Explosions of Biodiversity

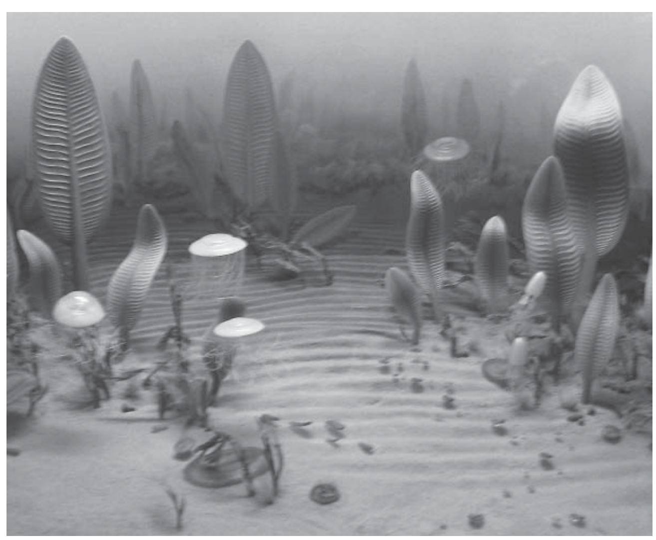
By John A. Catalani

In paleontology, when one speaks of explosions of biodiversity, it is generally assumed that one is speaking of the Cambrian Explosion. This is understandable because this "initial" radiation in both morphological disparity (range in utilized body plans) and diversity of taxa set the stage for the subsequent players in the game of life on Earth. However, we now recognize two other "explosions" in the early history of life – one that occurred before the Cambrian Explosion, named the Avalon Explosion (the time of origin of the Ediacara Biota), and one after, called the Great Ordovician Biodiversification Event (GOBE). Even though the Cambrian Explosion gets most of the press, each of these diversifications was significant for several reasons. First, they occurred at or near the beginning of multicellular life and, second, they (well, the last two anyway) deter-mined the shape (body plans) and evolutionary history (phylogeny) of life on Earth, culminating in all that we see today – and that is just plain cool.

The Ediacara "Biota" (some paleontologists do not like the term "biota" because Ediacaran fossils vary widely in size, shape, and construction) has been, since its discovery in 1946 in Australia (although examples of the fauna were found early in the twentieth century in Namibia), enigmatic in terms of body-plan organization and relationships to present-day organisms. The Ediacaran fossils occur in rocks of the upper Ediacaran Period (see Catalani, 2005, for background on this period) deposited approximately 575-542 million years ago (Ma) and have now been found at dozens of localities across five continents. Forms range from small (centimeter-size), somewhat amorphous blobs to very large (meter-size) fronds and discs. The frond and disc fossils reveal a structure quite unlike anything alive today. These organisms consisted of a quilted surface sometimes described as having an "air-mattress" morphology and, as far as can be determined, lacked a mouth and gut. It has been proposed that gas exchange (as well as food intake) in these organisms occurred by diffusion through their external surface instead of through internal surfaces as occurs in most animals today. This unique morphological architecture led Adolf Seilacher to propose that these animals were a "failed experiment" in biological organization that had no analogue with present-day life forms. In several papers (Seilacher 1989, 1992), he proposed that the Ediacaran organisms should be placed in a separate phylum that he originally termed "Vendozoa" (the Ediacaran Period has also been referred to as the Vendian) and then later renamed it Vendobionta. The most recent evaluation of the Ediacara Biota suggests that it consisted of "a mixture of stem- and crown-group radial animals, stem-group bilaterian animals, 'failed experiments' in animal evolution, and perhaps representatives of other eukaryotic kingdoms" (Narbonne, 2005: 421).

The Ediacara Biota, which appeared just after the end of the Gaskiers glaciation (the last glaciation of the so-called "Snowball Earth") and disappeared around the start of the Cambrian Period, actually consisted of three distinct assemblages (see Narbonne, 2005, for a much more detailed description). The oldest (approximately 575-560 Ma) is termed the Avalon Assemblage. Fossils show that these organisms were constructed of modular elements forming, among others, frond-shaped colonies that lived in deep water. The shallow-water White Sea Assemblage (approximately 560-542 Ma) displayed the most diverse biota composed of frond-shaped as well as segmented organisms. The Nama Assemblage (approximately 549-542 Ma) also consisted of shallow-water organisms but of relatively low diversity. Speculations that attempt to explain the appearance and diversification of the Ediacara Biota include the presence of significant amounts of oxygen that reached deep water for the first time, the Acraman bolide impact event (South Australia), and the breakup of the supercontinent Rodinia.

In the most recent study of the Avalon Assemblage (and one of the two new papers that provided the incentive for this essay; the other concerns the GOBE and is detailed below), Shen and colleagues (2008) compared the radiation

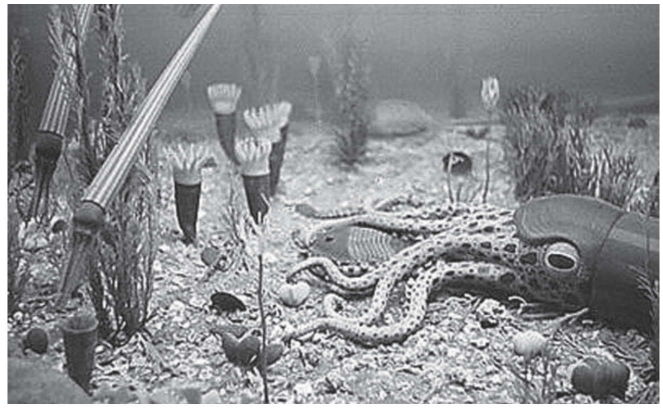


Reconstruction of the Ediacara Biota (courtesy of Joshua Sherurcij, via Wikimedia Commons).

of body plans of the Ediacara Biota to that of the Cambrian Explosion. They termed this rapid increase in disparity the "Avalon Explosion" in which virtually the complete range of Ediacaran body plans evolved in the Avalon Assemblage and was maintained with little change in the two subsequent assemblages. Taxonomic diversity, however, increased, gradually reaching its peak in the White Sea Assemblage, then decreased in the Nama Assemblage. The authors conclude that "the marked parallels between the Cambrian and Avalon explosions suggest that the decoupling of taxonomic and morphological evolution is not unique to the Cambrian explosion and that the Avalon explosion represents an independent, failed experiment with an evolutionary pattern similar to that of the Cambrian explosion" (p. 84).

The Cambrian Explosion (very approx. 542-520 Ma although some researchers speculate that the actual "explosion" was compressed in time at around 530-520 Ma) documented the initial emergence of life in its more-or-less familiar form. During this radiation event, all but one of the phyla that characterize life on Earth today made their first appearance. From studies of trilobites, it appears that variation in morphological form was particularly strong at this time, leading to an explosion in disparity. As with the Ediacara Biota, the process of innovation and diversification of body plans was rapid at the beginning of the Cambrian Explosion. Subsequent preening of body forms resulted in many that became the foundation for succeeding animals as well as some that, for one reason or another, did not survive. Other studies suggest that at this time the rates of molecular evolution were exceptionally high. Some paleontologists have proposed that many of the morphological forms that arose during the Cambrian Explosion cannot readily be assigned to an existing phylum. This is not to say that they represent, as proposed by Gould (1989), separate and distinct phyla, just a period of experimentation in body form. Others maintain that most of the problematic forms can be assigned to existing phyla and that the morphological disparity evident in the Cambrian is not much different than that seen today. This also raises the question as to just what constitutes a phylum, but I will defer that question to those much more qualified than I. Be that as it may, it is obvious that there was an unprecedented radiation of body forms at the expense of taxonomic diversity during the Cambrian Explosion.

Several theories have been proposed to explain the Cambrian Explosion including high rates of molecular evolution (as mentioned above), continued oxygenation of the oceans, and the acquisition by animals of the ability to secrete hard shells (biomineralization) in response to predation. It is also probable that the seeds for the Cambrian Explosion were sown well before the Cambrian Period and, therefore, before the advent of biomineralization, which would have severely limited the formation of recognizable fossils. Some have even suggested that the "Cambrian Explosion" is merely an artifact of the invention of biomineralized. That might be, but all of



Reconstruction of an Ordovician sea floor (courtesy of National Aeronautics and Space Administration, via Wikimedia Commons).

these diverse organisms had to radiate at some point and the limited time available, geologically speaking, points to some type of "explosion."

Needless to say, although I am fascinated with the earlier two "explosions," the Great Ordovician Biodiversification Event holds a special and intense interest for me because it is during this time that my beloved nautiloids lived, died, and were fossilized. The Ordovician (approx. 489-443 Ma) radiation is different than either the Ediacaran or Cambrian "explosions" for several reasons. First, the earlier two both experienced a radiation of body plans, disparity, at the expense of taxonomic diversity, whereas during the GOBE only one new phylum, Bryozoa, originated but taxonomic diversity increased dramatically. Second, the Ediacaran and Cambrian radiation events were restricted in time, geologically speaking, with all groups diversifying at about the same time for each event, whereas the GOBE radiations, although occurring in definite pulses, were spread pretty much throughout the entire Ordovician. Therefore, the origination of most of the phyla and classes of animals, as well as a varied set of body plans, in the Cambrian set the stage for the Ordovician radiations to fill niche spaces with a diversity of species. The GOBE, it is generally acknowledged, was characterized by the greatest increase in biodiversity in the history of life – there was a two-fold increase in taxonomic orders, a three-fold increase in families, and a nearly four-fold increase in genera (Webby *et al.*, 2004: 9). Nautiloids, for example, were represented at the beginning of the Ordovician by only one order but, by the time the Late Ordovician rolled around, had radiated into at least ten orders – nine of which are represented in the Platteville rocks that I have been studying and collecting for the past 30 years. Additionally, nautiloids diversified into a wide range of shell shapes and species and reached their all-time peak diversity at this time. The potential of several groups that experienced their initial radiations during the GOBE, however, was not fully realized until long after the Ordovician. For example, the bivalves, a group that would become an important component of post-

Paleozoic faunas, evolved most of their shell forms during the Ordovician radiations (many bivalves representing both epifaunal and infaunal types are found in the carbonate rocks of the Platteville alongside my nautiloids).

This lesser known event, when compared to the Vendian and Cambrian explosions, finally received its due when a monumental volume (Webby *et al.*, 2004) was published that covered all taxonomic groups, summarized environmental and tectonic aspects of the Ordovician world, and defined a global stratigraphic framework and a standard timescale that allowed the taxonomic studies to be compared. Although the time slices utilized by the book's authors had been determined using radiometric dating techniques, all of the global stages still had not been officially named when the volume was published. In 2007, however, the International Subcommission on Ordovician Stratigraphy (ISOS) finally agreed on a set of names for these global stages after almost 30 years of deliberation. Defining these units was complicated by the highly provincial nature of Ordovician faunas, the uneven occurrence and distribution of reliable radiometric dates, and the search for appropriate type sections that would suitably illustrate each stage. It is now possible to place local, regional, and continental series and stage names into a global context. Consequently, the Platteville rocks (which were probably deposited in only 1-2 million years, by the way) that contain the abundant and diverse molluscan fossils that I collect are part of the Turinian Stage of the Mohawkian Series (North American designation), the Caradoc Series (British terminology still used as a point of common reference), and the Sandbian Stage of the Upper Ordovician Series (global designation). Comprehending the various terms that are used to designate the same rock unit can be overwhelming at first, but when placed on a chart, the hierarchical logic becomes clear, or at least it does to those of us that are true Ordovician geeks.

As stated above, the GOBE occurred in definite pulses of radiations. Although the most intense diversification took place during the Mid (when referring to a time series Mid is used, when referring to a rock series Middle is used) to Late Ordovician (a duration of around 28 million years), taxonomic radiations lasted virtually the entire period (nearly 46 million years). Additionally, the GOBE was taxonomically selective – some groups diversified robustly whereas others experienced only moderate diversification. The first pulse of radiations commenced slowly late in the Early Ordovician

Continued – see Explosions, page 35

Explosion – continued from page 30

then picked up dramatically early in the Mid Ordovician until a plateau in diversity was experienced for the rest of this stage. The second pulse followed this plateau with an even greater rate of diversification during the beginning of the Late Ordovician with peak diversity in the middle of the Late Ordovician. A minor decline in diversity was experienced after this peak. The final pulse occurred near the end of the Late Ordovician when radiations again increased dramatically reaching the highest diversity peak in the entire Ordovician just before the end-Ordovician mass extinction – an event second only to the end-Permian mass extinction in severity. A post-Ordovician recovery initiated a period of relatively stable diversity (the so-called "Paleozoic Plateau"), broken significantly only by the end-Devonian mass extinction, which lasted until the massive end-Permian extinction event.

As with other radiation events described above, a plethora of possible causal factors have been proposed to explain the GOBE. These factors include, but are not limited to, intrinsic biological factors, increased volcanism that resulted in an influx of continental nutrients into the oceans, an areal increase in hard substrata, plate movements, and escalation in the partitioning of marine habitats. Now, in another recent paper, Schmitz and colleagues (2008: 49) suggest an interesting explanation for the onset of the GOBE. The authors claim "that the onset of the major phase of biodiversification ~470 Myr ago coincides with the disruption in the asteroid belt of the L-chondrite parent body – the largest documented asteroid breakup event during the past few billion years." The 470 Ma that they emphasize corresponds approximately to the middle of the first GOBE pulse – specifically, the Mid Ordovician increase in the rate of diversification described above. The asteroid breakup, they say, caused an elevated rate of meteorite bombardment which lasted for 10-30 million years after the initial breakup. Evidence, compiled from sections in Sweden and China, for this event includes rocks enriched with an isotope of osmium commonly found in meteorites, the recovery of unaltered chromite grains with an elemental composition distinct from terrestrial chromite, and the discovery of abundant fragments of the meteorites that were incorporated into the rocks that were laid down at this time. Additionally, from an analysis of impact craters on Earth, it appears that "impacts may have been more common by a factor of 5-10 during the Middle Ordovician compared with other periods of the Phanerozoic" (p. 52). The authors also compiled data on fossil brachiopods contained in rocks of the same age from Baltoscandia and concluded that, for this region at least, the onset of the two events, meteorite bombardment and brachiopod diversification, "seems to coincide precisely" (p. 52). It has been claimed by others, however, that the initial diversification of the GOBE started before the sustained bombardment.

So, how can impacts cause faunal diversifications instead of the extinctions that are popularly presumed to have resulted from them? It turns out that hard evidence for impact-caused extinctions for all but the end-Cretaceous event is tenuous at best. Apparently, there is a size threshold below which impacts disrupt ecosystems but do not initiate mass extinctions. Schmitz and colleagues state that "more minor and persistent impacts could generate diversity by creating a range of new niches across a mosaic of more heterogeneous environments" (p. 52). In other words, the niche partitioning initiated by the numerous impacts resulted in more diverse environments that, in turn, fostered speciation events. Admitting that these conclusions are speculative, the authors maintain that the most reasonable explanation is that numerous and persistent impacts caused modifications in Earth's biota. This cause and effect scenario is an intriguing possibility but has by no means been proven – stay tuned for further developments.

I consider myself fortunate to have been exposed (no pun intended) to Ordovician rocks when growing up. The collecting that I began as a hobby has escalated into a passion for the nautiloid (and other molluscan) fossils contained in these rocks. Little did I know then that I was benefiting from the results of the greatest taxonomic diversification in the history of life on Earth. The nearly 60 species of nautiloids that I have amassed over the years are a testament to this unique event.

Further Reading

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