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The Cambrian Explosion: How Much Bang for the Buck?

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THE RISE OF ANIMALS: Evolution and Diversification of the Kingdom Animalia by Mikhail A. Fedonkin, James G. Gehling, Kathleen Grey, Guy M. Narbonne, and Patricia Vickers-Rich. Baltimore, MD: Johns Hopkins University Press, 2007. 327 pages; includes an atlas of Precambrian Metazoans, bibliography, index. Hardcover; \$79.00. ISBN: 9780801886799.

THE CAMBRIAN EXPLOSION: The Construction of Animal Biodiversity by Douglas H. Erwin and James W. Valentine. Greenwood Village, CO: Roberts and Company, 2013. 406 pages; includes one appendix, references, index. Hardcover; \$60.00. ISBN: 9781936221035.

DARWIN'S DOUBT: The Explosive Origin of Animal Life and the Case for Intelligent Design by Stephen C. Meyer. New York: HarperCollins, 2013. 498 pages; includes bibliography and index. Hardcover; \$28.99. ISBN: 9780062071477.

By the time that Darwin published *On the Origin of Species* in 1859, the principle of biotic succession had been well established and proven to be a powerful aid to correlating strata and deciphering the history of Earth, to which the rock layers testified. However, for Darwin, there remained a major issue regarding fossils for his comprehensive explanation for the history of life. The problem was this: the base of the Cambrian period, originally defined by Adam Sedgwick, was signified by the presence of trilobites, as well as other macroscopic fossils such as linguliform brachiopods and some strange echinoderms. These exotic and aesthetic remains were fairly easy to spot, but problematic in that they were blatantly the remains of complex multicellular organisms overlying rocks in which there were no remains of simpler organisms.

Later on, this dramatic appearance of complicated macroscopic fossils would become known by the shorthand expression "Cambrian explosion." Because the dispute between Sedgwick and Roderick Murchison on the boundary between the Cambrian and Silurian systems had not been fully resolved by 1859, Darwin considered these fossils "Silurian" (and thus for him, the issue would have been labeled the "Silurian explosion"!); Darwin confessed to some puzzlement:

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Consequently, if my theory be true, it is indisputable that before the lowest Silurian stratum was deposited, long periods elapsed, as long as, or probably far longer than the whole interval from the Silurian age to the present day; and that during these vast, yet quite unknown, periods of time, the world swarmed with living creatures. To the question why we do not find records of these vast primordial periods, I can give no satisfactory answer.¹

Of course, even during Darwin's day, the presence of large packets of strata lying below the Cambrian were discerned by field geologists; but the seeming absence of fossils in these layers left them resistant to description and analysis.

The perceived magnitude of this dramatic difference was given a boost by the discovery of two extraordinarily well-preserved Middle Cambrian fossil biotas. These two localities are the well-known Burgess locality of British Columbia, discovered in 1909 by Charles D. Walcott of the Smithsonian Institution; and the Chengjiang locality, Yunnan Province, China, discovered by Hou Xianguang in 1984. These are classic fossil "lagerstaetten" (bonanzas), formed as very fine-grained sediments (Burgess locality: the Stephen Formation; Chengjiang locality: the Maotianshan Shale) that were deposited in anoxic environments, providing exceptional preservation of soft anatomy as well as intricate hard structures. Supplemented by contemporaneous fossil assemblages from western Utah, Russia, Greenland, Australia, and elsewhere, these biotas have enabled us to analyze morphology for many dozens of exotic creatures and to reconstruct these in three dimensions.

We thus have been *blessed* to obtain a fairly synoptic picture of the broad taxonomic diversity, morphological complexity, and ecological relationships present in the Middle Cambrian underwater world. The biota includes sponges, sea pens, brachiopods, priapulid and sipunculan worms, onychophorans, many diverse arthropods, sea cucumbers, stalked echinoderms, and chordates. Notably, a large group of magnificent creatures that exhibit morphologies intermediate between onychophorans and arthropods, termed "lobopods," have been discovered. At present, about a dozen extant multicellular animal phyla, plus a few completely extinct phyla, are established from these contexts.

In 1989, Stephen J. Gould provided a popular introduction to the Burgess fauna (the Chengjiang fauna was not yet appreciated) and interpreted its significance for the history of life with his book *Wonderful Life: The Burgess Shale and the Nature of History* (hereafter referred to as *Wonderful Life*).² *Wonderful Life* was illustrated with drawings by Marianne Collins of the Royal Ontario Museum, which elegantly highlighted the strangeness and beauty of these animals. Gould recounted the history of discovery of the Burgess locality by Walcott and provided a resume of what was then known about the biology of these organisms. He then used this account as a springboard to a sermon on the nature of the course of evolution. Notably, he argued that the fauna served to illustrate just how quirky the record revealed life's history to be, illustrated by his metaphor of "replaying life's tape" (pp. 45-52). Gould argued that if we could somehow rewind history and then set it going again, we would see different sorts of surviving lineages—and lineages perhaps dramatically unlike our own. My favorite quote is the following:

We cannot bear the central implication of this brave new world. If humanity arose just yesterday as a small twig on one branch of a flourishing tree, then life may not, in any genuine sense, exist for us or because of us. Perhaps we are only an afterthought, a kind of cosmic accident, just one bauble on the Christmas tree of evolution. (p. 44)

Gould went one step further and argued that the Cambrian diversification event provided the single most significant episode of elaboration of phyletic-level body plans in Earth's history; from that point on, the story was primarily one of deletion of animal lineages. (This last claim was hyperbolic from the start; for example, the kingdom Plantae *did not yet exist* in the Cambrian. If we were literate intelligent plants, how would we evaluate this claim?)

Gould was taken to task on several fronts by critics, most notably, Simon Conway Morris.³ Conway Morris had devoted many years to the understanding of the Burgess soft-bodied animals, and he is regarded today as one of the world's authorities on the Cambrian biota. He argued that natural selection could predictably favor adaptations that promoted motility, sensory organs, feeding, and ultimately intelligence. Thus, the course of life was less fluky and more predictable. Conway Morris has

continued to persuasively argue this case, but that is another story. Meanwhile, there is general consensus that *Wonderful Life* stimulated a larger effort to really fathom the early history of life's diversification. But the elegant picture of Middle Cambrian biodiversity provided by the Burgess and Chengjiang lagerstaetten has left many with the impression that the Cambrian revolution is much more threatening to Darwin's synthesis than he could appreciate.

But there is more to the story ...

During the past 150 years, intensive field exploration and occasional episodes of serendipity have provided us with a clearer picture of the kinds of life which existed prior to the Cambrian, as well as rounding out a Cambrian bestiary. While the appearance of visible multicellular life in the rock record is not as abrupt and single-stepped as Darwin and

his contemporaries observed, the life forms during the long interval of 600–500 million years before the present (hereafter I will use the geologic convention of "Ma" for "millions of years before the present") have posed other very interesting problems of interpretation. There exists now a dynamic subdiscipline within paleontology devoted to the understanding of Precambrian and Cambrian life forms.

Our understanding of the Cambrian biodiversification event, as well as relevant biological events prior to the Cambrian period, has been greatly clarified since 1859 by the development of radiometric dating techniques. Through the application of several diverse techniques to Precambrian rocks, we now have a chronologic framework to order these biotic clues (fig. 1).⁴ A nomenclature is in place so that communication between scientists around the globe can occur. A familiarity with these terms is necessary for grasping the flow of the narrative in the volumes

Era	Period	Time before present (in Ma)	Age	Faunas/Notes	
Phanerozoic	Ordovician	485		Major diversification of articulated brachiopods; nautiloid cephalopods New echinoderms classes: sea stars, sea urchins Phylum Bryozoa appears in rock record	
		490	Stage 10		
	Cambrian			Jiangshanian	Archaeocyaths, helicoplacoids go extinct
				Paibian	
				Guzhangian	
				Drumian	
				Stage 5	Burgess biota
				Stage 4	
				Stage 3	Arthropods radiate; Trilobites
				Stage 2	Chengjiang biota
		521	Archaeocyaths flourish; vertical <i>Skolithos</i> burrows		
		529	"Small shellies"		
		541	Fortunian	<i>Treptichnus</i> burrows	
Neoproterozoic	Ediacaran			550–542 Ma: Nama Ediacaran assemblage, including <i>Cloudina</i>	
				560–540 Ma: "Classic" Ediacaran assemblages, incl. <i>Kimberella</i> Horizontal bedding-plane tracks	
				570 Ma: Doushantuo Fm. preserved microfossils	
				578 Ma: Avalon-style Ediacaran: Rangeomorphs + <i>Thectardis</i>	
				635 Ma: Chemical biomarkers of sponges	
		(635)	↓		

Figure 1: Chronology of Significant Biodiversification Events, Late Neoproterozoic through Early Phanerozoic Periods. Note: The Neoproterozoic-Phanerozoic boundary equals the Precambrian-Cambrian boundary.

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under review. This nomenclature is understood to be a working tool, and hence definitions become modified as more data come in. At present, geochronologists split Earth's history into four large eons: Hadean (4600–4000 Ma); Archean (4000–2500 Ma); Proterozoic (2500–541 Ma); and Phanerozoic (541 Ma–the present). The Cambrian Period (which has been subdivided into ten stages encompassing 541–485 Ma) was originally perceived due to the appearance of macroscopic, complex life forms (e.g., trilobites), thus marking the beginning of the Phanerozoic (which is from the Greek for “visible life”) and delineating the Proterozoic-Phanerozoic or Precambrian-Cambrian boundary. The Proterozoic Eon is divided into three eras: Paleoproterozoic, Mesoproterozoic, and Neoproterozoic. The last, the Neoproterozoic Era, spans the time frame from 1000–541 Ma; its uppermost unit has been christened the Ediacaran Period (635–541 Ma). In this essay book review, I adhere to the Cambrian stage nomenclature adopted by the International Commission on Stratigraphy; this nomenclature has displaced a prior functional set of terms adopted from the biostratigraphy of the Siberian platform (e.g., Tommotian, Nemakit-Daldynian) which may be familiar to some of this audience.⁵

The record of life during the Archean and early Proterozoic is highly relevant to the biological/ecological events which began during the Neoproterozoic, but can only be briefly mentioned here. Microfossils preserved in the Apex Chert of western Australia, dated to 3450 Ma or slightly older, are regarded as the earliest clear evidence of life, although carbon from earlier deposits may be of organic origin.⁶ Thinly laminated rock structures termed “stromatolites” are located in rocks of the same age and younger, extending up into the present. In today's world, these mats are the products of complex miniature ecosystems involving many types of cyanobacteria, other types of bacteria, and algae. By the late Paleoproterozoic, organic-walled unicellular structures, collectively termed “acritarchs” (from the Greek *akritos*, “uncertain”), are present. Later acritarchs of Mesoproterozoic age include recognizable representatives of the green, red, and brown algal clades; some may have been dinoflagellates. Acritarchs exhibit diversity rises and declines during the Mesoproterozoic and Neoproterozoic, and later abundance during the Cambrian and Ordovician periods.⁷ Diverse acritarchs would have been part of a Neoproterozoic and Cambrian

phytoplankton and hence significant as components in evolving marine food webs during that time. A protracted history of the transition of Earth's surface geochemistry to that correlated to an oxygenated atmosphere can be traced through several types of mineral indicators, revealing that these humble photosynthetic organisms are implicated, at least to some extent, as participants in the first major ecological transformation of our planet.

Only within the past fifteen years has the significance of sponges and sponge-like creatures for Neoproterozoic ecologies been appreciated. Lipids (“biomarkers”), which are today created by sponges, have been discovered in Neoproterozoic sediments >630 Ma in age. “Spongiomorph” body fossils are now known from several intervals within the overall Ediacaran and earliest Cambrian. I use the term spongiomorph because anatomical, biochemical, and genetic evidences reveal that the group of organisms that we all learned as Phylum Porifera is, in fact, a paraphyletic group; our living sponges are relicts of a radiation of erect water-filterers, an initial diversification of metazoans into a colonial lifestyle.⁸ Thus, for around 100 million years prior to the classic “Cambrian explosion,” sponges would have been filtering the water column. They would have transferred large volumes of accumulated dissolved organic carbon and deposited it as sediments as they died.

During the late 1940s, Reginald Sprigg, an Australian mining geologist, discovered a suite of enigmatic fossils in sandstones located in the Ediacara Hills, Flinders Ranges, South Australia. These fossils consisted solely of impressions of several types of organisms which must have been fairly flat and flimsy during life. Since that time, several diverse biotas resembling those of Ediacara have been discovered. Other principal biotas are known from Newfoundland, Namibia, and several locations in Russia; smaller biotas are known from Charnwood, England, and several locations in the Rocky Mountains of western North America. All these fossils are dated to the late Proterozoic and are collectively referred to as the “Ediacaran” biota. After a complicated and lengthy discussion on nomenclature, the latest Proterozoic period was christened the Ediacaran Period, after these creatures. (The lower boundary of the Ediacaran period, however, is defined by a global climatic event, the Marinoan glaci-

ation.⁹) The fossils themselves have also engendered a long and complicated discussion as to their nature and significance. By far, the best single reference now available on these fossils is the volume, *The Rise of Animals*, which is discussed below.

While preservation of most Ediacaran biotas occurs as impressions, a few fossil biotas scattered in time through the late Precambrian have been discovered that preserve detailed anatomy in fine-grained sediments. This is true especially of the fossil biotas in the Doushantuo Formation, originally described during the 1970s and now known from several localities in southern China. The Doushantuo formation shales and phosphorites, dated to 570 Ma, elegantly preserve acritarchs, multicellular algae, and significantly, animal embryos of uncertain affinity.¹⁰

Meanwhile, during the last fifty years or so, our biostratigraphic picture of the early Cambrian also has been transformed by the realization that trilobites, long considered as the signature Cambrian organism, appear globally in the record *after* other shelled creatures and *after* complex traces of motile organisms. Lingulate brachiopods with phosphatic shells, small football-shaped echinoderms termed “helicoplacoids,” and tiny conical tubes termed “hyoliths,” among others, are found in deposits devoid of trilobites and below strata with abundant trilobites. Biostratigraphers now set the appearance of trilobites as the beginning of Cambrian Stage 3, at around 521 Ma (fig. 1). The Chengjiang fossils are assigned to Cambrian Stage 3 and the Burgess fauna assigned to Stage 5.

Already by the middle nineteenth century, biostratigraphers had added to the list of Cambrian actors a group of puzzling fossils termed “archaeocyaths” (Greek for “ancient cup”). These one- to two-inch-long, perforated cup-shaped or tubular fossils are now understood to be an extinct sponge group which created stout calcareous skeletons. This group blossomed in the early Cambrian, and together with diverse algal groups produced one of the earliest undoubted ecologic reef associations.¹¹ Nearly all archaeocyathan taxa were extinct by the end of Cambrian Stage 2, and the last few did not make it into the Ordovician.

Accompanying the archeocyaths were a large group of tiny tubular phosphatic fossils, plus a series

of smaller plates and spines which must have become detached from skeletons.¹² They are mostly extracted from lower Cambrian phosphate deposits; some were probably originally composed of calcium carbonate, but have been replaced by phosphate minerals. These tiny fossils, typically 1 to 2 mm in largest dimension, are collectively known as the “small shellies.” These skeletal remains are common in Cambrian Stage 1, achieved peak diversity in Cambrian Stages 2 and 3, and decline thereafter (fig. 1). Some of the isolated plates were eventually matched to dermal armor in middle-Cambrian organisms found in the Burgess or Chengjiang biotas, such as the onychophoran-like *Microdictyon*. Some of the tubes are probable annelid dwelling tubes. Some of the tiny shells exhibit microstructure which mark them as primitive brachiopods, while others are probable molluscs. And a further revelation: the tiny tube *Cloudina* (named after Precambrian paleobiologist Preston Cloud) and a few others are abundant in the uppermost Ediacaran, at least back to 548 Ma, in the Nama Group of southern Africa.

Furthermore, traces of various kinds of burrows and trackways appear in lower Cambrian sediments of Stage 1 and 2, again prior to the appearance of trilobites. Some of these are vertical burrows, evidently the products of creatures endowed with muscles and a hydrostatic body cavity. Some of the horizontal burrows exhibit scratch patterns suggestive of legs—although we do not understand what legged creatures were around to produce them. The appearance of the vertical burrow *Treptichnus pedum* was recognized by the International Commission on Stratigraphy during the 1990s as the boundary marker for the beginning of the Cambrian period. (Trace fossils are assigned binomial labels but not higher taxonomic categories. In most cases, they are not assumed to be the product of a specific biologic taxon, but rather a potential group of taxa.)

Thus, it is very important to understand that the “Cambrian Explosion,” evidently a real and profound phenomenon, occurred during a protracted series of major ecosystem transitions which occurred over the period 600–490 Ma (and indeed, beyond, through the Ordovician Period, fig. 1). This Proterozoic/early Phanerozoic ecological context provides an important perspective with which to evaluate any attempt to explain Cambrian biodiversification.

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THE RISE OF ANIMALS: Evolution and Diversification of the Kingdom Animalia by Mikhail A. Fedonkin, James G. Gehling, Kathleen Grey, Guy M. Narbonne, and Patricia Vickers-Rich.

This elegant volume is unquestionably the best available comprehensive resume of what is known about the Ediacaran creatures. Nearly every page includes a photograph (most in color) or a colored illustration, for a total of 480 figures in 256 initial pages. In addition, there is a 31-page atlas of Precambrian metazoans, with photos for most of the approximately 250 taxa described. The volume even contains a foreword by the science-fiction author Arthur C. Clarke.

The Rise of Animals begins with two background chapters: the first on the Hadean/Archean Eons, the second an overview of the Proterozoic. The next eight chapters treat the major biotas, followed by a chapter on the minor but significant localities. Chapter 12 examines the trace fossils, with their implications for motility of the Ediacaran creatures. Chapter 13 provides an overview of the microfossils, many of these organic-walled plankton, from the deposits. Chapter 14, by Patricia Vickers-Rich, is a nice, succinct discussion about what is currently known and unknown about the transition into the Cambrian world.

As noted previously, almost all of the Ediacaran fossils are impressions. These manifestly demonstrate that there were very few organisms which possessed hard skeletons during that interval of time. Careful attention to the details of bedding surfaces reveals that the organisms which left the impressions were often preserved under slimy mats of algae. Many of the Ediacaran creatures (e.g., *Rangia*) were frondose. The oldest Ediacaran assemblages, preserved in eastern Newfoundland, were composed of fronds ("rangiomorphs") which exhibit fractal branching at three or four scales. Their sedimentological context argues for a deep-water habitat, below the photic zone; thus they were not photosynthetic nor did they house photosynthetic symbionts.¹³ They are believed to have obtained their nutrition osmotically through direct absorption from seawater.¹⁴ Hans Pflug proposed that many or most of the Ediacaran frondose creatures were a unique phylum (christened the "Petalonomae") of osmotrophic organisms; Adolf Seilacher went one step further, considering these an extinct kingdom of life, the Vendobionts.

Later Ediacaran soft-bodied biota may have been sessile comb jellies (Phylum Ctenophora). A few forms (e.g., *Charniodiscus*) contain tiny tubes which may have housed zooids, implying these were sea pens (Phylum Cnidaria). Other Ediacarans (e.g., *Aspidella*) are disk-shaped impressions. Early on, they were interpreted as medusans. As more and more specimens became available, most were revealed to be holdfasts for the frondose organisms. Some of the disks (e.g., *Tribrachidium*) have three arms. They have been claimed to be jellyfish, echinoderms, and sponges, and remain problematic. Others are broad, flat, segmented impressions (e.g., *Dickinsonia*). These do not possess stalks and are interpreted alternatively as petalonomans which lay flat during life, or segmented worms of uncertain affinity (perhaps flatworms).

True sponges with a meshwork of spicules are preserved: *Palaeophragmodictya*, from the classical Ediacaran area of south Australia. The conical fossil *Thectardis* from the Avalon assemblage is also probably a sponge.

Some of the segmented organisms exhibit a mid-line keel and head-shield-like structure which leads some workers to believe that these were early non-skeletonized arthropods (e.g., *Parvancorina*). Some of the Chenjiang and Burgess arthropods resemble *Parvancorina*, for example *Naraoia*, which is a non-calcified strange trilobite with only two dorsal shields.

The fossil *Kimberella quadrata* is an elongated (up to six inches long), "boat-shaped" form with a distinct frill around the edges. It possessed a stiff but unmineralized integument, and is associated with traces of scratching which match those created by modern algae-rasping molluscs such as chitons and monoplacophorans. *Kimberella* is known from several Ediacaran localities; more than eight hundred specimens have been obtained from the White Sea region of Russia.

Thousands of Ediacaran fossils have now been obtained, and these document a marine world which is ecologically very different from that of today. There are no traces of deep burrowing, nor of grazing on the fronds. So, at least part of the explanation for the patent transformation into the world of the Cambrian lies in the elaboration of new ecological

niches, which literally undermined and shredded the placid, stable-surface world of the Ediacaran.

The Ediacaran ecosystems of circa 580–540 Ma are still enigmatic. Comprehensive studies of sedimentation patterns combined with fossil clues demonstrate subtle variation in ecologies that correlate with water depth. There were changes over time in the Ediacaran world, too, as new actors came on the scene. *Kimberella* represents an advance guard of a phalanx of sediment plowers and croppers which would ultimately decimate the flimsy, helpless Ediacarans. And the basal Cambrian small shelly fauna, with hard parts appearing simultaneously across a diversity of biotic forms, probably represents a response to croppers which possessed teeth.

However, we do appreciate that some of our standard marine invertebrate phyla are evidenced during the late Precambrian: sponges early on, then diploblastic organisms such as ctenophores and cnidarians, and later, early molluscs, flatworms, and possibly arthropods. These Neoproterozoic representatives require that any comprehensive look at the Cambrian “explosion” must expand the time frame of this biodiversification event into one that took place over several tens of millions of years and involved a cascade of ecosystem transformations pushing a series of turnovers in major ecological actors.¹⁵

THE CAMBRIAN EXPLOSION: The Construction of Animal Biodiversity by Douglas H. Erwin and James W. Valentine.

Valentine is emeritus professor at the University of California, Berkeley; some aspects of his long (approaching fifty years) career are briefly discussed in the review of *Rereading the Fossil Record* in this issue of *PSCF* (p. 263). Erwin is a curator of paleobiology at the Smithsonian National Museum of Natural History. Like *The Rise of Animals*, this volume is elegantly illustrated. There are over seventy very clear photographs of Ediacaran and Cambrian fossils, plus numerous elegant reconstructions, colored graphs, and anatomical figures. The two dozen life-like organismal reconstructions by Quade Paul and the line art by Tom Webster add considerably to the reader’s vision of what life forms were like in these strange ancient seas. The appendix, prepared by

Sarah Tweedt, is a compilation of first appearances of major metazoan clades in the fossil record.

The Cambrian Explosion is organized into four parts. Part I outlines the stratigraphic and paleoenvironmental context of the Ediacaran and Cambrian world. Part II, consisting of three chapters and 160 pages (occupying nearly half of the book), is a detailed look at the life of these periods. Part III focuses on explanatory possibilities, in the form of changing ecologies and different genomic regulatory mechanisms. Part IV consists of two chapters summarizing the late Proterozoic and Cambrian biotic revolutions.

Part II (chaps. 4–6) reviews the Ediacaran and Cambrian biota. Chapter 4 lays out the basic taxonomic/morphological framework for classifying these organisms and for grouping them into higher biological categories. Body architectures are illustrated with crisp, multicolor diagrams. A scheme for the classification of metazoans (multicellular animals) is elaborated. This scheme has emerged over the past thirty years through a concerted multidisciplinary examination of the key similarities and differences in major invertebrate groups, much of which was summarized in Valentine’s masterful 2004 opus, *On the Origin of Phyla*.¹⁶ Then, in chapters 5 and 6, the groups of Ediacaran and Cambrian organisms are described and illustrated as ecological assemblages, and on a group-by-group basis. Along the way, Erwin and Valentine explain just how the architectures of individual organisms fit into our emerging phylogenetic picture for Metazoa. The top-quality photographs, reconstructions, and clear discussion of these taxa make chapters 5 and 6 the best single one-stop overview of the “explosion biota” to be had.

The book has several other strengths, beyond the clarity and aesthetic value of the illustrations and the extensive treatment of the biology of these organisms in Part II. One is the detailed discussion of the changing ecology of the marine world in the Proterozoic and early Phanerozoic (chaps. 3 and 7). This involves summarizing data from sedimentology, various geochemical indicators (e.g., sulfur minerals) of such important environmental parameters as atmospheric oxygenation, evidences for Neoproterozoic climate swings, and seafloor sediment stability. These environmental evidences dovetail

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with the clues from the biota, including traces of activity, to provide a picture of changing ecosystems over this period spanning more than 100 million years. As one case in point, noted above: there are no marks of predation on the Ediacaran creatures. The appearance of marine mineralized skeletons is, on the one hand, an indicator of increased oxygen concentrations (permitting the metabolic levels necessary for depositing skeletons), and, on the other hand, a new ecological context: biting, rasping, and drilling.

Other major ecological changes include deeper burrowing:

The advent of burrowing in the very latest Ediacaran or earliest Cambrian led to a seafloor “agronomic revolution,” heralding the disappearance of the firm, microbially stabilized sediments of the Neoproterozoic and the increasing aeration and disturbance of sediments by the burrowers. (p. 225)

Yet a third highly significant biotic revolution was the appearance of mesozooplankton, linking pelagic and benthic ecosystems. Another was the colonization of microbial reefs by tubular shelled creatures, including the archaeocyaths, resulting in a complex, tiered architecture which provided numerous micro-niches ready for occupation. Based on an analysis of ecological spaces by Richard Bambach, Andrew Bush, and Doug Erwin,¹⁷ Valentine and Erwin identify twelve different ecological roles for Ediacaran organisms, expanding to thirty modes in the first half of the Cambrian. This expansion resulted in middle Cambrian food webs that, surprisingly, are highly similar to modern marine food webs, albeit with different actors.

Chapter 8, “The Evolution of the Metazoan Genome and the Cambrian Explosion,” probes the (obligate!) genetic system correlates of Cambrian biodiversification. Erwin and Valentine begin by noting the (unexpected) low number of human genes coding for proteins (<25,000). The key to understanding development of complex organisms lies not in single genes manufacturing proteins (which they term “housekeeping genes”) but rather in gene regulatory networks (GRNs).¹⁸ GRNs affect transcription, resulting in cascades of differentiating cell lineages, leading to major architectural or physiological systems. The “kernels” of these systems are modules which are highly conservative; an example provided

is the module which specifies endomesoderm development in both sea urchins and starfish (p. 275). Interestingly, this same kernel is present in zebrafish. In general, such kernels are conserved because tinkering with these will result in a nonviable organism. On the other hand, kernels can be interlinked with modular elements termed “plug-ins,” which can alter the sequencing of deployment of kernels or their interaction, ultimately influencing gene transcription. There is no doubt that these mechanisms are those that direct construction of major groups of body plans, and underlie the pattern that we are still elucidating for the relationships of phyla.

In Part IV, Erwin and Valentine sum up their review of Cambrian faunal diversification. In chapter 9, “Ghostly Ancestors,” they summarize the evidences which are currently available to reconstruct ancestral morphologies and genealogical connections among metazoans. Chapter 10, “Constructing the Cambrian,” provides an interpretation of the Ediacaran/early Cambrian phenomenon. They believe that only by integrating three distinct sources of data will we be able to understand the Cambrian diversification event: (1) historical changes in the physical environment; (2) elaborations in developmental mechanisms, particularly in GRNs; and (3) changes in ecological relationships over time, including the elaboration of new adaptive niches. While “the early evolutionary history of metazoans was characterized by a range of innovations unmatched by subsequent Phanerozoic evolution” (p. 319), Erwin and Valentine believe that we are making significant headway in constraining our explanations for these innovations. The Cambrian diversification event is “a tractable but unresolved problem” (p. 330).

Erwin and Valentine admit that there is much yet to be deciphered concerning the Precambrian-Cambrian biotic transition. They see two major unresolved questions:

First, what evolutionary processes produced the gaps between the morphologies of the major clades? Second, why have the morphologic boundaries of these body plans remained relatively stable over the past half a billion years? (p. 330)

They later term these correlated issues “the conservative and clumpy nature of body plans” (p. 332). The

answer, they believe, must involve (historically) fixed discontinuities in patterns of GRNs.

It is the exact when and how these discontinuities were fixed that will continue to provide controversy and impetus to further paleontological field work. Right now, as best we can fathom, these genetic innovations occurred either prior to the advent of mineralized tissues, or during the initiation of this event (i.e., the time of the “small shellies”). Thus we await revelations which might be provided by just the right fossil bonanza, such as preservational circumstances like those of Chengjiang, but dated to 530 Ma, 550 Ma, or 560 Ma. In the meantime, for the best current introduction to the Proterozoic-Cambrian transition and to the fascinating organisms inhabiting the seas way back then, go to this volume.

DARWIN’S DOUBT: The Explosive Origin of Animal Life and the Case for Intelligent Design
by Stephen C. Meyer.

Meyer, a philosopher of science with a PhD from Cambridge University, is director of the Discovery Institute’s Center for Science and Culture. At less than half the price of Erwin and Valentine’s volume, there must be a trade-off, and it comes in the number and quality of illustrations. Meyer’s volume features a center section containing twenty-three very nice color plates: 1–3 are photos of the Chengjiang locality; 4–23 are of Cambrian organisms, mostly from Chengjiang. There are about two dozen good black-and-white photos of Ediacaran or Cambrian organisms, plus many line drawings and diagrams drafted by Ray Braun. Some of the line drawings are a bit rough. There are also thirty-eight pages of dense endnotes which grant greater detail to statements made in the course of the narrative.

Part I, “The Mystery of the Missing Fossils,” consisting of seven chapters with 150 pages, is an extended review of the Precambrian-Cambrian transition, including a history of paleontological discoveries. Chapters 2 and 3 provide a survey of the Burgess and Chengjiang biotas. Chapter 4, “The Not Missing Fossils?,” looks at the Ediacaran biota. Part II, “How to Build an Animal,” consists of seven chapters treating the role of genes in organismal development, and why Meyer and others are not impressed with classical neo-Darwinian mechan-

isms as potential explanations for the origin of the Cambrian body plans. Part III includes six chapters explaining why the author feels that intelligence must be provided from without in order to account for the genetic programming necessary to rapidly produce the Cambrian biota. Thus, much of the book is a polemic. Just as in the case of *Wonderful Life*, an opinioned work which had many faults but which engendered much useful labor and thought, this book must be examined from many different angles.

A signal component in Meyer’s thesis is the notion that “the main pulse of Cambrian morphological innovation occurred in a sedimentary sequence spanning no more than 6 million years” (p. 73). Meyer cites geochronological studies by Samuel Bowring (MIT) and colleagues, and by Doug Erwin and colleagues.¹⁹ The first study, by Bowring et al., established that the Manykaian stage lasted no less than ten million years, while the Tommotian and Atdabanian stages lasted five to ten million years. Translating into standardized stage dates, the Tommotian plus Atdabanian are the upper part of Stage 2 plus Stage 3, together accounting for at least ten million years. But the Cambrian Stage 1, roughly equivalent to the Manykaian-Daldynian, contains the record of the rapid expansion of the “small shelly fauna” in which we discern elements of the “classic” Cambrian fauna, such as brachiopods, molluscs, and onychophorans. Erwin et al. deliberately include Cambrian Stage 1 along with the very latest Ediacaran in their designated interval for diversification, thus identifying a biodiversification period “with a dramatic rise over about 25 million years in the first several stages of the Cambrian ...”²⁰ Meyer’s claim for a span of “not more than 6 million years” represents a minimalist interpretation of these two articles, and particularly the more current Erwin et al.

The absence of any discussion of the “small shellies,” along with the stratigraphic subdivisions of the uppermost Ediacaran and Cambrian Stage 1, represents a significant lacuna in Meyer’s treatment of the Cambrian explosion. Moreover, while the surface trails of the Ediacaran receive a few pages of discussion (pp. 81, 85–6), the transition to deeper burrowing requiring muscles and/or a hydrostatic skeleton at the beginning of the Cambrian also goes disregarded. Thus, these significant evidences that

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many kinds of poorly mineralized multicellular animals were living and dying in the earliest Cambrian seas are not made available to the reader. Only by ignoring these evidences can the claim of “not more than 6 million years” be sustained.

There is also no discussion of changing early- to mid-Cambrian ecologies, which, in fact, opened many environmental niches. Such significant innovations as ecological reefs and new planktonic food webs, which would provide new adaptive niches, are simply not mentioned. This general glossing over of significant stratigraphic and paleoecological data helps one to understand the exasperation expressed by paleontologist reviewers such as Donald Prothero.²¹

Chapter 6 is a critique of our fallible efforts to thoroughly understand the phylogenetic organization to life.

My point in summarizing these disputes is to simply note that the molecular and anatomical data commonly disagree, that one can find partisans on every side, that the debate is persistent and ongoing, and that, therefore, the statements of Dawkins, Coyne, and many others about all the evidence (molecular and anatomical) supporting a single unambiguous tree are manifestly false. (p. 124)

There are ongoing disagreements, to be sure, but some confusion is to be expected when we consider that the further back we probe the initial branching events, the more similarities we expect to see across the boundaries of what we can today easily distinguish as phyla. In fact, the detailed anatomy provided by the Chengjiang and Burgess biotas is proving to be of huge help in resolving our understanding of the branching, hierarchical structure to living creatures.²²

In Part II, “How to Build an Animal,” Meyer mounts a step-by-step critique of standard neo-Darwinian accounts for the origin of phylum-level body plans. Meyer takes his time and builds a case showing that standard “bean-bag” genetics cannot provide the kinds of integrated developmental systems that the metazoan radiation demands. Chapter 13, “The Origin of Body Plans,” concludes with a discussion of Eric Davidson’s work on GRNs.²³

Davidson’s findings present a profound challenge to the adequacy of the neo-Darwinian mechanism. Building new animal body plans requires not just new genes and proteins, but new GRNs. (p. 268)

Chapter 14 explains why epigenetic processes in development are important, and why modern evolutionary biology has become much more pluralistic. Many of those who “have raised questions about the adequacy of the standard neo-Darwinian mechanism, and/or the problem of evolutionary novelty in particular” are briefly mentioned, for example, Brian Goodwin, Gerd Mueller, Stuart Kauffman, and Rudolf Raff. Interestingly, several paleontologists are included in Meyer’s list of skeptics, including Simon Conway Morris, Robert Carroll, Doug Erwin, and James Valentine (p. 287).

Meyer, following Goodwin, Mueller, and others, is absolutely correct that epigenetics is important for understanding organismal development and animal forms. But I think that the average reader of chapter 14 will be underinformed. Meyer begins the narrative in chapter 14 by outlining the experiments of Hans Spemann and his PhD student Hilda Mangold in the 1920s on developing newts, plus some important subsequent studies during the middle-twentieth century, which demonstrated the significance of the cellular chemical environment for gene expression during development. (Chemical gradients across the developing embryo which determine which genes are expressed are often termed “developmental morphogenetic fields.”) Meyer then moves on to the

groundbreaking collection of scientific essays entitled *Origination of Organismal Form: Beyond the Gene in Developmental and Evolutionary Biology*, edited by two distinguished developmental and evolutionary biologists, Gerd Mueller, of the University of Vienna, and Stuart Newman, of New York Medical College [published in 2003] ... Mueller and Newman not only highlighted the importance of epigenetic information for the formation of body plans during development; they also argued that it must have played a similarly important role in the origin and evolution of body plans in the first place. (p. 272)

As they and others in their volume maintain, neo-Darwinism lacks an explanation for the origin of organismal form precisely because it cannot explain the origin of epigenetic information. (p. 273)

Meyer relates,

I first learned about the problem of epigenetic information and the Spemann and Mangold experiment while driving to a private meeting of Darwin-doubting scientists on the central coast of California in 1993 ... On our drive, I asked [Johnathan] Wells why developmental biology was so important to evolutionary theory and to assessing neo-Darwinism. I'll never forget his reply. "Because," he said, "that's where the whole theory is going to unravel." (p. 273)

Certainly it is true that many of the primary architects of the neo-Darwinian synthesis downplayed embryology. But Spemann received the Nobel Prize in 1935 for his work, and the study of morphogenetic fields in development has been standard fare in laboratories and embryology texts since his day. (I first learned about Spemann's experiments in 1973, in an undergraduate class in vertebrate embryology at a state university.) It is a fact that our understanding of gene regulation has grown exponentially since 1970, and that biologists such as Goodwin, Raff, and Davidson have been discovering more and more complexity in the regulation of the developmental process. But, while it is true that Goodwin and others believe that their discoveries pose a major challenge to neo-Darwinian orthodoxy, this does not cause them to abandon their belief that the history of life can be explained as the outcome of biological processes! Indeed, many evolutionary biologists and paleontologists are looking to build the notions provided by morphogenetic fields and developmental constraints into a larger synthesis. Meanwhile, I suspect that the average (nonbiologist) reader will come away from chapter 14 with a mistaken impression that this previously innocuous or neglected topic has just now been revealed to completely overturn our understanding of the history of life.

Part III, "After Darwin, What?," builds a case for considering intelligent design (ID) as a reasonable potential resolution to the enigma of the Cambrian explosion. Chapters 15 and 16 consider non-Darwinian materialistic explanations, such as Stuart Kauffman's suggestion that self-organizational principles dictate the direction for life. I think Meyer makes a good case that self-organizational principles do not get us very far in explaining morphogenesis of intricate organisms. Chapter 17 defends the notion that ID should be at least considered as a reasonable explanation for (some potential) phenomena; chap-

ter 18 looks for "Signs of Design in the Cambrian Explosion." The work of Doug Erwin and Eric Davidson, already noted above, is pivotal. Meyer believes that developmental GRNs, with their intricate circuitry and multiple feedback systems, are too complex to have arisen piecemeal, even granting millions of years culminating in the Cambrian event. Here we have the focal point of the long argument. Chapters 19, "The Rules of Science," and 20, "What Is at Stake," are a plea for a reconsideration of the role of design. Chapter 20 begins with a visit by Meyer and his son to the Burgess site and is a brighter, more upbeat endnote for the volume.

I admit that, by temperament, I am inclined to see design in nature, and so I resonate with some of Meyer's arguments. I think he and I would concur that humans are not "baubles on the Christmas tree of life." I think he has developed a case for the inadequacy of standard "bean-bag" genetic approaches to the production of animal body plans. Does this negate a genealogical organization to life? No. And does the development of this strong case require a glossing over of the series of profound ecological changes which transformed the late Ediacaran world through the early Cambrian, into the middle Cambrian, and beyond? I hope not. A lack of real engagement with long spans of geologic time has long plagued the advocates of ID.²⁴ And, sadly, the lack of engagement with real time tends to divorce ID arguments from real creatures existing in real history, and perhaps counter-intuitively, render these arguments joyless. Meyer's examination of the Cambrian event employs dates, looks at several of the interesting taxa, and even concludes with a pilgrimage to the Burgess locality—but it could use a dose of pleasure in these wild and weird life forms.

Does *Darwin's Doubt* exhibit irritating flaws? Yes. Is the Erwin and Valentine book, *The Cambrian Explosion*, authoritative and more fun than *Darwin's Doubt*? Yes. But do I think that Meyer makes an argument that folks should think hard about? Yes.

Wonder-Full Life

Our knowledge of the Cambrian diversification event has grown enormously since *Wonderful Life* was published, while our real *wonder* over just what was going on keeps increasing. J.-Y. Chen, in a significant review article, notes that

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the transition of the two-segmental lobopodian head into the first arthropod head required a *quantum leap* (my italics) through multiple, synchronous events, including: transition of the first head appendage into the stalked eyes; specialization of the second head appendage into sensorial organs known as antennae; and displacement of the mouth into a ventral position of the antennal segment.²⁵

Erwin and Valentine, near the conclusion of *The Cambrian Explosion*, remark that “the pathway from sponges to eumetazoans is the *most enigmatic* [my italics] of any evolutionary transition in metazoans” (p. 324). One can continue to multiply quotes such as these. Conway Morris, in a recent review, states, “My main conclusion is that the Cambrian ‘explosion’ is a real event.”²⁶ Is this event, occurring over an interval of twenty-five or more million years, opaque to our efforts to discern normal causal processes operating in the past? Conway Morris, a few paragraphs following the quote above, concludes, “Does this course of events create a problem for Darwinism, even for evolution? I do not think so.”²⁷

How *do* we interpret God’s active providence in the affairs of the world of the past? As Christians, we understand that God is good and that his creation reflects that. But in the human world, we think that we can (or must) discriminate between God’s decretive will and his permissive will. Does God worry about which color shirt I put on this morning? I sometimes think our pondering over the direction of life is something like that. I believe God directed the course of life, but I am not sure whether he worries about putting together every bit of (just-right) pigment on the back of a dragonfly, or even about which particular flower that honeybee is going to pollinate, and so forth. Maybe he likes to watch how his creatures behave, just as he enjoys hearing us pray to him voluntarily. I am not sure that it is in our place to know. If that is so, perhaps our efforts to obtain certainty in seeing his design will end in frustration.

I do know that the life of the past praised its Creator, just as giraffes and oysters and prickly pear cacti do today. I think we are *blessed* to get glimpses of these ancient creatures, and also blessed to intelligently ferret out what was going on, even if this ferreting-out leads us up some dead ends from time to time. ★

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Notes

- ¹C. Darwin, *On the Origin of Species* (1859; reprint, Cambridge, MA: Harvard University Press, 1964), 307.
- ²S. J. Gould, *Wonderful Life: The Burgess Shale and the Nature of History* (New York: W. W. Norton and Company, 1989).
- ³S. Conway Morris, *The Crucible of Creation: The Burgess Shale and the Rise of Animals* (Oxford: Oxford University Press, 1998).
- ⁴Cf. J. G. Ogg, G. Ogg, and F. M. Gradstein, *The Concise Geologic Time Scale* (Cambridge: Cambridge University Press, 2008). Dates in this article and in figure 1 conform to those of the International Commission on Stratigraphy: see www.stratigraphy.org for further information.
- ⁵Ibid.
- ⁶J. W. Schopf, *Cradle of Life: The Discovery of Earth’s Earliest Fossils* (Princeton, NJ: Princeton University Press, 1999); and B. T. De Gregorio et al., “Biogenic Origin for Earth’s Oldest Putative Microfossils,” *Geology* 37 (2009): 631–4.
- ⁷De Gregorio et al., “Biogenic Origin for Earth’s Oldest Putative Microfossils;” and A. H. Knoll and S. Xiao, “Precambrian Lagerstaetten,” in *Palaeobiology II*, ed. D. E. G. Briggs and P. R. Crowther (London: Blackwell Publishers, 2003), 332–7.
- ⁸E. A. Sperling, D. Pisani, and K. J. Peterson, “Poriferan Paraphyly and Its Implications for Precambrian Palaeobiology,” *Geological Society of London Special Publications* 286 (2007): 355–68; and E. A. Sperling, K. J. Peterson, and M. LaFlamme, “Rangeomorphs, *Tectardis* (Porifera?) and Dissolved Organic Carbon in the Ediacaran Oceans,” *Geobiology* 9 (2011): 24–33.
- ⁹A. H. Knoll, M. R. Walter, G. M. Narbonne, and N. Christie-Blick, “The Ediacaran Period: A New Addition to the Geologic Time Scale,” *Lethaia* 39 (2006): 13–30.
- ¹⁰Knoll and Xiao, “Precambrian Lagerstaetten.”
- ¹¹B. R. Pratt, B. R. Spincer, R. A. Wood, and A. Yu. Zhuravlev, “Ecology and Evolution of Cambrian Reefs,” in *The Ecology of the Cambrian Radiation*, ed. A. Yu. Zhuravlev and R. Riding (New York: Columbia University Press, 2001), 254–74.
- ¹²A. C. Maloof et al., “The Earliest Cambrian Record of Animals and Ocean Geochemical Change,” *Geological Society of America Bulletin* 122 (2010): 1731–74.
- ¹³G. M. Narbonne, “Modular Construction of Early Ediacaran Complex Life Forms,” *Science* 305 (2004): 1141–4.
- ¹⁴Cf. M. A. S. McMenamin and D. L. S. McMenamin, *The Emergence of Animals: The Cambrian Breakthrough* (New York: Columbia University Press, 1990); and Sperling, Peterson,

and LaFlamme, "Rangeomorphs, *Thectardis* (Porifera?) and Dissolved Organic Carbon in the Ediacaran Oceans."

¹⁵D. H. Erwin and S. Tweedt, "Ecological Drivers of the Ediacaran-Cambrian Diversification of Metazoa," *Evolutionary Ecology* 26 (2012): 417-33.

¹⁶J. W. Valentine, *On the Origin of Phyla* (Chicago, IL: University of Chicago Press, 2004).

¹⁷R. K. Bambach, A. M. Bush, and D. H. Erwin, "Autecology and the Filling of Ecospace: Key Metazoan Radiations," *Palaeontology* 50 (2007): Pt. 1:1-22.

¹⁸E. H. Davidson and D. H. Erwin, "Gene Regulatory Networks and the Evolution of Animal Body Plans," *Science* 311 (2006): 796-800; and E. H. Davidson, "Emerging Properties of Animal Gene Regulatory Networks," *Nature* 468 (2010): 911-20.

¹⁹S. A. Bowring, J. P. Grotzinger, C. E. Isaachsen, A. H. Knoll, S. M. Pelechaty, and P. Kolosov, "Calibrating Rates of Early Cambrian Evolution," *Science* 261 (1993): 1293-8; and D. H. Erwin, M. Laflamme, S. M. Tweedt, E. A. Sperling, D. Pisani, and K. J. Peterson, "The Cambrian Conundrum: Early Divergence and Later Ecological Success in the Early History of Animals," *Science* 334 (2011): 1091-7.

²⁰Erwin, Laflamme, Tweedt, Sperling, Pisani, and Peterson, "The Cambrian Conundrum: Early Divergence and Later Ecological Success in the Early History of Animals." The full quote, which is partially extracted in this review, is the following:

A recompilation (SOM text 1 and table S1) of the first occurrences of all metazoan phyla, classes, and stem-classes (extinct clades) of equivalent morphological disparity (fig. 2, D and E) shows their first occurrences in the latest Ediacaran (by 555 MA), with a dramatic rise over about 25 million years in the first several stages of the Cambrian, and continuing into the Ordovician (figs. 1 and 3 and table S3). (p. 1091)

²¹D. Prothero, "Stephen Meyer's Fumbling Bumbling Cambrian Amateur Follies: Review of *Darwin's Doubt*," 2013, http://www.amazon.com/review/R2HNOHERF138DU/ref=cm_cr_pr_viewpnt#R2HNOHERF138DU.

²²Cf. Valentine, *On the Origin of Phyla*; and Douglas H. Erwin and James W. Valentine, *The Cambrian Explosion: The Construction of Animal Biodiversity* (Greenwood Village, CO: Roberts and Company, 2013).

²³Davidson and Erwin, "Gene Regulatory Networks and the Evolution of Animal Body Plans;" and Davidson, "Emerging Properties of Animal Gene Regulatory Networks."

²⁴M. Roberts, "Intelligent Design: Some Geological, Historical, and Theological Questions," in *Debating Design: from Darwin to DNA*, ed. W. A. Dembski and M. Ruse (Cambridge: Cambridge University Press, 2004), 275-93.

²⁵J.-Y. Chen, "The Sudden Appearance of Diverse Animal Body Plans during the Cambrian Explosion," *International Journal of Developmental Biology* 53 (2009): 737.

²⁶S. Conway Morris, "Darwin's Dilemma: The Realities of the Cambrian 'Explosion,'" *Philosophical Transactions of the Royal Society B* 361 (2006): 1077.

²⁷*Ibid.*, 1078.

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