

BOOK REVIEW

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The diversification of modern animals: Douglas Erwin and James Valentine on the Cambrian explosion

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When writing *The Origin of Species*, Darwin (1859, pp. 306-309) puzzled over the abrupt beginning of life's fossil record: after long, seemingly lifeless eras, an extraordinary diversity of marine life suddenly burst forth into the geological record. Nowadays, the trained minds of geologists and microbial biochemists see abundant evidence of microbial activity in these seemingly lifeless pre-Cambrian rocks: indeed, these microbes' photosynthesis and chemosynthesis transformed the chemistry of the oceans and the geology of their sediments (Fischer 1984, Konhauser 2007). Since Darwin's time, a pre-Cambrian biota of macroscopic multicellular organisms, the Ediacaran biota, has been discovered, although just what these organisms were, or even whether they were all aquatic, is far from settled (Knauth 2013, Retallack 2013, Xiao 2013). It remains true that the first organisms we can recognize as members of living phyla burst into the fossil record, in remarkable diversity, with disconcerting suddenness, in the Cambrian period, beginning 540 million years ago. What happened?

In *The Cambrian Explosion*, two paleontologists, Douglas Erwin and his former dissertation advisor James Valentine, document the explosion of diversity in the Cambrian, and the events leading up to it, in lavishly illustrated detail. This story begins with the origin about two billion years ago — by an Archaean incorporating bacterial symbionts capable of aerobic respiration — of

eukaryotes. Transforming bacterial symbionts into the microscopic power plants we call mitochondria made possible the evolution of large multicellular organisms with division of labor among their cells (Lane and Martin 2010). After outlining the plan of their book, they explain how one infers an evolutionary narrative from the geological record — how one tells the relative, and the absolute, ages of widely separated fossil deposits. They end the book's first section by discussing the environmental events (including two episodes when nearly all the earth froze!) associated with the gradual oxygenation of first the atmosphere, then the ocean, that set the stage for the explosive diversification of fossilizable life.

Their second section explores the early stages of metazoan evolution. First they consider what can be learned from molecular phylogeny, comparative analyses of the early stages of embryonic development, and the genetic bases of their differences. There are surprises here. Onychophora, once touted as the "missing link" between annelids and arthropods, turn out to be far more closely related to arthropods than to annelids (p. 95). The flatworm phylum, Platyhelminthes, and its best-known exemplar *Planaria*, are not mentioned in the text although they represent a basic stage in animal organization (Haldane & Huxley 1927, Hyman 1951): do the authors consider them a degenerate offshoot? (This is true for the 'acoels,' but not for all Platyhelminthes: see bottom panel of figure on p. 162 of Maxmen 2011). Subsequent developments in the fast-moving field of metazoan origins have sprung more surprises. It now appears that ctenophores (Rokas 2013, Ryan *et al.* 2013, Hejnol 2014, Moroz *et al.* 2014, Ryan 2014) — comb jellies or sea walnuts — rather than sponges (Srivistava *et al.* 2010) were the oldest (earliest-diverging) branch on the tree of

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animal life. Nevertheless, this chapter is a lovely introduction to many of the following chapters' *dramatis personae*.

This section concludes with two chapters on what the fossil record has revealed. The first chapter considers the last two hundred years before the Cambrian began, especially the last 97 million years — the Ediacaran period. Metazoans — including sponges — clearly evolved before the Ediacaran began. A variety of soft-bodied organisms appeared about 580 million years ago, evolved, diversified — and vanished from the face of the earth 40 million years later, just before the Cambrian began. There were no predators, no scavengers, and until the very end no burrowers among them, which no doubt allowed these fossils' excellent preservation. A few mobile animals appeared 14 million years before the Ediacaran ended: an animal that grazed, limpet-like, on the microbial mat that covered the sea bottom (p. 122); another that crawled on its digestive surface over the mat, *Trichoplax*-fashion, perhaps absorbing organic compounds from the mat (pp. 120-122). Otherwise, we have little idea how these organisms made their living, who they were related to, or why they died out.

The Cambrian tells a different story. Its beginning is defined by the first appearance of *Treptichnus* burrows, made by an animal with a front and a rear, and upper and lower sides (p. 143). A host of small shells, mostly of mollusks and brachiopods, appear with them (p. 149). Twenty million years later, the exquisitely fossilized remains of complex ecosystems appear — first Chengjiang in China, Sirius Passet in north Greenland and the Emu Bay shales in Australia 520-515 million years ago, then, ~ 10 million years later, the Burgess Shales of the Canadian Rockies (p. 155), made famous by Gould (1989) and Conway Morris (1998). The deposits include most living phyla possessed of fossilizable body parts (p. 154), including vertebrates like jawless fishes. A diversity of predators, burrowers and filter-feeders burst upon the scene (p. 177, Vinther *et al.* 2014). The Cambrian brought forth a huge diversity of forms, many destined to disappear as natural selection sifted the more from the less enduringly effective.

New ways of life demand new technologies, and only now are we learning how rapidly some of this technology developed. Many of these animals could move: some swam (pp. 196-7), others walked (pp. 190-191). Various animals soon evolved the abilities to detect, catch, eat and digest prey. The front appendages, 12 cm long, of the suspension-feeding anomalocarid *Tamisiocaris borealis* were good tools for straining plankton ~ 1mm in diameter from the water (Vinther *et al.* 2014). A Cambrian arthropod 3 cm long, *Alalcomeneus*, had a pair of chelicerae, two crude compound eyes 0.75 mm wide with 200 facets (ommatidia) apiece, and a nervous system much like that of fossil horseshoe crabs, *Limulus*, coordinating motor responses to sensory input (Tanaka *et al.* 2013). After *The Cambrian*

Explosion appeared, Cong *et al.* (2014) showed how the forebrain, optic nerves, and nerves of the two front appendages, here claw-bearing, of the 8 cm anomalocarid *Lyropanax* resembled that of modern onychophorans, and suggested how their innervation came to be reorganized in later ancestors of such mandibulate arthropods as grasshoppers and beetles. Isolated arthropod eyes ~ 8mm wide, with 3000 facets apiece, were discovered in Australia's Emu Bay shales (p. 216, Lee *et al.* 2011). These were organized like robberfly (Asilidie) eyes, and were adapted to see in dim light. Soon thereafter, meter-long *Anomalocaris*, swimming predators like their namesakes in the Burgess Shales, were found in the Emu Bay shales. Their 3 cm wide eyes, adapted for brighter light, had over 16,000 facets apiece (Paterson *et al.* 2011). These predators had more acute vision than most living arthropods. One of the most remarkable of the Cambrian dramas was the extraordinary strides of some animal groups toward sensing their surroundings, organizing them into valid pictures of their environment, and coordinating appropriate responses.

This book's next section explores the ecological and genetic aspects of diversification in the Ediacaran and especially the Cambrian. An underlying theme of the ecological chapter is the evolutionary innovations by which organisms transformed their environment (p. 223), transforming the sea into a more hospitable and productive home for life. The Cambrian was distinguished by the evolution of deep burrowers, predators, anti-predator defenses and metazoan reef-makers (p. 225). They document the spread of animals into ever more diverse ways of life (p. 233) and the evolution of food webs analogous in topology and complexity to modern marine shallow-water counterparts.

Erwin and Valentine try to explain Cambrian diversification without invoking competition (p. 249), which is odd, because they happily invoke natural selection (competition among genotypes) to explain evolution (p. 265). Vermeij (1995, 1999, 2004), whom they treat rather ungenerously, makes no such error, and provides a far better perspective for understanding the Cambrian's extraordinary developments. Innovation is favored by increased nutrient supply, and warming, which increases animals' metabolic rates and therefore their ability to secure these nutrients (Vermeij 1995). The Cambrian opened with a major marine transgression (Peters and Gaines 2012), likely caused by eruptions of submarine volcanos (Vermeij 1995), which increased both temperature and nutrient supply. Deep burrowing, which began in the Cambrian, recycles nutrients which would otherwise be buried beyond reach; predation, another Cambrian innovation, enhances resource turnover: both processes amplify productivity (Vermeij 1995). The coevolution between anti-herbivore defenses and ways to penetrate them must have increased diversity in the Cambrian, as it does today (Ehrlich and Raven 1964).

The benefits ecosystem dominants derive from increased ability to sense and respond to their environment (Vermeij 1999) are wonderfully illustrated by the Cambrian's meter-long apex predator *Anomalocaris*, with its pair of 3-cm-wide eyes, capable of vision clearer than that of most modern arthropods (Paterson *et al.* 2011). Indeed, the development in anomalocarids of awareness of their surroundings and the ability to respond quickly and appropriately (Cong *et al.* 2014) — a story still being assembled — is not the least of the Cambrian's achievements.

The authors, both paleontologists, devote more discerning attention to the genetical side of their story. Indeed, ever since the days of Charles Darwin and Richard Owen, geologists have debated both the centrality of adaptation and natural selection's role in its origin (Osborn 1934, Simpson 1944, Gould and Lewontin 1979, Gould 1985, Schindewolf 1993) — often, sadly, in an ecological vacuum. Without downplaying the role of natural selection, the authors — like Samuel Butler and William Bateson — act as if the central problem in the origin of species is the origin of variation. There is much to be gained by doing so: there is no other way to see how natural selection could bring forth the Cambrian explosion.

The Cambrian explosion was not driven primarily by the origin of new genes. The unicellular eukaryote ancestors of metazoans — choanoflagellates, presumably had ~ 9100 genes (p. 251), governing metabolism, cellular construction, reproduction, control of their mitochondrial guests, and coordination of the cell's physiological and behavioral activities (p. 254). Ctenophores, now considered the first metazoans to diverge from the “main line,” and sponges evolved many more genes, mostly by gene duplication (p. 266). The two genotyped ctenophores have 16,548 (Ryan *et al.* 2013) and 19,523 (Moroz *et al.* 2014) protein-coding genes respectively; the fruit fly *Drosophila* has 14,601 (p. 253) and human beings ~ 25000 (p. 251). Genes come and go. Although 2000 *Drosophila* genes evolved after the origin of flies, most *Drosophila* genes were in early metazoans (p. 272). Moreover, the reactions these genes' proteins catalyze have not changed since, although the location, timing and function of these reactions can differ greatly in different classes or phyla. Moreover, similar genes orient the body axis in flies and mice. Similar genes coordinate gut formation in both flies and sea urchins, although mouth and anus have different developmental origins in the two groups (p. 285). Despite the difference between the compound eyes of insects, the simple eyes of human beings, and the better-organized simple eyes of squid, the development of all these eyes is governed by the same genes.

Despite their similar numbers of genes, and the similarity in the sets of genes controlling the basic outlines of their corresponding organ systems, a sea anemone

has 15 types of cells, a human being, ~ 400; and human beings have brains capable of conceptual thought, which sea anemones lack. The difference between sea anemones and human beings is largely governed by the greater subtlety and complexity of the mechanisms by which the activities of different genes are localized, timed and coordinated in human beings. The main actors in this drama are transcription factors, which govern when and where a gene programs the catalysis of the protein it encodes, and signaling pathways, which coordinate the functions of different transcription factors both within a cell and among an animal's cells (p. 258). Regulation could be quite complex. Some subcircuits of regulatory genes, “kernels” which “define the spatial pattern of part of the embryo's development,” are too intricately organized to change (p. 275). Kernels characterize phyla or groups of phyla (p. 277), and may limit their group's array of evolutionary options. Much Ediacaran and Cambrian evolution (not all!) hinged on how these transcription factors and signaling pathways deployed old genes in newer, subtler, more intricately coordinated ways. Cambrian diversification largely reflected divergent uses of these newer, subtler, better coordinated control mechanisms. How this appears to have been accomplished is not easy reading, but it makes a fascinating story.

This book's final section includes a chapter reconstructing the early stages of metazoan evolution and another on what factors drove the explosive diversification of the Cambrian. Choanoflagellates possess both metazoan-type transcription factors and metazoan-type signalling pathways (p. 297): the relevant genes appeared long before they acquired their current functions. The fact that ctenophores, with muscles and nerves (Moroz *et al.* 2014), evolved before sponges, which lack both, may simplify the authors' story. Although sponges lack complex gene regulatory networks, they have a few components of six of the seven major signaling pathways (p. 297), more pathways than the ctenophores do (Ryan *et al.* 2013). Both sponges and ctenophores can restrict a gene's expression to certain regions or tissues (p. 297, Moroz *et al.* 2014). Just as tunicate larvae revealed the relationship of their sessile filter-feeding adults to vertebrates (pp. 93-94), so sponge larvae may reveal the contribution of sponges to metazoan evolution better than their adults do. Indeed, the radially symmetric, three-layered larvae of the genotyped sponge *Amphimedon queenslandica* has twelve cell types, and it can steer in response to light (Adamska *et al.* 2011). One of its signaling pathways specifies its front and rear, another, its top and bottom (p. 303). One need not deny that ctenophores are basal metazoans to suspect that Nielsen (2008) was onto something in calling us, and other. Bilaterians, derived sponge larvae. Erwin and Valentine

are surely right to conclude (p. 298) that ancestral metazoans could specify and localize different cell types in order to make organized bodies with division of labor among their cells.

Once past the ctenophores and the sponges, the story of metazoan evolution stands out a little more clearly. Although *Trichoplax* has no gut, muscles or nerves, and only 11,514 protein-coding genes (p. 253), they have some genes that influence the development of gut, muscles and nerves, many transcription factors, and other genes important in the development of bilaterians (bilaterally symmetric animals) (p. 299). *Trichoplax* must have more complex ancestors. Cnidarians have many genes that mediate the development of tissues and organs, especially those of the mesoderm, the middle layer, in bilaterians. Is the distinction between having two layers, as in cnidarians, and three layers of tissues, as in bilaterians, that fundamental?

The latest common ancestor of snails, onychophora, nematodes and human beings had ganglia that foreshadowed brains, and Hox genes that caused differential development along various parts of the animal's long axis. They had genes modern animals use to make eyes, but these genes may only have produced light-sensitive cells (p. 317). These ancestral bilaterians had the evolutionary capability to cope with the consequences of becoming larger and lowering their surface-to-volume ratio (p. 310) even though larger animals must have ways of conveying oxygen and food to all their cells, removing these cells' wastes, integrating sensory impressions, and coordinating appropriate responses.

The last chapter starts with with the reflection, well worth reading however obvious it may seem once read, that the Cambrian explosion must reflect a match between environmental opportunity and the functional ability and evolutionary capacity of organisms to exploit it (p. 320). The authors believe that metazoans appeared over 750 million years ago (p. 323) and had evolved the required abilities before the Cambrian began (p. 326), a conclusion amply justified by their reflections on the ability of early bilaterians to evolve large size (p. 310). If so, what opened the "opportunity window" when the Cambrian began? The great marine transgression of Peters and Gaines (2012)? The activities of some organisms presumably created opportunities for others (p. 328), making the Cambrian explosion a chain reaction, an autocatalytic process.

The Cambrian was the era when modern phyla evolved: modern classes and orders mostly appeared in the Ordovician, or later (p. 330). Did the Cambrian witness the mother of all adaptive radiations, of which the radiations of silverswords and drepanidine honeycreepers into the opportunity-rich habitats of the Hawaiian Islands (Carlquist 1980) are but shadows? The authors are

reluctant to agree. First, the body plans of the Cambrian appeared so quickly, were so distinct "from the beginning" (which, sadly, we do not yet really know), and lasted so long — the half-billion years to the present (p. 330): they find this beyond the common for adaptive radiations. That the Cambrian sees no species swarms like the cichlid fishes of Lake Victoria (p. 339) is no surprise. Such swarms presuppose effective sexual selection and sensory capacities sufficient to distinguish appropriate mates from a host of similar but inappropriate ones (Seehausen *et al.* 1997, 1998), abilities not yet evolved in the Cambrian. Metazoans are, however, societies of cells. In animal societies one distinguishes social selection, governing behavior to one's fellow group members, which are both rivals and mates on which one's own future depends from selection for behavioral and functional characteristics appropriate to the outside world (West Eberhard 1979). Similarly, this book's authors distinguish internal selection, favoring appropriate multiplication and development of, and harmonious coordination among, an animal's cells and organs from external selection favoring effective exploitation of, and responses to, the animal's surroundings (p. 331). Might internal selection commit different clades to distinct body plans (p. 331)? Finally, the authors think of an adaptive radiation as a sequence of competition-avoiding innovations that fills a pre-existing adaptive zone. The Cambrian explosion, however, was an interacting set of chain reactions where new adaptations opened opportunities for other adaptations to different zones, often destined to be exploited by members of different clades. Fisher (1930, pp. 38-40) devised a toy model of factors influencing a new mutation's chance of being favorable, which may be a useful framework for understanding the Cambrian explosion. This model suggests that in a population barely capable of exploiting an opportunity, which lacks better competitors, mutations of substantial effect, would have a meaningful chance of being favorable in the opportunity-rich Cambrian world, even though in today's competitive world they would be disasters. Under such circumstances, evolution would be very rapid. Moreover, the more varied a clade's opportunities, the more severe the trade-offs involved in exploiting one opportunity rather than another, and the stronger the selection for diversification and reproductive isolation between exploiters of different opportunities (Fisher 1930, pp. 123-129). Is there any reason why these principles would not apply to the autocatalytic chain reactions of the Cambrian explosion?

The Cambrian explosion is one of the most astonishing and fascinating events of evolutionary history. The authors have gone to enormous trouble to tell the story comprehensively and clearly. They have told the story well, and their story gives biologists a great deal of food for thought.

Competing interests

The author declares that he has no competing interests.

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