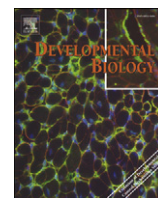


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## Evolutionary uniformitarianism

Douglas H. Erwin\*

Department of Paleobiology, MRC-121, National Museum of Natural History, PO Box 37012, Washington, DC 20013-7012, USA  
 Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA

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### ABSTRACT

I present a new compilation of the distribution of the temporal distribution of new morphologies of marine invertebrates associated with the Ediacaran–Cambrian (578–510 Ma) diversification of Metazoa. Combining this data with previous work on the hierarchical structure of gene regulatory networks, I argue that the distribution of morphologies may be, in part, a record of the time-asymmetric generation of variation. Evolution has been implicitly viewed as a uniformitarian process where the rates may vary but the underlying processes, including the types of variation, are essentially invariant through time. Recent studies demonstrate that this uniformitarian assumption is false, suggesting that the types of variation may vary through time.

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### Introduction

The ubiquity of morphological discontinuities between clades of organisms has troubled evolutionary biologists since Cuvier and Darwin and remains one of most important questions in evolutionary biology. Why is it that the distribution of morphologies is clumpy at virtually all scales? Although both Darwin and the proponents of the Modern Synthesis expected an 'insensible' gradation of form from one species to the next, this is only sometimes found among extant species (for example, among cryptic species) and is rare in the fossil record. Gradations in form are even less common at higher levels of the Linnean taxonomic hierarchy. Explanations for this clumpy distribution of morphologies fall into three classes: neo-Darwinian extrapolation in which morphological disparity reflects gradual divergence followed by the disappearance, through extinction or non-preservation, of intermediate forms; a hierarchical view of macroevolution where species sorting or selection drives evolutionary trends (although it is not clear how this produces a non-uniform distribution of morphologies); and various formalist or structuralist schools where major evolutionary transitions reflect structural or physical requirements, with selection entering only as a secondary sorting mechanism. Generally absent from each of these approaches is consideration of the possibility that the nature of the evolutionary process, as distinct from the organisms on which evolution acts, has itself evolved over time (Erwin, 2004; Erwin and Davidson, 2009).

The spectrum of morphologies among multicellular, differentiated organisms is a small portion of the range of possible morphologies. This is evident both by inspection of B-grade science fiction movies and, more scientifically, by studies of theoretical morphospace, which

construct a range of morphologies that do not currently exist and have never evolved (McGhee, 1999; Niklas, 2009). The variety of potential but currently unrealized forms can be divided into different categories: some morphologies are simply unachievable within existing developmental processes (a third pair of appendages in vertebrates, for example) or because of constructional limitations; other potential forms represent once existing but now extinct organisms (trilobites, or sauropod dinosaurs); and a final, probably infinite class, is those morphologies which could in principle exist but for whatever reason have simply not evolved.

Evolutionary biologists have generally explained the clumpy distribution of morphologies in one of two, non-exclusive ways: the disappearance of intermediate forms via extinction, and the limited search space examined through evolution. While it is demonstrably true that many morphologies have disappeared through extinction, this argument assumes that morphologies within a clade will become more similar as we move back through time closer to the origin of the clade. This assumption was, rather provocatively, exploded by Gould (1989), who used the soft-bodied animals of the mid-Cambrian Burgess Shale fauna as a case study to argue that the dominant pattern of morphologic evolution was one of maximal early morphologic diversity (now termed disparity), followed by a later increase in the number of species or other taxa (taxic diversity, often genera in the fossil record). Gould argued that this qualitative pattern was not consistent with a gradual increase of possible morphologies through adaptive evolution (which he characterized as the 'cone of expanding morphology'), but rather a rapid definition of the potential morphologic space of a clade followed by exploration of that defined space.

Gould's claims were robustly challenged by evolutionary biologists and paleontologists (Briggs et al., 1992a,b; Fortey et al., 1997; Wills, 1998). But the most useful work was done by developing quantitative techniques for assessing morphologic disparity and comparing it to

\* Fax: +1 202 789 2832.

E-mail address: [Erwind@si.edu](mailto:Erwind@si.edu).

taxonomic diversity (Foote, 1992, 1993, 1994, 1997, 1999; Wesley-Hunt, 2005) see review in (Erwin, 2007). These studies quantitatively substantiated Gould's intuitive conclusion: morphologies really are unevenly distributed at the origin of a clade. In the majority of cases studied, morphologic disparity greatly exceeds taxonomic diversity in the early history of a clade. This result could only be the result of sampling artifacts if one were to posit that unusual morphologies were more likely to be preserved and recovered than morphologies similar to one another, which is hard to credit. Such studies have demonstrated that the apparent gaps between morphologies are not simply due to extinction of once-intermediate forms.

The exploration of morphologies through a morphospace has not been random, but has been guided to greater or lesser extent by selection. Consequently, large regions of morphospace may never have been sampled by evolution (Thomas and Reif, 1991; Thomas et al., 1993) either because the morphologies were never generated by development, or because nearby morphologies were stuck on a local adaptive peak. Since functional studies suggest that many morphologies can accomplish essentially the same functional task (Wainwright et al., 2005) at least some morphologic disparity may have no functional consequences.

Here I explore growing evidence that a significant factor in the clumpy nature of morphology is systematic, time-inhomogeneous patterns in types of variation upon which natural selection and other evolutionary processes could act. I present a new compilation of the first occurrences of marine invertebrate phyla, classes and equivalent stem groups during the Ediacaran, Cambrian and Ordovician, focusing on the Ediacaran–Cambrian (579–490 Ma) diversification of animals. The pattern of first appearances confirms earlier suggestions for an abrupt, asymmetric pattern of morphological innovation during the early Cambrian. Using higher Linnean taxa as proxies for morphologic innovation has several inherent limitations: 1) We can only identify the pattern of successful morphologic novelties, and thus cannot directly assess whether morphologic variability was greater. Morphologic novelties must also be ecologically and evolutionarily successful in order to persist into the fossil record, although I do not address this issue here. 2) Although one cannot unambiguously identify the processes involved in generating this asymmetric pattern of origination, empirical data on the structure of developmental gene regulatory networks (GRNs) provides a reasonable mechanistic hypothesis: these morphologic innovations reflect the establishment of recursively wired GRNs for regional patterning of the developing embryo. Many of the novel morphologies that have been recognized as higher taxa at the level of phyla and classes contain unique architectures that must be underlain by distinctive regional patterning mechanisms in development. Although the claim that these regional patterning features are underlain by particular structures in developmental GRNs is a hypothesis and requires additional support, current empirical data supports the hypothesis (discussed further below). Thus to the extent that novel morphologic structures reflect the underlying structure of developmental GRNs, we can use the distribution of distinctive morphological architectures as a proxy for their generation.

This specific example fits into a larger pattern of the refocusing of selection during the major evolutionary transitions. Evolutionary biologists have always acknowledged that evolution is a historical, path-dependent process in which the order of adaptations and even the success of specific mutations may depend upon the order in which they occur (Stern, 2010). While recognizing the importance of 'constraints' (although the definition is rather mushy) and acknowledging the role of path-dependence, the implicit assumption of most evolutionary biologists has been that there are not systematic variations in the types of evolutionary change through time. I argue here that this assumption can be traced to Darwin and his colleagues and that it developed for specific methodological reasons, akin to the development of uniformitarianism in geology.

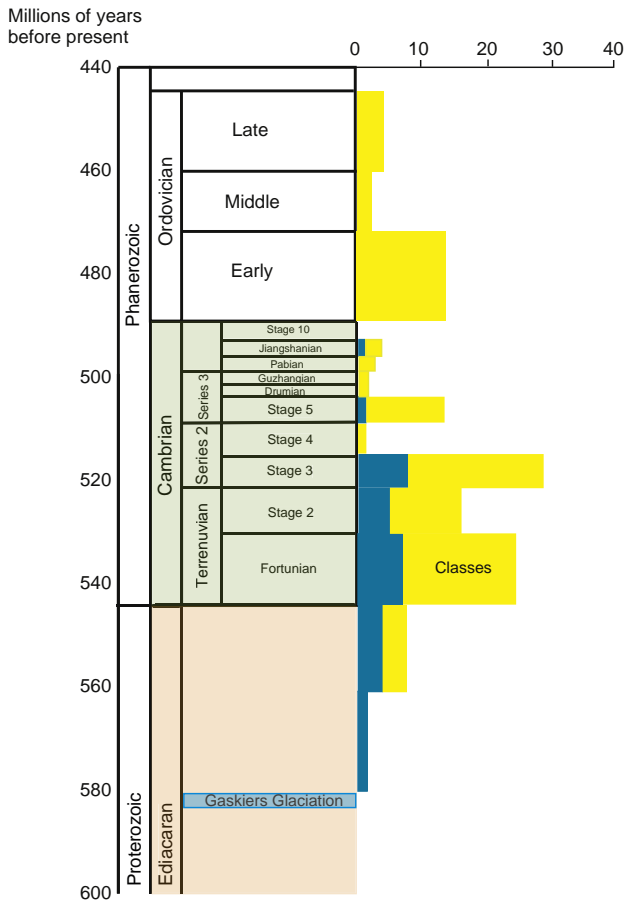
## Ediacaran–Cambrian patterns of morphologic innovation

The early diversification of metazoans during the Ediacaran–Cambrian periods established all major clades, including the first vertebrates. The fossil record of this diversification spans 579–510 Ma, although molecular clock evidence suggests that many of the divergences began earlier (Peterson et al., 2008). This complex episode involved extensive environmental, geochemical and paleo-ecologic changes (Erwin, 2005), as well as the formation of the developmental mechanisms required for the advent of complex morphogenesis (Davidson, 2006; Davidson and Erwin, 2006; Davidson and Erwin, 2009).

Although the Ediacaran–Cambrian diversification of animal life has been the focus of intensive investigation for the past several decades, there has not been a systematic compilation of the patterns of origination of higher clades since 1987 (Erwin et al., 1987) and many papers have continued to use family and generic compilations based on the work of Sepkoski in the late 1990s (Sepkoski, 1992, 2002), e.g. (Knoll and Carroll, 1999). Since that time many new clades have been described, our understanding of metazoan phylogeny has been revolutionized, and both Ediacaran and Cambrian stratigraphy and the temporal framework have been heavily revised. Much of current work on fossil diversity has emphasized family and generic patterns (Sepkoski, 1997), and more recently sample-standardized treatments have been applied (Alroy, 2010; Alroy et al., 2008; Alroy et al., 2001). Cambrian generic diversity for the south China region has been compiled (Li et al., 2007) but there is currently no global generic compilation. However, here I focus on morphologic innovation that is better captured by the more inclusive Linnean taxonomic categories of phylum and class. I present a new compilation of phylum and class-level originations and cumulative diversity during the Ediacaran, Cambrian and Ordovician (Figs. 1 and 2). This is part of an ongoing project to reassess patterns of higher-level origination through the Phanerozoic. This new data is presented using the newly revised Cambrian stratigraphic framework with greatly improved global correlations, which differs considerably from older usage based on the Siberian Stages (Babcock and Peng, 2007; Zhu et al., 2009).

Since the mid-1980s phylogenetic methods have substantially changed our approach to systematics and this may in part explain why there have been no compilations of Ediacaran–Cambrian data over the past several decades. Many stem groups have been recognized but few new classes and phyla have been described. Although the reliance on trees that is reflected in the emphasis on stem groups has greatly improved our understanding of phylogenetic patterns, it poses a problem for compiling diversity patterns. For example, 21 different classes have been described for the Phylum Echinodermata, but many of these are short-lived, if morphologically distinctive, groups known only from the Cambrian or Ordovician periods. These are recognized as classes only because they were described many decades ago. Today many of these echinoderm clades would be recognized as unranked stem groups within the Echinodermata. This difference in no way changes their morphologic distinctiveness, or the unique developmental programs likely required to produce these morphologies, but reflects the evolution of taxonomic bookkeeping. Compare these groups to many newly recognized panarthropod clades that are equally distinctive morphologically, but have been treated as stem groups rather than extinct classes (Edgecombe, 2010).

Data was compiled from the primary paleontological literature on the earliest described genera from all Ediacaran–Cambrian and Ordovician phyla and classes (compilation of data for orders is ongoing) and equivalent stem groups (see Supplemental Information). The higher-level phylogenetic relationships are based on recent molecular studies, and where disputes exist about the basis for some clades, these are noted in the Supplemental Information. The Ediacaran records pose several challenges. There is no generally



**Fig. 1.** First occurrences of phyla, classes and equivalent ranked stem-clades during the Ediacaran, Cambrian and Ordovician periods.

accepted phylogeny for elements of the soft-bodied Ediacara biota, although several monophyletic clades have been identified (dickinsoniids; rangeomorphs) as well as a number of likely polyphyletic groups (Xiao and Laflamme, 2008). Work currently in progress with M. Laflamme will present a preliminary grouping of the Ediacara macrofossils. In this work because of the phylogenetic uncertainty I have been relatively conservative in identifying phylum and class-level groups. Consequently, little emphasis should be placed on the relative lack of higher-level originations during the Ediacaran. In addition, the Ediacaran has not yet been subdivided into stages. Following Narbonne (2005) I have grouped the Ediacara macrofossils into three assemblages: the Avalon, White Sea-Ediacaran and the Nama. These assemblages were originally thought to be temporally distinct (Narbonne, 2005), but they may overlap to some degree (Grazhdankin, 2004).

For Cambrian occurrences, using a variety of stratigraphic sources, I correlated the original descriptions into the recently established 10 Cambrian stages (Zhu et al., 2009). Although not all of these stages have been formally defined, the basis of the boundaries of the stages have been established and this provides a basis for provisional correlation. A number of issues remain to be resolved, however, including the precise correlation between many of the earliest Cambrian beds in south China and in Siberia. Where correlations were uncertain I have been conservative and chosen the younger alternative. The classic Ordovician stages were used. Since the goal has been to identify the pattern of early occurrences rather than generic diversity, I have not used a locality-based approach, nor have I sample-standardized the data (Alroy et al., 2001). While the Paleobiology Database Project (PDBD; PDBD.org) has become an essential part of much research on diversity in the fossil record, it was

not set up to easily track first occurrences, and the temporal bins established by the PDBD project average about 10 Ma in duration, longer than the new Cambrian stages. Consequently I have used data from the PDBD as a source but where possible have checked the original publications. The PDBD ID number, when available, has been cited in the Supplemental Information.

Stem groups within phyla were tabulated as classes, and stem groups within classes are tabulated as orders, and are not considered further here. Two Cambrian stem groups were recognized at the phylum level, the Cambrian lobopods and the Phylum Vetuocolia. Phylogenetic studies of the rich fossil record of lobopods indicate that the extant phyla Tardigrada and Onychophora are a depauperate remnant of a once-richer clade (Edgecombe, 2010) and so they are treated here as a single clade with separate classes. There are a number of problematic groups, such as the putative Phylum Coeloscleritophora, which are probably polyphyletic. As noted in the Supplemental Information, these groups have generally not been counted, and do not appear in the results. They are listed in the SI for completeness. Inclusion of these taxa would simply increase the numbers noted below.

## Results

Ediacaran originations are relatively few, reflecting the uncertainties about the phylogenetic placement of most Ediacaran fossils. A major pulse of origination is evident in Cambrian Stage 1, largely of small skeletonized fossils known as the 'small shelly fossils' (Bengtson, 2005; Steiner et al., 2007), followed by the first appearances of many clades in Cambrian Stage 3, corresponding to the exquisite soft-bodied preservation of the Chengjiang biota in southern China (Hou et al., 2004). A later, smaller pulse is associated with first appearances in the Burgess Shale fauna of British Columbia, Canada. The only later occurrence of a durably skeletonized phylum is the Bryozoa in Cambrian stage 9. Twelve phyla are known only from the Recent and four phyla first occur in the fossil record after the late Cambrian: one each in the Carboniferous, Jurassic, Cretaceous and Eocene. New classes continue to occur, albeit at a lower frequency, later into the Cambrian and during the Ordovician radiation (Fig. 1). A number of classes first appear much later in the record, but many of these are non-durably skeletonized clades: three in the Silurian and Carboniferous, and one in each of the Permian, Jurassic, Cretaceous and Eocene. At least 25 classes are known only from the recent. All of these groups are non-durably skeletonized and evidence from molecular phylogenies and molecular clocks suggests that the lineages they represent arose by the early Paleozoic, so it is not surprising that they have a poor fossil record.

This pattern may well understate the rapidity of the originations of these clades. The pulses in stages 3 and 5 reflect the unusual preservation potential of the Chengjiang and Burgess Shale faunas, which record a number of groups that would otherwise be missing from the fossil record. Consequently they represent minimum ages for the first appearances of these clades. The lower bounds on the appearance of many of the bilaterian clades are unclear (see review in Davidson and Erwin, 2010). *Dickinsonia* has recently been suggested to be an acoelomorph (Sperling and Vinther, 2010), which may be basal deuterostomes (Philippe, 2011) rather than along the main branch of metazoan evolution (Baguana and Riutort, 2004). In addition, *Kimberella* is likely a primitive mollusk (Fedonkin et al., 2007; Ivantsov, 2009). If these assignments are correct (and at least that of *Kimberella* to the molluscs seems secure) then the protostome-deuterostome divergence must predate about 560 Ma; bilaterians likely existed by 555 Ma (Fedonkin et al., 2007; Martin et al., 2000) and perhaps earlier (Chen et al., 2009). The burst in the morphologic complexity of trace fossils (the burrows and trails that record the behavior of various animals) near the base of the Cambrian strongly suggests that macroscopic bilaterians larger than about 1 cm in

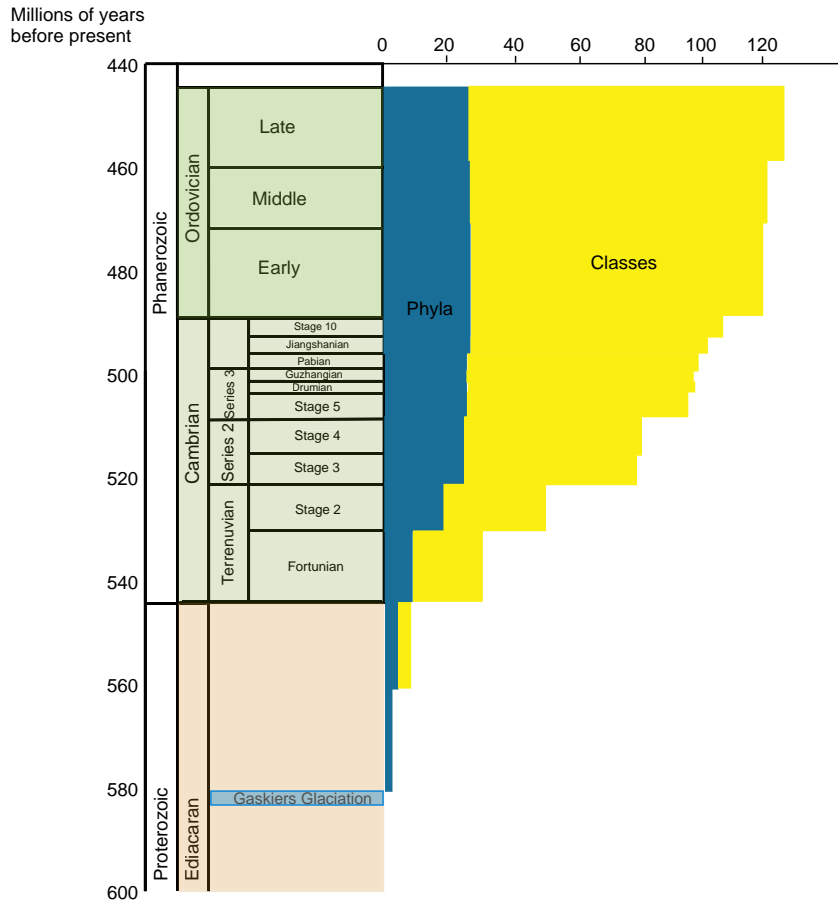


Fig. 2. Cumulative diversity of phyla, classes and equivalent ranked stem-clades during the Ediacaran, Cambrian and Ordovician periods.

diameter are unlikely to have been present before this time (Jensen et al., 2005; Seilacher et al., 2005).

Although the fossil record strongly indicates the rapid origination of the novel morphologies recognized in Linnean systematics as phyla and classes, such evidence does not allow us to distinguish between differences in the rate of generation of these morphologies and their rate of success. In other words, it is theoretically possible that such novel morphologies have been produced continuously throughout the Phanerozoic (the past 542 Ma) but were, perhaps for ecological reasons, simply more successful during the early Cambrian. However, combining insights from the fossil record with comparative studies of developmental gene regulatory networks provides a new perspective on the generation of these morphologies, and on evolutionary processes.

### The structure of developmental gene regulatory networks

Studies of developmental gene regulatory networks (GRNs) have revealed considerable structure suggesting that evolutionary changes are not uniformly distributed across the network. The best-studied examples come from endomesoderm in the developing sea urchin larvae, where the GRNs consist of a series of subcircuits that specify various spatial domains, control intracellular signaling, and eventually run differentiation gene batteries (Davidson, 2006; Peter and Davidson, 2009; Davidson, 2010). Among these subcircuits are highly conserved and recursively wired components that establish domains for subsequent developmental patterning. These have been termed kernels, and they appear to be associated with the establishment of regional patterning systems early in the history of major metazoan clades. These kernels, once formed, appear to be remarkably refractory to subsequent evolutionary change. In essence, selection

is shifted from the genes themselves to the kernel. Within the kernels that have been identified this far (admittedly small in number, but sufficient for a prediction about what will be found as others are identified) variation has been shifted to other parts of the developmental GRNs, both upstream and downstream from the kernels.

The conclusion from studies of developmental GRNs is that the formation of the distinctive kernels associated with regional pattern formation in the developing embryo closely coincides with the origin of phyla and classes during the Ediacaran–Cambrian. Indeed the formation of these kernels and their recursive wiring has been chiefly responsible for the formation and subsequent stability of these distinctive clades (Davidson and Erwin, 2006; Davidson and Erwin, 2009; Davidson and Erwin, 2010; Erwin and Davidson, 2009). This conclusion has at least two important implications: First, it indicates that the pattern of maximal early morphologic disparity in many metazoan clades and the early appearance of so many phyla and classes corresponds with patterns of morphologic innovation. Thus the ecological argument, that the temporal asymmetry of originations reflected changing probabilities of success, fails. This does not mean that ecological factors did not play a significant role in the Ediacaran–Cambrian metazoan diversification, only that they are not a sufficient explanation for the post-Cambrian decline in major morphological innovations. Second, the establishment of these kernels early in the history of metazoan evolution suggests a temporal change in the type of developmental variation exposed to selection and drift, indicating that aspects of evolutionary change are not uniformitarian.

### Uniformitarianism in geology and evolution

The implicit uniformitarianism of evolutionary biology results from two assumptions about the nature of the discipline: that



establishing evolutionary biology as a science required unifying laws and principles, and that particular evolutionary trajectories were historical and thus path-dependent. For such ambitious men as Charles Lyell, Huxley and other 19th century natural scientists, if geology and biology were to be as accepted as sciences, they had to follow the logical structure of physics, and that mean identifying laws and principles that did not vary in space or through time. Although Darwin's *Autobiography* is not always a reliable guide to the development of his thinking, I think he captured an important point when he wrote, following the precepts of Lyell: "Everything in nature is the result of fixed laws". Lyell was a close colleague of Darwin, and deeply influenced Darwin's approach to science. As he was completing the first edition of his *Principles of Geology*, Lyell wrote to Sir Roderick Murchison, another well-known geologist:

"It [the book] will not pretend to give an abstract of all that is known in Geology, but will endeavour (sic) to establish the *principles of reasoning* in the science, & all my Geology will come in as illustration of my views of those principles... *no causes whatever* have, from the earliest time to which we can look back, to the present, ever acted but those *now* acting, & that they never acted with different degrees of energy from that which they now exert." (Lyell to Murchison, 15 Jan 1829).

Lyell's views were not widely shared among his contemporaries. In his review of Lyell's book William Whewell wrote:

"Have the changes which lead us from one geological state to another been, on a long average, uniform in their intensity, or have they consisted of epochs of paroxysmal and catastrophic action interposed between periods of comparative tranquility? These two opinions will...divide the geological world into two sects, which may perhaps be designated as the Uniformitarians and the Catastrophists" (1832, p. 126).

Whewell's review makes clear that he does not find Lyell's argument particularly convincing, and indeed some historians of this era argue that Lyell may have been almost alone in holding a strong belief in uniformitarianism (Rudwick 2008). Most geologists acknowledged that the rates and intensities of geological processes had varied considerably over time. The complexity of the argument in the early to mid 19th century has been obscured over the years, as Whewell's catastrophists have been conflated with earlier geological theorizing. Whewell's review really seems to distinguish between Lyell's uniformity of rate and the views of many other geologists that rates had varied considerably over geologic time. In the absence of robust means of telling time in the geologic record (which ultimately was resolved with the discovery of isotopic decay and then the rapid advent of radiometric dating) there was no way of deciding the issue. Lyell's concern was a real one, however. The development of a rigorous science of geology required some basis upon which to evaluate hypotheses, and Lyell's argument was the best basis for testing hypotheses about past history was our understanding of processes currently operating.

### Essentials of uniformitarianism

The geological uniformitarianism of Lyell conflates two philosophically distinct ideas (Gould, 1965; Simpson 1970). The first, methodological uniformitarianism, is the argument for the spatial and temporal invariance of natural laws. In other words, the laws of physics and chemistry apply everywhere through time and space, and the speed of light, for example, has not varied over time. This is nothing but an underlying, implicit principle of science (although there are physicists exploring the limits of these assumptions). If laws

were subject to alternation they would not be terribly useful as operating principles for the Universe.

Substantive uniformitarianism holds that the current conditions of the earth reflect a uniformity of rates and material conditions through time and space, and has a more checkered intellectual history. Although it was central to Lyell's view of the history of the Earth, it is false, and indeed it was widely known to be false even by many of Lyell's colleagues in the 1830s (Rudwick, 2008). The rates of various geological processes vary widely today over the surface of the Earth and have varied widely through geological time. Remarkably however, the catchphrase "the present is the key to the past" has been drilled into the heads of unfortunate young geology students ever since Lyell. Many geologists view uniformitarianism as having been a bulwark against catastrophism (incorrectly). Geology student are often taught that the law-like principles of geology espoused by Lyell and codified as uniformitarianism were the crowning argument against older and more biblical views of geology that invoked rapid changes in the surface of the Earth. Yet as Rudwick makes clear, catastrophism had largely been rejected by the savants of the early 19th century well before the work of Lyell. Uniformitarian perspectives have had a pervasive effect on many historical disciplines.

### Temporal perspectives in evolutionary thought

Lyell, however, deeply influenced Darwin, and just as Lyell invoked uniformitarianism as part of his efforts to make geology a science, I believe Darwin followed suit in his development of evolutionary thought. Huxley famously wrote to Darwin immediately before publication of *The Origin*, suggesting that Darwin had adopted a gradual view of evolution too unreservedly. But as the subsequent history of evolutionary thought demonstrated, Darwin was right to be concerned about the assumptions required to do evolutionary biology. Many, if not most, biologists quickly accepted the reality of evolution. There was far greater reticence in accepting natural selection and the principle mechanism of evolutionary change. The late 1800s was a time of many competing evolutionary mechanisms, not all of them readily accessible to experimental test (Bowler, 1992).

The importance of a rigorously experimental view of evolution was thus clear to both geneticists and other evolutionary biologists during the early 1900s. By the time of the Modern Synthesis, they took advantage of some 70 years of confusion about mechanism to assert the importance of rigorously testable hypotheses. Although the term 'macroevolution' originally was applied to mechanisms that produced profound morphological discontinuities (in other words, it addressed the origin of variation), by the time of the modern synthesis macroevolution had become primarily about pattern, particularly as exhibited by the fossil record. There is a remarkable echo of Lyell in Dobzhansky's discussion of microevolution and macroevolution. Dobzhansky wrote: "There is no way toward an understanding of the mechanisms of macroevolution, which require time on a geological scale, other than through a full comprehension of the microevolutionary processes...for this reason, we are compelled at the present level of knowledge reluctantly to put a sign of equality between the mechanisms of macro- and micro-evolution" (Dobzhansky, 1937, p. 12; emphasis added). Note that Dobzhansky clearly recognizes the possibility that macroevolution could involve different processes and mechanisms than microevolution, but he acknowledges that from a practical standpoint in 1937 he could see no empirical or experimental approach to the issue. Dobzhansky and his colleagues were concerned with developing a rigorous, experimental science of evolutionary biology. In the face of ideas such as orthogenesis (already fading by the late 1930s) and Goldschmidt's ideas about macromutation, ensuring that there was a strong mechanistic base to evolutionary theorizing was as important then as it is today (Erwin, 2000, 2010).

Despite the best efforts of [Simpson \(1944\)](#) to articulate an expanded view of evolution, with micro-, macro- and quantum evolution, there were relatively few efforts to develop a coherent theory of macroevolution until the work of [Gould, Eldredge, Stanley, Valentine, and Jablonski](#), beginning in the 1970s. By this time the argument had largely shifted from the sources of morphologic variation to one of differential success of species and clades. In the 1970s the punctuated equilibrium model of speciation disconnected within-species adaptive evolution from inter-species evolutionary dynamics ([Gould, 2002](#); [Gould and Eldredge, 1993](#)). This quickly led to proposals for selection at the level of species (although not without some confusion about the difference between differential sorting of species and true species selection) ([Cracraft, 1985](#); [Jablonski, 2005, 2008](#); [Stanley, 1975](#); [Vrba, 1989](#); [Vrba and Eldredge, 1984](#)). The critical point here is that most (but not all, see [Jablonski \(2007\)](#)) of the work on macroevolution has been concerned with the differential success of species through time, rather than with mechanisms for the generation of variation that might explain significant morphologic innovation.

Structuralist approaches to evolution merit only the briefest comment. Some have argued that physical forces such as surface tension and other factors have been the dominant factor in generating organismal form with selection playing a relatively insignificant role. This idealistic view descends from the work of [D'Arcy Thompson \(Arthur, 2006; Thompson, 1942\)](#) and has been considerably elaborated ([Goodwin, 1990](#); [Muller and Newman, 2005](#)). While there is little doubt that physical factors such as surface tension and the physical dynamics of cellular interactions influence the developing embryo, the absence of rigorous experimental work and the agnosticism toward the role of genes and genomes among structuralists has necessarily limited their impact on evolutionary theory. Some structuralists have articulated an explicitly non-uniformitarian view of evolution, suggesting that physical forces primarily played a role early in animal evolution, perhaps during the Ediacaran Period. [Newman and colleagues](#) posited a 'pre-Mendelian' phase of animal evolution where physical forces dominated evolutionary change, before the takeover of development by genetic systems ([Newman et al., 2006](#)). This claim is of course vitiated by the extensive homologies between choanoflagellates and metazoans in signaling pathways, transcription factors, and other developmental mechanisms ([King, 2004](#)).

Thus a uniformitarian approach may have been politically necessary early in the history of evolutionary thought as a counterweight to various non-Darwinian approaches to evolution. And it is certainly the philosophic position most compatible with a strongly experimental basis for evolutionary theory, but there is no *a priori* reason why it should be correct. Today geologists acknowledge many processes that are more evident in deep time than they are today, and paleontologists often discuss 'non-analog' situations: periods during which the earth acted very differently than it does today. Examples of such non-analog conditions include anoxic oceans and global warm periods ([Bottjer, 1998](#)). As an anonymous paleontologist once remarked: "The present is only a hypothesis about how the world works". Reexamination of the uniformitarian assumptions of evolutionary biology may suggest alternative approaches to several problems in evolutionary biology.

## Major evolutionary transitions

The packaging of variation by kernels to influence patterns of evolution across developmental GRNs is not the first example of asymmetric patterns of variation in the history of life. Indeed, this may be the dominant process involved in major evolutionary transitions. In a seminal book [Maynard Smith and Szathmáry \(1995\)](#) argued that increases in biological complexity can largely be traced to eight major

evolutionary transitions, each of which involved new ways of packaging and transmitting information between generations:

- Replicating molecules → populations of molecules in compartments
- Independent replicators → chromosomes
- RNA as gene and enzyme → origin of the genetic code
- Prokaryotes → eukaryotes
- Asexual clones → origin of sex
- Protists → multicellularity with differentiated cells
- Individuals → colonies
- Primate societies → human societies (language)

The first three transitions on the list involve aspects of the origin of life, and while the list obviously does not include such events as the invasion of land by plants and animals or the origin of flight by insects, flying reptiles and birds, it does include transitions that involved how information was transmitted between parent and offspring. The first eukaryotic cells captured and incorporated once free-living protists to produce the intracellular chloroplasts and mitochondria that can now replicate only as part of the host cell. Similarly, when sex evolved, asexual eukaryotic lineages that once replicated on their own were now part of a sexually interbreeding population.

[Maynard Smith and Szathmáry](#) recognized that the object of selection had changed through the history of life, and these changes involved packaging formerly independent entities so that they can only replicate as part of some larger whole. In each of the transitions above there is a loss of the ability for independent replication. This created the potential for conflict between replication at different levels: if cell lineages are trying to replicate this may be in conflict with the whole organisms need to grow before replicating (and such runaway cellular proliferation is the basis of cancer). [Maynard Smith and Szathmáry](#) observe that the entities that exist within some larger whole may eventually lose the potential for independent reproduction. For example, although DNA still persists in mitochondria, many genes have been transferred to the nucleus of the host cell so that today it is impossible for mitochondria to live on their own. Similarly, the transition from protists to multicellular organisms required the development of mechanisms to corral the selfish tendencies of individual cells for the good of the larger organism, but one benefit (although it may not have been the initial basis of selection) was the development of cellular differentiation to produce the complicated forms with a diversity of organs, tissues and cell types. This book has sparked a minor industry in examining major evolutionary transitions ([Crespi, 2004](#); [Michod and Nedelcu, 2003](#); [Okasha, 2006](#)).

Along with this loss of independence came a greater division of labor and the possibility for increased specialization. The origin of eukaryotes, for example, involved the establishment (via symbiosis) of the mitochondria and chloroplast as energy-producing organelles within a eukaryotic cell, a distinct nucleus encompassing genetic material and a host of other specialized structures. These intracellular subunits could each specialize in ways that were not previously possible. Such a division of labor is a characteristic feature of these evolutionary transitions. A second characteristic is the development of new ways of transmitting information. [Maynard Smith and Szathmáry](#) recognized a distinction between two different levels of complexity in transmitting information. In the first, only a few distinct states can be transmitted, as with a mineral crystal 'seeding' the formation of similar crystal structures from a supersaturated solution. In the second, systems of 'unlimited heredity' can transmit a potentially infinite variety of types of information. This changes information flow between generations and also the entities upon which selection acts.

[Maynard Smith and Szathmáry](#) almost entirely ignore both ecological dynamics and changes in the physical environment, and their potential role in the major evolutionary transitions. This neglect was addressed by [Knoll and Bambach \(2000\)](#) who described an alternative set of 'megatrajectories' keyed to increases in ecological

complexity. Their list has some overlap with Maynard Smith and Szathmáry, and includes:

- Increasing efficiency of life processes [Origin of life]
- Prokaryotic diversification
- Diversification of unicellular eukaryotes
- Aquatic multicellularity
- Invasion of land
- Origin of intelligence.

Knoll and Bambach focused on the dimensions of ecological complexity, including the interactions of organisms in ecological food webs, the flow of energy, nutrients and important elements such as carbon sulfur and phosphorus, and steadily increasing volumes of biological material (biomass). At each successive level the degree of ecological complexity increases, and new dimensions are added to how life utilizes the environment and to the ways in which some organisms construct and modify their environment. Importantly, while the lower levels necessarily had to precede the higher levels, there was nothing inevitable about higher levels such as the invasion of land. The result is a series of transitions that progressively increased the overall diversity of life and the complexity of ecological interactions, but none of these transitions are associated with changes in the locus of selection. To the extent that they are non-uniformitarian it is because each of these innovations changes, to a greater or lesser degree, the nature of the environment in which organisms find themselves.

## Discussion

In this contribution I have focused on two aspects of non-uniform evolutionary change: the formation of highly recursive patterns within developmental gene regulatory networks, and the major evolutionary transitions. Each of these involves changes in the locus of selection, and patterning the sorts of variation upon which selection can act. It is unlikely that these examples exhaust the possibilities of asymmetric patterns of variation in the history of life. For example, horizontal gene transfer has been an important contributor to evolutionary variation among bacteria and archaea, and has also played a significant role among unicellular eukaryotes (Boto, 2009; Keeling and Palmer, 2008; Zhaxybayeva and Gogarten, 2004). This allows for the rapid transfer of evolutionary novelties between lineages. Because of the difficulty in identifying ancient gene transfer events, it seems to have been difficult to rigorously assess whether the incidence of successful gene transfers and whether the pattern of integration has varied over time. In other words, as genome organization has become more structured, has there been a systematic bias in the pattern of integration of new genes? These will be promising avenues to explore.

Traditional evolutionary theory is essentially non-uniformitarian. While it acknowledges the historical nature of evolutionary biology, until recently little attention has been paid to the issue of the impact of changing evolutionary dynamics through time. The pattern of origination of metazoan phyla and classes is highly non-uniform through the Phanerozoic, with an overwhelming bias towards the Cambrian and Ordovician. In the past non-paleontologists have attempted to rescue uniformitarian explanations by 'explaining away' this empirical pattern as a result of various biases. Both taxic and quantitative morphometric approaches have established that the pattern is accurate reflection of the appearance of morphological novelties. By combining this information on the pattern of morphologic evolution with mechanistic information from comparative studies of modern developmental GRNs, a new, non-uniformitarian view of evolution emerges. From this perspective, the growth of developmental networks has progressively structured the nature of accessible developmental innovations overtime. As kernels (and perhaps other patterns) formed early in the evolution of metazoa, these established the characteristic architectures recognized in the

fossil record. Subsequent evolutionary change appears to have been influenced by the persistence of these regulatory networks.

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