynamics and little apparent diversity: after the period, they show both diversity and rapid turnover. Peterson and Butterfield think the morphological diversity of the Ediacaran acritarchs is a signature of biological interaction, in particular, a response to predation of protists by early animals.

In summary: our best guess of the pattern of the Metazoan radiation goes something like this. Metazoans probably existed for 80–100 million years or so before the base of the Cambrian. But their ecological and morphological diversity was low. Only a few of the

living Metazoan lineages had separated before the Cambrian, and most of these early animals were simple, without much in the way of complex tissues, organs, or musculature. They were, perhaps, mostly very small as well. However, the size and organisational complexity of the Last Common Ancestor of the bilaterian clades – ''the Urbilateria'' – remains controversial. After the Cambrian, there was a genuinely rapid ecological, phylogenetic, and morphological radiation. A raft of morphological complexes had evolved by the mid-Cambrian; complexes that had existed at best in very rudimentary form at the Ediacaran-Cambrian boundary. The Cambrian Explosion is no illusion. However, it was probably the period in which many of the modern phyla acquired their crown group characteristics rather than the period in which those clades first diverged from their sister taxa. It was, in all probability, an extraordinary period for the evolution of novelty. Puzzles remain. Why did animals remain, collectively, small and unobtrusive for the best part of 100 million years when there was room at the top? After all, the post-Cretaceous radiation of the mammals has taken only two-thirds that time. If unobtrusive microfauna lived for 80 million years or more without much expansion in size or complexity, this suggests the existence of a right wall blocking the evolution of larger and more complex Metazoa. We should look for an external environmental barrier or constraints internal to the Metazoan clade. There remain phenomena to be explained.

5.   MINIMAL MODELS OF THE CAMBRIAN RADIATION

The Metazoan radiation resulted in the evolution of a dazzling array of morphological novelties: it was a period in which the space of evolutionary possibility expanded. I noted in Section 1 that minimalist models of novelty emphasise the role of the external environment in explaining possibility-expanding innovations. Key innovations are ordinary changes in extraordinary times. Theories of the Cambrian explosion that emphasise the role of external environmental triggers fit minimalism. According to this line of thought, armour (say) was indeed a key innovation. But in the generation of relevant variation and its establishment in local populations, the spread of biomineralised structures in (for example) stem group

brachiopods looked just like any other small adjustment to local circumstances. The difference between the Cambrian and other periods of animal evolution lay not in the processes through which variations arose and spread in local populations, but in the global extent and importance of driving environmental change. The revolution was a revolution in circumstances, a revolution in what was necessary.

There are quite plausible theories of this kind. One idea is that the Metazoan radiation was initiated by an injection of new resources into the ecosystems of the late Proterozoic world. One such resource is oxygen. Atmospheric oxygen is a biological product: it is not an ancient feature of the world. A threshold level of oxygen is needed to power the aerobic metabolisms of (most) animals. While tiny animals can live in low-oxygen environments, large, active, or well-armoured animals cannot. So one traditional hypothesis was that the radiation was triggered by oxygen's reaching that threshold (Nursall 1959). Knoll discusses this idea sympathetically, arguing that there is indeed geochemical evidence for an increase in atmospheric oxygen in the late Proterozoic, after the youngest of the three severe global ice ages that preceded the Ediacaran biota. The evolution of that biota might well (he argues) have been triggered by that oxygen pulse (Knoll 2003, 217–20).

There are other versions of this resource-driven view of the radiation. Vermeij argues that major pulses of evolutionary innovation are caused externally, by sudden pulses in the availability of resources (Vermeij 1995). In particular, he thinks that the time of Metazoan evolution is characterized by two great innovation revolutions: one from the Cambrian to the mid-Ordovician, the other in the mid-Mesozoic. Undersea volcanism generated a large pulse of extra resources, and those pulses led to biological revolutions.[11] He argues that an external mechanism must play a crucial role in the Metazoan radiation, for many innovations occurred independently in several lineages, for example, the evolution of a skeleton, rapid and controlled locomotion, the capacity to burrow.

The evolutionary dynamics of one lineage are often sensitive to change in others. Perhaps then the Metazoan radiation is an effect of runaway coevolutionary interactions. A key innovation in one lineage triggers coevolutionary responses in others. Those responses themselves may include further key innovation, inducing

feedback-driven diversification. There is a raft of mutually com-
patible suggestions along these lines. The most widely discussed one
is based on the invention of macropredation, a breakthrough that
triggered a host of defensive counteradaptations and hence further
adaptations for predatory lifeways (Vermeij 1987, McMenamin and
McMenamin 1990). Building shells and skeletons certainly takes off
in the Cambrian: that era saw the evolution of hard structures in
bivalves, molluscs, brachiopods, arthropods. There are two more
recent ideas: Bilaterians with a true body cavity invented the ca-
pacity to tunnel through the substrate both for food and for refuge,
destroying one community type (based on sediments stabilized by
microbial mats) and establishing others. There was a biological
revolution in the nature of the sea floor (Bottjer et al. 2000). Most
recently, Andrew Parker has argued that the Cambrian radiation is
a central nervous system revolution. The invention of true vision is
the invention of a special kind of active agency. Through vision,
agents get fast, accurate, and positional information about their local
environment, and that sets up selection for rapid, guided response.
The result is the evolution of a new kind of agent, one whose
behaviour in both foraging and defence is guided by specific and
up-to-date information about its local environment. No other sense
modality has this combination of range, specificity, and speed of
information transmission (Parker 2003).

Such explanations fit with minimalist models of the Cambrian
radiation. The selective environment changed in an important,
sustained, and global way. Those changes affected different lineages
in similar ways: perhaps they eased resource constrains on all of
them; perhaps all the Metazoan lineages for the first time were at
risk from predation. Thus broadly similar responses evolved in
parallel in different Metazoan lineages. As they stand, though, these
externalist models are incomplete: they give no account of the ori-
gins and establishment of the striking morphological innovations –
the key innovations – characteristic of the Cambrian radiation.
Minimalist models presuppose rather than deliver a minimalist
account of the origins of novelties. Yet the morphological innova-
tions of the Cambrian are truly extraordinary. Moreover, once we
recall there are alternatives to minimalism other than models
invoking macromutations delivering a whole functioning new
system in one go, there is no reason to suppose some minimalist

account of novelty *must be true*, even if we do not know what it is. Thus we shall consider in the next section an extended argument for the claim that the bilaterian novelties of the Cambrian depended on fundamental changes in Metazoan developmental systems. We cannot exclude the possibility that key Cambrian innovations really did originate and establish in just the same way that (say) variations in the facets of trilobite compound eyes evolved and established. But in the light of these developmental considerations, it is likely that the Metazoan radiation arose through some form of complex feedback among (a) exogenously caused environmental changes, (b) biotically triggered environmental changes, (c) changes in evolvability. In the next section I discuss the idea that the Cambrian explosion depended on a developmental revolution, and then return to the key problem for this chapter: what does this radiation show about the relationship between microevolutionary process and macroevolutionary pattern?

6.   THE DEVELOPMENTAL REVOLUTION HYPOTHESIS

Sean Carroll has argued that the diversification pulse of the Cambrian represents a change in developmental program rather than a change in selective regime. He, like others, emphasises the importance of modularity to evolutionary possibility. Innovations that increase the space of evolutionary possibility are made possible (or perhaps, much more probable) by modular construction. If the development of one structure is largely independent of the development of others, those structures can vary independently of one another; the structures can be independently modified. Such developmental compartmentalization decouples phenotypic traits from one another, enabling a lineage to escape from developmental constraints that would otherwise limit the range of variation. Moreover new structures can be made by repetition followed by differentiation, as with arthropod limbs. Carroll argues that there is evidence for an increase in complexity in arthropod limb design (and hence arthropod ecological versatility) since the Cambrian, and he interprets this as an instance of modular development's allowing repetition followed by differentiation (Carroll 2001; see also Lewontin 1985, Kauffman 1993, Wagner and Altenberg 1996). On Carroll's view, these

evolutionary changes cannot be understood as the replacement of one allele by another in the context of invariant systems of gene regulation and expression. The Cambrian radiation (and, more generally, the evolution of novelty) requires evolutionary changes in how genes are used as well as changes in the genes themselves. They are essentially evolutionary changes in gene regulation (Carroll 2005).

Carroll has defended one version of the idea that the Cambrian radiation is a radiation in development. But the most articulated developmentalist explanation of the Cambrian radiation is due to Eric Davidson. The Metazoan radiation is really a radiation of one deep branch of the Metazoans. The sponges and jellyfish did not experience an explosive increase in diversity and disparity; that burst took place in the bilateral animals (Knoll and Carroll 1999). Major morphological innovations separate these developmentally simple sponges and jellyfish ("the diploblasts") from the earliest bilaterally symmetrical animals ("the Urbilaterians"). These include a through-gut, a third germlayer, a centralized nerve chord, a body vascular system, primitive organs. Eric Davidson and his colleagues have suggested that these morphological innovations and the diversification that followed from them depended on a developmental revolution. That developmental revolution is the crucial evolutionary change that made the Cambrian Explosion possible (Peterson et al. 2000, Peterson and Davidson 2000, Erwin and Davidson 2002).

Many adult bilaterians develop from larvae that live as very small, but free-living members of the plankton. This life history is known as indirect development, as juveniles are morphologically and ecologically very different from the adults into which they develop. Such larvae consist of only a few thousand cells. They have only ten to twelve cell types. Moreover, they are organizationally simple. They do not have multilayered, organisationally complex internal structures. Finally, these larvae develop in a distinctive way. Their genes are turned on early in development, and thus cell lineages differentiate early, with about ten rounds of cell division. Cells find their final position and role in the organism under local signalling control. In contrast to the standard developmental pattern of adult bilaterians, these larvae do not first differentiate into embryonic regions prior to cell differentiation. The *Hox* genes control this system of developmental regionalisation on the front-to-back axis in adult bilaterians, and those genes are not active in these larvae.

Davidson thinks that the developmental mode exemplified by these planktonic larvae is a relic of the earliest bilaterians, and argues that development with early differentiation and local control suffices only for this grade of morphological complexity. More complex morphologies required a developmental revolution that had two key ingredients. One is regional regulation, and hence delayed cellular differentiation. Crucial genes determining cell type are not switched on until after developmental regions are established. The other is the evolution of a population of "set-aside" cells: cells that retain all their potential for cell division and that are not committed to specific cell fates. These set-aside cell populations exist in the larval form of indirectly developing bilateria, and adult morphological structures are recruited from those set-aside cells. Contemporary adult bilaterians share a developmental recipe that includes a differentiated axis of symmetry from front to back and a system of recursive regionalization. The developing embryo is divided into a set of regions, each of which is under fairly independent developmental regulation. Often these regions are further subdivided until the specific details of adult morphology are constructed.

So how did the developmental revolution take place? Davidson's evolutionary narrative goes something like this: Early-differentiation embryogenesis evolved after the Cnidaria split off from the stem Metazoa. The third tissue layer of the embryo, the endomesoderm, then evolved, and this was crucial to the later evolution of structurally complex organs, for these have their developmental origin in this third layer. After the Ctenophora split off from the stem, bilaterian symmetry and the *Pax-6* genes (involved in vision) evolved. The final innovations, just prior to the crown group radiation of the bilaterian phyla, was the evolution of a full *Hox* cluster with front-to-back differentiation and set-aside cells. *Hox* genes evolved earlier, when the cnidarians split from the basal Metazoans, but they did not originally function to control front-to-back differentiation. The full *Hox* complement with the contemporary *Hox* functions evolved relatively late.

This narrative leads to their portrait of the common ancestor of the extant bilaterian clades: the common ancestor, that is, to the vast majority of multicelled animal designs. Morphologically, the creature was small; perhaps very small, and possibly pelagic. But it

was more structurally complex than its Cnidarian sister group. The common ancestor had a mesodermal layer, a central nervous system, and two-ended gut with a mouth and anus. It thus had a front-to-back axis. These are genuine bilaterian homologies not shared by jellyfish. Moreover, some common developmental mechanisms were available to the common ancestor, including the *Hox* system, not just for basic body, front-back, and up-down differentiation, but for structures attached to the body. Thus the morphological similarities between the bilaterian phyla in part depend on crucial and very deep morphological homologies. But they are also the result of parallel evolution working with a homologous developmental toolkit. Many organ systems across the bilaterians as a whole – heads, hearts, sensory systems – are analogs not homologs. But the cell types of which these organs are composed are homologs and explain some of their functional similarities, as do these homologous developmental mechanisms. The common ancestor had the developmental toolkit needed for a complex morphology. But it was not itself complex. While the common ancestor was itself likely to be a relatively small and simple organism, it was preadapted to morphological differentiation in response to the right biotic and abiotic triggers.

As it was initially formulated, the developmental revolution hypothesis entails a puzzle of its own. What selected for these developmental changes? As Graham Budd and Soren Jensen (2000) argue, if developmental innovation *preceded* morphological innovation, the selective advantages of the developmental innovations of set-aside cells, modular developmental regulation, and the *Hox* system are obscure. What was the function of these innovations if they preceded rather than postdated or accompanied growth in size and complexity of bodily organization? Davidson and his colleagues place these developmental changes very deep in the bilaterian stem lineage, long before any trace fossil evidence of bilaterian morphological innovations. They seem to commit themselves to the idea that these animals were minute and nondescript even at the completion of the developmental revolution (Peterson et al. 2000, 12).

There is, however, a natural modification of the idea of the developmental revolution that leads to a more integrated conception of the radiation. Davidson thinks that early-differentiation embryogenesis is not sufficiently powerful to build adult, crown group

bilaterian body plans. That could mean that it is simply impossible to build an adult crown group bilaterian by this mode of development. But perhaps the constraint is less absolute than that. Perhaps early-differentiation development can build only a somewhat simple version of an adult bilaterian; for example, one without a complex sensory system or complex locomotor-manipulation system. Alternatively, perhaps the primitive mode of bilaterian development can build complex adults only at the cost of a high rate of developmental error. This more modest view of developmental constraints on complexity leads to a natural ratchet hypothesis: a positive feedback between developmental and morphological change. Early bilaterian morphological innovations (for example, the two-ended gut) would select for improved developmental control, to reduce the rate of disastrous developmental errors. Once these evolve, they permit the evolution of further early bilaterian novelties, which in turn select for further improvements in developmental control, and so on. Early elements in the bilaterian body plan did occur first. But the limits on early-differentiating development in constructing such bodies selected for the key elements of the developmental revolution, both to make development more reliable and to support specific adaptive complexes grafted onto the basic plan.

7.   FINAL THOUGHTS

The key point – the take home message – is that minimal models are indeed minimal, and they can be enriched in a variety of ways. One is by extending temporal scale: on microevolutionary time scales, we can often treat features of both the environment and development as fixed. But these are not fixed on macroevolutionary time scales. In particular, it is unlikely that we can in general model the evolution of novelty in a classically Dawkinsian way, by thinking of alternative alleles as difference makers: one replaces another as each makes a consistent, selectable phenotypic difference, but only relative to a fixed developmental and genetic environment. In the evolution of possibility-expanding innovations, these environments are not fixed. The individualist perspective on selection is sometimes too limiting. It is clear that transitions in individuality require group selection of some kind. But it may well be the case that the structure and organization of species themselves are both important

and no simple reflection of within-population change in the constituent demes from which species are formed. It is arguable that species structure plays a role in explaining fine-grained macroevolutionary patterns, for example, the punctuated-equilibrium pattern of typical species life histories (Eldredge 1995, Sterelny 1999b).

Let me finish by connecting these general morals to the Metazoan radiation. First: the origination of the Metazoans involved a transition in individuality, and hence requires a multilevel perspective on evolution. There will have been a period in the early evolution of the Metazoans when the fitness of individual cells within a protoanimal and the fitness of that protoindividual in a population were both important. Second: the radiation of the Metazoans was not an evolutionary radiation taking place within a fairly constant environment. The radiation, whatever its causes, profoundly changed both the selective and the physical environment. Likewise, the Cambrian radiation was evolution in a changing developmental environment. Davidson may not have correctly identified the primitive mode of bilaterian development or the sequence through which the contemporary bilaterian developmental toolkit was built. But it is clear that the radiation involved profound developmental change, for while protist preadaptations for complex development were important, the radiation required the evolution of both cellular differentiation and vertical complexity, as cells are organised into tissues, organs, and organ systems. Very early, simple Metazoans have few cell types: Placazoa have four; sponges have five cell types; cnidarians have ten. Valentine estimates that stem group bilaterians had between twelve and forty cell types, depending on the phylum. Crown group bilaterians have many more (Valentine 2004, 74–75). There is nothing like this in the protist world. Hence the evolution of Metazoans, especially the bilaterians, required a major revolution in developmental control. One cannot model this evolutionary transition as the result of the substitution of variant alleles for their predecessors in a relatively fixed developmental environment. There were crucial changes not just in organisms' genetic complement but in the ways genes are used. Finally, there is the open issue of novelty. Were the crucial novelties of the Cambrian radiation built unobtrusively, with their significance only becoming apparent later? The extent to which we can fit the evolution of novelty into the

gradualist framework of minimal models remains open. But if Carroll or Davidson is right, some novelties – phenotypic icebergs – really are different, for their evolution is accompanied by changes in the developmental architecture that make further changes much more likely.

NOTES

1. Gould has written here of ''extrapolationism'' (Gould 2002). I have avoided this term because Gould's work suggests that there is a single contrast between minimalist and extended models of the micro/macro relationship, one that turns on the acceptance or rejection of high-level selection. In contrast, I think there are a number of ways of going beyond minimalism, and some of these have nothing to do with levels of selection.

2. Such properties can be important without species selection's being important, in part because species-level properties may not be heritable.

3. There is considerable debate about the history of life, even at a coarse grain of analysis. It is not surprising that the issue of progress has always been contentious (see Ruse 1996). But even more technical claims about complexity and diversity have generated rich debate: see, for example, McShea 1998a, Knoll and Bambach 2000, Benton 2006.

4. In fitting the *Spread of Variation* view within a minimalist framework, I part company with Dan McShea's important and influential work on these issues. We both think the crucial element of minimalism is local determinism: for minimal models to be adequate, the fate of a lineage depends on the fate of its constituent taxa, and their fate in turn depends on local circumstances. But we have different views on how to identify local determinism. For example, unlike me, McShea counts sensitivity to a left wall of minimal complexity as a *violation* of local determinism: he thinks of it as a feature of the global environment affecting all taxa. See McShea 1996, Alroy 2000, McShea 2000.

5. This may exaggerate the uniqueness of the protist threat to bacteria. There is predation in the bacterial world, and hence probably in ancient bacterial environments. Bacteria predate by lysing and envagination. In the first, a mob of bacteria release an enzyme that causes the membrane of the prey species to breach, spilling the contents of the cell and thereby making the amino acids, nucleic acids, and other building blocks of metabolism available for acquisition. In the second method, a bacterium bumps into, surrounds, takes in, and lyses a smaller microbe (Lyons, personal communication).

6. In saying this, it is important to distinguish between large-effect mutations and macromutations. Large-effect mutations involve significant quantitative changes in existing traits; macromutations involve the single-step creation of new structures. Recent population genetics has embraced the idea that large-effect mutations are important causes of ordinary evolutionary change. Minimalist models are certainly not committed to the view that all structures are built by tiny increments over countless generations. For a good discussion of the resources available to minimalism, see Leroi 2000.

7. For, first, stem-group organisms will not fit taxonomic stereotypes derived from crown group organisms. Second, they will look strange because our sense of a normal-looking organism – for instance, a normal crustacean – is derived from our exposure to a host of crown group crustaceans. Our pattern recognition heuristics are trained on crown group taxa. There remains, as Dan McShea points out to me, the possibility that these early animals are weird, disparity-expanding organisms not just because they fail to fit taxonomic stereotypes but because they have an extraordinary load of unique traits. He may be right; unfortunately, we lack ways of making such intuitions of weirdness rigorous.

8. Simple versions of this approach obviously make risky simplifying assumptions about the constancy of rates of change across times and between lineages. But those concerns can be addressed by using a variety of different genes and different calibration points. For a systematic discussion of the reliability of various clocks and their application to the radiation of the Metazoans, see Bromham 2003.

9. The defenders of the deep dates dispute this, arguing that the (relatively) recent divergence times estimated by Peterson and company depend not on the choice of calibration taxa, but on the treatment of the fossil dates as the maximum age of divergence, as if the first appearance of a fossil in the record was the first appearance of

that organism on Earth (Blair and Hedges 2005). Peterson responds in Peterson and Butterfield 2005.

10. Nothing extraordinary, so long as the preservation potential of soft-bodied organisms has not changed radically over the Ediacaran-Cambrian boundary. This assumption may not be safe: there are Ediacaran fossils of early-stage embryos, and these are of tiny organisms. Moreover, it has been argued that the Ediacaran fossils were formed only because Ediacaran preservation conditions were very different from those of the Cambrian and subsequent eras (Narbonne 2005).

11. There seems to be a serious problem with this idea, for the innovation mechanism rests on the idea that until the resource budget increases, innovations are too expensive. A pulse of resources into the environment eases resource-based constraints on potential innovations. But this assumes that an increase in overall productivity leads to an increase in *per capita* access to resources. But if population growth keeps pace with the growing resource envelope, then the per capita availability of resources may not change. Vermeij notes this problem (1995, 134), but then ends up responding to a different problem, the idea that a sudden resource spurt may be destabilizing, a possibility he argues is confined to relatively undiverse ecosystems.