The Cambrian Explosion and the Origins of Diversity

By Anirudh Penumaka

> *"During the Cambrian 'explosion,' life on Earth underwent a massive surge that created all of the major phyla of organisms that exist even today"*

"There is a grandeur in this view of life." Darwin famously wrote these words about his theory of evolution, and indeed there is something astounding about the idea that change is the only constant of life, mirroring yet also transcending the change we can see in the fleeting length of human lifetimes (1). Over billions of years, and as the result of a calculus we are only beginning to untangle, life evolved from simple, single celled forms into complex organisms, some of which are capable of emotion, thought, and strikingly, consciousness. But this slow march of gradual change by means of natural selection may not be that—a slow march—after all. Evolution may instead proceed through periods of long stagnation, interspersed with periods of incredible and rapid diversification to generate the vastly different organisms that inhabit the Earth today. During these periods of fast evolutionary progress, there is often a linked major environmental change or fundamental modification to the organisms themselves which suddenly open the door for many new forms of life to arise. A specific period of increased evolution, commonly called the Cambrian "explosion," occurred approximately 560 million years ago (2). Life on Earth underwent a massive surge that created all of the major phyla of organisms that exist even today. Life, which had been primarily unicellular, quickly became multicellular, and organisms evolved much more complex morphologies than had previously existed (2).

The Cambrian explosion witnessed the appearance of diverse phyla including those characterized by mineralized skeletons such as Arthropoda, Echinodermata, Mollusca, and Brachiopoda, in addition to phyla made up of soft bodied species such as Annelida, Onycophora, and Priapulida (3). In his book Wonderful Life, Stephen Gould discusses two contrasting theories about the Cambrian explosion. The first, the artifact theory, holds that there were definite Precambrian ancestors to phyla accorded a Cambrian origin; however, by coincidence these ancestors were not preserved in the fossil record, leading us to errantly conclude that there was a period of rapid divergence of life (4). Although, it has been suggested that the Cambrian explosion may artificially appear in the fossil record because of changes in the process or rate of fossilization during this time, this objection does not represent the predominant opinion. The major events of the Cambrian explosion are thought to have occurred over a period of just 20 million years, a very small amount of time in evolutionary terms (2). Fundamental theories explaining the Cambrian explosion fall into the broad categories of changing environmental conditions and far reaching genetic modifications.

▲ **Figure 1.** Artist redering of Cambrian period species.

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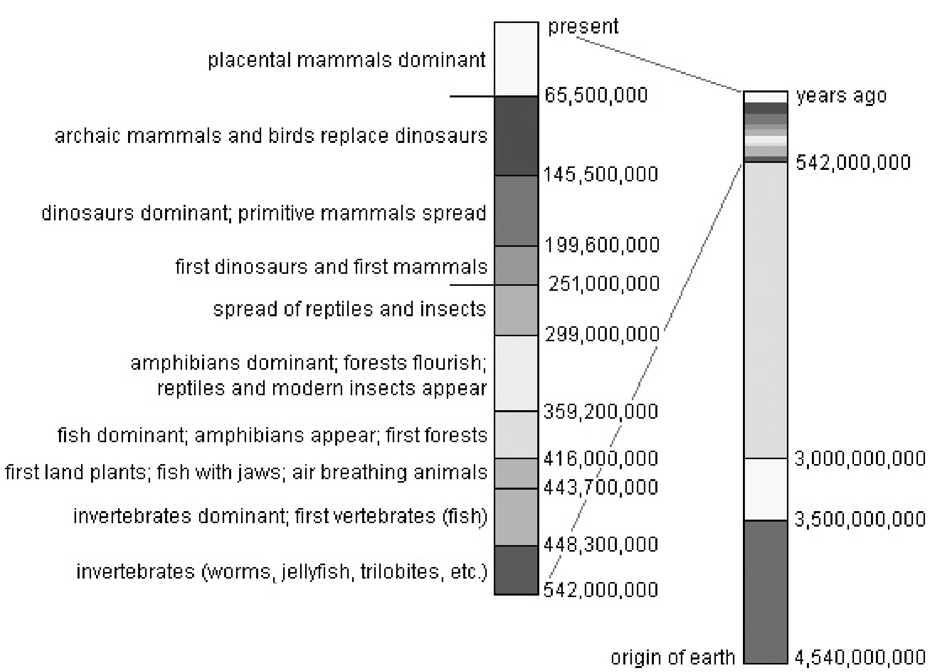
An increase in atmospheric oxygen concentration appears to be a major trend that long preceded the Cambrian explosion. Oxygen first appeared in significant amounts on Earth 2.3 to 3 billion years ago, when various microorganisms released oxygen into the atmosphere. Cyanobacteria greatly contributed to the release of free oxygen in the atmosphere through their photosynthetic processes (5). A second major oxygenation event, which occurred approximately a billion years ago, was a strong driving force that supported the development of complex organisms during the Cambrian era (6). During the past 700 million years, atmospheric oxygen levels have remained relatively stable at the 21% that is observed today (7). The link between rising oxygen levels and complexity is confirmed by a number of events. For instance, oxygen levels rose from 10% to 21% about 425 million years ago, and at this same time, vertebrates evolved and attained many of their essential features (6). Approximately 300 million years ago, a period of higher oxygen content in the atmosphere was associated with an increase in the size of insects (8). Higher amounts of oxygen meant larger body sizes could be achieved without constraints due to the unavailability of oxygen to support tissues, and also allowed for hardened skeletons to develop. A group led by Guy Narbonne published a study in 2007 which asserts that glaciers covered much of the Earth more than 580 million years ago, and thereby prevented the increase in oxygen levels until they began to melt. Narbonne suggests that the melting of these glaciers before the Cambrian released a large amount of nutrients into the oceans (9). The increase in nutrient content allowed small organisms, called phytoplankton, to proliferate; these organisms released oxygen into the atmosphere to raise the atmospheric oxygen concentration (10). A group called the Ediacara biota, which are fossils of soft bodied and complex organisms, initially arose during the period when glaciers were melting, suggesting that the evolution of these more complex forms is closely tied to the oxygenation event. Saltzman *et al.* discuss the fact that during the Cambrian and Ordovician periods, there were separate instances of "plankton and animal diversification" that is referred to as the Great Ordovician Biodiversification Event (7). Authors of this study suggest that the oxygen levels rose in a later part of the Cambrian era, which also had a profound impact on the chemical reactions defining the composition of the oceans and the diversity of marine organisms (7).

One of the major problems with assessing the importance of the oxygen hypothesis is that it is not possible to accurately predict how much oxygen the primitive organisms requiring oxygen actually used. The divergence of prokaryotes and eukaryotes occurred about 1.5 billion years ago, and oxygen may have been important in that very early major transition (6). Indeed, there has been evidence that free oxygen is a driving force for cells to evolve a compartmentalized format. Fluck *et al.* made the important observation that the DNA molecules must reside in the protected confines of the nucleus, away from the high energy reactions and oxidative stress that occur in the mitochondria (11). A consequence of the compartmentalized architecture of eukaryotic cells is that there must be major differences in the reduction-oxidation potentials in the different compartments of the cell. A rapid increase in the levels of oxygen may have placed selection pressure in favor of compartmentalization precisely because of the protection offered by compartmentalization against the effects of a reactive species such as oxygen (11). If oxygen was such a powerful driving force for the transition to eukaryotes, then it is also reasonable to hypothesize that further increases in oxygen levels may have influenced an even greater push toward a multicellular level of complexity. Acquisti *et al.* have suggested that cells need oxygen in order to "maintain novel communication-related transmembrane proteins." A major piece of evidence for this theory comes from the fact that transmembrane proteins tend to contain higher oxygen levels than do other proteins (10). Communication between the compartments of the cells requires specialized transmembrane protein; therefore, the compartmentalized cells required the presence of higher levels of oxygen before they evolved. Just as transmembrane proteins were important for the development of compartmentalization, these proteins also play an important role in the communication between cells in multicellular organisms (10). Therefore, the higher levels of atmospheric oxygen were required for eukaryotes, and eventually multicellular organisms, to evolve.

Furthermore, the complexity of the prevailing organisms appears to be positively correlated with the gradual appearance of an aerobic respiration mechanism (5). Increased levels of atmospheric free oxygen have to be linked to increased "network complexity" that cannot be achieved with anaerobic processes (12). In fact, many scientists claim that oxygen not only facilitated development, but also created an entirely new set of processes that were entirely oxygen dependent. The increased levels of oxygen just prior to the Cambrian era may have led to natural selection acting on the pathways involved in anaerobic respiration to preserve some parts of these pathways and also to forge new pathways that were entirely dependent on oxygen (12). The ability to utilize oxygen was tremendously beneficial to organisms because respiration using oxygen can yield four times the amount of energy as corresponding non-oxygenic pathways. Although oxygen can result in more efficient processes, the side effect of releasing radical oxygen elements had to be addressed (13). Selection eventually remodeled older systems to protect against the effects of oxygen radicals, and these systems passed very early in the history of life to "all three domains of life" (12).

Along with environmental changes, genetic changes in the form of homeotic (Hox) genes may also have been responsible for the sudden expansion of body forms. Homeotic genes are responsible for the basic segment morphology of many organisms, so the expansion of this set of genes meant that a common tool box of body architecture could be modified to produce a broad range of species (14). All of the phyla during the Cambrian period had clusters of Hox genes that contained between four and thirteen individual genes (15). Hox genes are found only in the kingdom Animalia, and most likely arose through repetitive "tandem gene duplication" (16). More specifically, organisms that had segmented body forms had greater numbers of Hox genes. The phyla that emerged during the Cambrian era had "very similar sets of Hox genes," suggesting that Hox genes did not become duplicated during this period (16). The major function of Hox genes is to lay the foundation for the production of more specialized cell types through further downstream signaling cascades, and to place the resulting tissues in the proper orientation. In evolution, acquiring a new function does not necessarily mean the development of genes that are entirely novel, because previously existing genes can simply be co-opted, or duplicated and modified to produce a very different gene with a different function (14). Hox genes are unique to metazoans, and the Hox gene families that arose during this period of time are



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▲ **Figure 2.** Summary of animal life since the end of the Precambrian period.

shared among many types of organisms. It is very possible that the Cambrian explosion occurred as a result of a critical mass of accumulated genetic changes that were suddenly utilized to lead to the rapid divergence of organisms into far more complex organisms (14). Even before the Cambrian explosion, the signaling pathways for basic metazoan body plans may already have been established. Gould and others point to the same line of reasoning. In other words, rather than evolving a separate addition or new gene for each new body pattern or body segment, the pattern of regulatory networks and Hox genes was already in place, and smaller modifications in the regulatory genes and control elements were used to effect changes to the body plans (17). Ohno highlights the fact that, with a liberal assumption of a steady mutation rate of 1 base pair per billion, it would take 10 million years to achieve a 1% change in the genetic material. Considering that the Cambrian explosion occurred in only 20 – 50 million years, this enormous event could not be explained simply by ordinary mutations in specific genes (15). Instead, Ohno suggests that the organisms belonging to even diverse phyla formed during the Cambrian explosion could have "nearly the identical genome" and that the immense variety was actually due to "differential usage of the identical set of genes" (15). For instance, under this scenario, arthropods and vertebrates would have a common ancestor approximately 560 million years ago. Therefore, the common ancestor would have had time to evolve regulatory pathways that provided opportunities for modifications to these pathways for generating "major morphological innovations" (15).

Because there were so many new types of morphological patterns during the Cambrian and it seems unlikely that this could occur simply through an instance of greatly accelerated duplication of Hox genes initiated by some genetic change. Distinct phyla can have different collections of Hox genes, which were modified over time to produce many new body patterns observed during the Cambrian explosion. However, researchers also make the important point that even ancient species, such as the protosome-deuterostome ancestor, had a set of Hox genes. Therefore, simply possessing these genes was not enough "to trigger a metazoan radiation" (17). To produce the radiation, there would also have to have been alterations to the way the Hox genes were put together, as well as in the regulation of Hox gene expression and their downstream signaling pathways (17). The rapid evolution of unique morphologies during the Cambrian era probably involves a number of explanations, yet it is also relevant to explore why this period of evolutionary creativity did not persist for longer. Erwin *et al.* suggest an explanation for why the biological innovation during the Cambrian period eventually came to a stop, rather than continue to create ever more diverse body forms (3). An important point is that the creation of new forms of organisms created a new landscape of predatory, competitive, and indirect interactions that cannot be easily characterized, but that profoundly influenced future evolutionary events. The authors suggest that available ecological niches may have become filled, meaning that even when new forms developed, they could not become established because the ecosystems already reached their ecological limits. A more subtle explanation is that the complexity and interdependency of pathways and regulatory mechanisms had evolved to a point where major modifications could no longer take place without being maladaptive in a larger sense (3).

The two major prevailing theories regarding the Cambrian explosion are not mutually exclusive; in fact, it may have been the case that both rising oxygen levels and fundamental genetic changes nurtured an environment that set the stage for the Cambrian explosion to occur. Sixty years ago, scientists could not say with any certainty what caused the dinosaurs to become extinct. Ingenious techniques involving observations of iridium in the geological record led to the theory of a cataclysmic asteroid impact to explain the demise of dinosaurs 65 million years ago. It appears that understanding of the Cambrian explosion is at a similar stage, where there are many lines of evidence, conjecture, and theory, but, unlike the single explanation of an asteroid impact, the Cambrian explosion may be an emergent property of the many simultaneous changes taking place at the time. It is often said that species alive today are only a small fraction of the species that once lived, and there is perhaps no greater testament to the power of evolution that even with such destruction, nature still bursts with diversity and prolific creativity. Understanding the Cambrian explosion retains great importance because the basis of many of our archetypal beliefs and sense of awe about the beauty of living things was conceived during this time. In our attempt to search back through the tree of life to divine those still mysterious events that influenced life, we also search for our own origins and our own evolution. H

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