The Cambrian Explosion: The Construction of Animal Biodiversity.

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persistence. In this domain, however, cooperation also plays a crucial role: "Cooperation and competition are partners in cultural change" (p. 257).

Although the author is clear to make distinctions among the domains of evolutionary change, development, learning, and cultural change, what is emphasized in *Cells to Civilizations* is that, at the appropriate level of abstraction, their similarities can be enlightening. There is much more in this book that I have not mentioned. It is replete with biological examples—from the stripes of zebras to plant genetics—that illustrate the author's claims, all accomplished with clarity and grace. *Cells to Civilizations* is an intelligent and entertaining book by a distinguished biologist.

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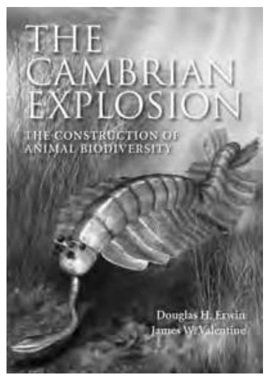
BREAKTHROUGH ON THE CAMBRIAN EXPLOSION

The Cambrian Explosion: The Construction of Animal Biodiversity. Douglas H. Erwin and James W. Valentine. Roberts and Company, 2013. 416 pp., illus. $48.00 (ISBN 9781936221035 cloth).

Three unsolved problems, above all others, command the attention of the scientific community. The first is whether there is or was life on Mars. The second concerns the origin of life. The third—arguably the most difficult of the three to answer—is what happened during the Cambrian explosion. In their book *The Cambrian Explosion: The Construction of Animal Biodiversity*, Douglas H. Erwin and James W. Valentine present a courageous effort to address this third problem. The book's subtitle pays homage to the closing paragraphs of *The Origin of Species by Means of Natural Selection*, in which Darwin reflected that "elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us" (Darwin 1872 [1859]). Why did these elaborate forms, so different from one another, appear so suddenly in the Cambrian Period of the Paleozoic Era?



Fossils occurring at the base of the Cambrian confront Darwinism with its greatest challenge. Do they constitute a fatal stumbling block for theories of morphological evolution for which the natural selection of small changes over geologic time is posited? Darwin admitted in *Origin* (1967 [1859]) that the sudden appearance of complex animals was problematic for his evolutionistic schema. No surprise then that Darwin was the first scientist to rationalize away the abrupt appearance at the outset of the Cambrian with an appeal to the incompleteness of the fossil record. Darwin compared the rock record to a damaged folio volume, for which we have only a page here and a paragraph there.

Charles D. Walcott, who famously discovered the Burgess Shale fossils in British Columbia, Canada, attempted to address Darwin's difficulty by proposing the *Lipalian interval*—a vast stretch of geologic time not represented by strata. Walcott realized that a gap in the record would rescue Darwin's schema by providing a ready excuse for the missing ancestors. Field studies, however, have shown that many Precambrian–Cambrian stratigraphic boundary sections show no evidence for such a gigantic gap.

In one of the great ironies in the history of science, Walcott's discovery of the Burgess Shale had a result diametrically opposed to his Lipalian gambit. Burgess creatures look distressingly modern. Making matters worse, the 1985 discovery of Early Cambrian soft-bodied fossils of the Chengjiang biota in the Yunnan Province of China further compounds the problem. Chengjiang reveals fossils even more modern looking than those of the Burgess Shale, among them being the first fossil fish, *Myllokunmingia*.

Erwin and Valentine admit that the creatures of Chengjiang are "no less complicated than those of today" (p. 327), thus recognizing the danger of the Darwinian view. They argue (unconvincingly, in my opinion, considering that soft-bodied fossils also occur in the Proterozoic) that these "newly opened taphonomic windows [Burgess and Chengjiang]… have surely made the explosion appear to be more abrupt than was actually the case" (p. 328). It is here that the primary purpose of the book becomes clear. Their effort to defend neo-Darwinism shows that gradualistic evolution is no mere straw man but, rather, a strong bias among top paleontologists. They uncritically accept Zhu and colleagues' (2008) assignment of the spiral Ediacaran *Eoandromeda* to the ctenophores as support for gradual evolution across the Cambrian boundary. *Eoandromeda* is far better assigned to the weird Ediacaran vendobiont clade. Implying that cnidarian cnidae are "derived" products of sequential evolution, Erwin and Valentine ignore that cnidae are the evolutionarily abrupt result of a symbiotic acquisition of microsporidians.

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Phylogenetic telescoping is a phenomenon whereby the putative ancestral forms appear at the same time or even later than the descendants. Telescoping is rampant in the Cambrian, yet Erwin and Valentine make scant mention of this. I offer three examples to prove my point: First, consider whether echinoderms represent a well-behaved phylum in conventional evolutionary terms. Zhang and colleagues (2013) reinterpreted the Chengjiang metazoan *Cotyledion tyloides* as a stem-group entoproct. A close look at the stem reveals oval sclerites with marginal borders strikingly similar to the oval stem sclerites of the Cambrian echinoderm *Gogia*. The sclerites of *Cotyledion* therefore appear as fossils before the well-mineralized gogiid sclerites. This seems to fulfill the neo-Darwinian expectation that the ancestral trait precede the crown-group trait by an ample margin.

Second, Erwin and Valentine make a case that asymmetrical echinoderms preceded and were ancestral to pentameral (2–1–2 ambulacra) echinoderms. Therefore, asymmetrical echinoderms (*Helicoplacus*) were precursors to echinoderms with one ambulacrum and two branched ambulacral pairs. Similar to the *Cotyledion*-to-*Gogia* progression, the *Helicoplacus*-to-pentameral scenario is a tempting potential match to expectations. The fossil record does not match this expectation, however. Erwin and Valentine note that the earliest well-mineralized "endoskeletons of echinoderms first appear as disarticulated plates" (p. 168). One of these fossils (Sprinkle's 1973 figure 18, plate 25) shows the ambulacral bifurcation. This is a case of phylogenetic telescoping, in which the crown group appears before the putative stem (*Helicoplacus*).

Third, *The Cambrian Explosion* states that gene expression supposedly becomes "increasingly inflexible" because of the establishment of metazoan developmental kernels. The authors note that kernels are "refractory to modification once they form" (p. 275). Their solution to this dilemma is to describe a combination of the advent of the *cis*-regulatory evolution of genome networks and an immutable codification of the developmental kernels. There is, however, evidence that *cis*-regulatory features and developmental kernels were already in place at a very early date. Ediacarans appeared 585 million years ago (Kaufman et al. 2007). The fauna includes the oldest known chitons (McMenamin 2011). As members of Polyplacophora, these fossils indicate that *cis*-regulatory networks and developmental kernels were already functional. In a key admission that undermines their main thesis, Erwin and Valentine state that there "simply may not be any viable phenotypic variation within the developmental kernels for selection to act upon" (p. 331).

This presents us with a serious conundrum. Extant animal groups appear early in Ediacaran times, but somehow, the explosion proceeds without warning, evidently by processes that do not (or, if we believe in the rigidity of developmental kernels, cannot) require the agency of natural selection. Although Erwin and Valentine acknowledge the magnitude of these morphological gaps, they miss the main message of the explosion—namely, that it represents a singularity in the history of life.

Unwarranted gradualistic assumptions abound throughout this book. A mention of Darwin's finches and the Miocene horses may remind readers of comfortably gradualistic cases in which neo-Darwinism seems to apply, but recent investigations now suggest that this synthesized theory is, in fact, indefensible (e.g., Newman and Bhat 2008, Fodor and Piatelli-Palmarini 2011). What will develop in its place is less clear.

Darwin once remarked that Jean-Baptiste Lamarck's concept of a complexifying force was "useless." Perhaps we should now give renewed scientific scrutiny to Lamarck's rendering of the phenomenon of "*la force qui tend sans cesse à composer l'organisation*" ("the force that tends to ceaselessly create order"). Berg (1969 [1926]) stressed that natural selection does not explain evolutionary change. He proposed that the primary mechanism was "directed mass mutations." This hard-to-fathom concept takes on a new resonance as we confront what exactly took place.

The Cambrian Explosion may well be the last serious attempt to explain the Cambrian event from an exclusively neo-Darwinist perspective. Despite this limitation, the book is a superb summary of the data associated with this problematic period. In one sense, Darwin was right: Evolutionary changes are indeed "produced by laws acting around us." In strictly scientific terms, we must admit that we understand neither the nature of these laws nor whence they came.

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