

Cambrian Explosion of Life: the *Big Bang* in Metazoan Evolution

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Despite the protracted history of life on earth spanning well over 3.8 Ga, fossil record of the Precambrian (> 543 Ma) largely documents only microscopic life. The mostly simple Precambrian life forms were followed by a sudden explosive radiation of multicellular animals at the turn of the Cambrian period (543-490 Ma) between 530 and 520 Ma ago, when almost two-thirds of the animal phyla make their dramatic appearance in the fossil record. This unusual and amazing burst of macroevolutionary change is called the Cambrian explosion.

In all probability life originated on earth ~ 4 Ga ago (Giga annum = 10^9 years; see Sukumaran, *Resonance*: October and November 2001). Despite this long history, multicellular life (the terms *metazoans*, *multicellular animals* and *animals* are synonymous) appears first in the fossil record (see *Box 1*) only between 530 and 520 Ma (Mega annum = 10^6 years), after a gap of nearly 3.5 Ga since the origin of life. Amazingly, when they arrived, they arrived in profusion and geologically very abruptly. The sudden and explosive diversification of life forms at the early Cambrian period as documented in the fossil record is called the Cambrian explosion. Palaeontologists, evolutionary biologists and geneticists hotly debate the causes of this extraordinary event in the evolutionary history of life.

Recent advances in genetics and molecular biology have shed new light on genetic controls of body plan development (see *Box 2*) in metazoan phyla. New fossil discoveries and molecular techniques (see *Box 3*) have also brought in controversies: do the metazoans have deep evolutionary roots in the Precambrian or do the palaeontological data confirm a major evolutionary mile-

Keywords

Fossils, evolution, macro-evolution, development.



Box 1. The Fossil Record and Evolution

The particles of gravel, sand and mud, which are collectively called sediment, are transported by flowing water and glaciers and eventually settle in layers at the bottoms of rivers, lakes and oceans. Shells and other remains of life also settle along with these sediments. As the sediments accumulate they bury shells, bones, leaves, pollen, and other bits and pieces of living things. With the passage of time, the layers of sediments are compacted by the weight of overlying sediments and cemented together to become sedimentary rocks like shale, limestone and sandstone. The buried remains of life become fossils. Successive rock layers contain different groups or assemblages of fossil species. By studying the fossils present in the oldest sedimentary rocks to the present it is possible to get a crude idea of the progression of life through the ages and thus the trend in evolution.

post in the early Cambrian? Besides, molecular evidence shows that regulatory genes that control development of morphology in animals are fairly similar in all phyla, but give rise to very disparate body plans. These advances are providing new lines of evidence to look into the origin of metazoans and thereby into the mystery of the Cambrian explosion.

Darwin's Dilemma

According to Darwin's theory of evolution (*Box 4*), species evolved from simple to complex forms largely through natural selection. During Darwin's time fossils older than the Cambrian were little known and it was generally believed that life itself originated in the early Cambrian. Subsequent fossil discoveries threw considerable light on life prior to the Cambrian confirming the continuous presence of life on earth right from its advent

Box 2. Animal Body Plans

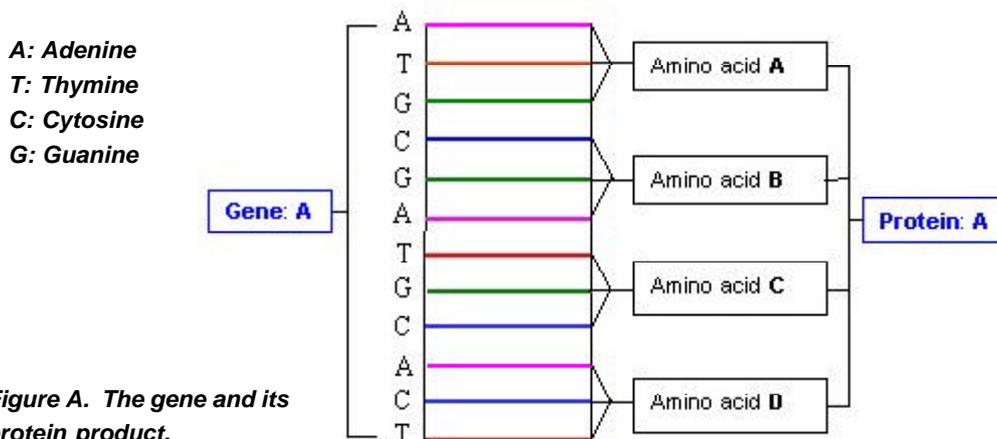
All members of the kingdom *Animalia* show distinct architecture on which their body is built. It is based on this architecture (also called body plan or bauplan) that the *Animalia* is divided into different Phyla, each Phylum characterized by a unique body plan. Phylum represents the highest biological category in the kingdom *Animalia*. The major body plans are: cell aggregate body plan (corals and jelly fish), body sac plan (coelenterates and flatworms) and tube-within-a-tube plan (crustaceans, insects, trilobites and vertebrates).



Box 3. Molecular Dating

According to the *neutral theory* of molecular evolution postulated by Motoo Kimura most of the nucleotide substitutions in genes arising out of mutation are selectively neutral or of little functional consequence to the organisms. This theory was slightly modified later to accommodate the observation that most molecular evolution involves slightly deleterious substitutions rather than strictly neutral ones.

The molecular data consist of long sequences of nucleotide bases in the nucleic acids that make up the genetic text in DNA. Segments of nucleotide sequences that code for a particular protein are called genes (Figure A). While genes are nucleotide sequences, their protein products are amino acid sequences. Mutations in genes produce variations in proteins. For instance, the protein haemoglobin is present in many species of animals and its function is to carry oxygen from the lungs to various parts of the body through the blood. But the amino acid sequence of haemoglobin is not the same in all species. The difference is due to mutation and is a measure of the time elapsed since the species separated from a common ancestor in the course of evolution. This method of inferring the divergence time of clades from a common ancestor by means of gene/protein sequencing is called *molecular dating*. The time is calibrated against well-dated fossil data of Phanerozoic era, which is then extrapolated to estimate the time divergence of phyla.



4 Ga ago. The abrupt appearance of diversified life at the beginning of the Cambrian period was not explainable if life evolved gradually as envisaged by Darwin, under the influence of the geologist Lyell. Gradualism, of course, is not central to the notion that life forms evolve largely through natural selection, and Darwin's friend T H Huxley had argued that Darwin should drop his insistence on evolutionary change being gradual.

Darwin had no answer to this puzzle and he was hopeful that future explorations would unearth evidence for the continuity of life and eventually solve the problem of Cambrian explosion. However, despite over 150 years of exploration since Darwin, the mystery remains.

The Earliest Metazoans

The Cambrian life was totally unlike that of the Precambrian (*Figure 1*). Single-celled microbes ruled the earth almost in the entire Precambrian and fossil remains of single-celled organisms occur in the oldest sediments dated 3.5 Ga. Metazoan fossils predating the Cambrian explosion are not totally rare. Among the earliest signs of metazoans are small circular discs from northwestern Canada that date from 610 to 590 Ma. Trace fossils in the form of animal trails and markings are described from rocks as old as 600 Ma and these constitute the unequivocal palaeontological evidence for earliest metazoan life. The earliest known shelly (with a protective outer shell) metazoan fossils are simple tube-like structures called

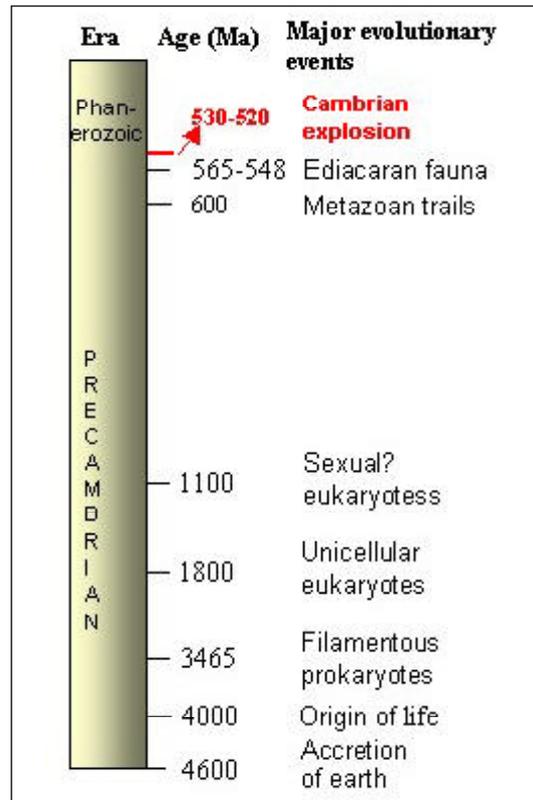


Figure 1. Major events in the history of life.

Box 4. Darwinism, Natural Selection and Neo-Darwinism

According to Darwin's classical theory of evolution (*Darwinism*), life evolved from simple to complex forms largely through natural selection, a process by which variants better able to survive and reproduce in a given environment become more common in a population over generations. Following the advances in classical genetics in the early 20th century, genetics and the theory of natural selection were welded together into what is often called the Neo-Darwinian Synthesis in the 1940's and 50's. In this view, the ultimate source of new genic variation is mutation, although in sexually reproducing organisms, genetic recombination in itself produces numerous variants in each generation. The Neo-Darwinian synthesis provides an adequate explanation for micro-evolutionary change i.e. changes over generations by which a population of a species adapts to its environment. What has remained controversial is whether micro-evolutionary changes are sufficient to explain – in the long term – changes at the macro-evolutionary level i.e. the evolution of new species or higher taxonomic groups. (For a more detailed description of some of these concepts see *Resonance*, Vol.7, No.11, pp.8-17, 2002 and Vol.8, No.2, pp.6-18, 2003).



Box 5. Trace Fossil Evidence from India

While the timing of metazoan divergence remains controversial, the discovery of suspected metazoan trace fossils from central India has added a new dimension to the controversy. Seilacher and group (1998) have reported fossil markings from Precambrian sandstones of central India that have been interpreted as burrows excavated by metazoans. Because these sandstones were thought to be older than 1000 Ma, these markings were regarded as the oldest fossil evidence of metazoan life. If these are really metazoan tracks, this discovery pushes back the origin of multicellular animals to well beyond 1100 Ma, almost doubling the time span of the metazoan fossil record. The controversy deepened further with the report by Rasmussen and coworkers (2002) that this sandstone was deposited 1.6 Ga ago indicating that complex animals probably evolved a full 1Ga before the Cambrian explosion.

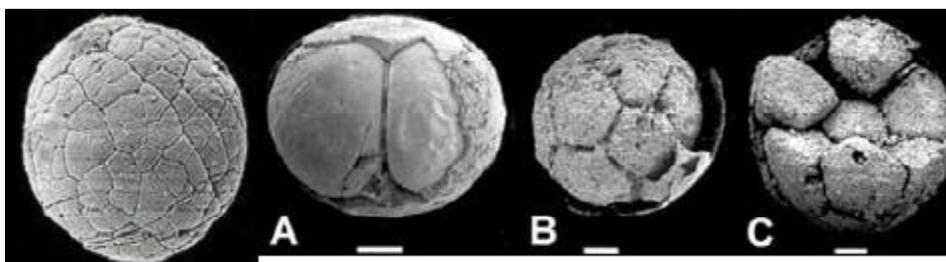
cloudinids that first appear near the end of Precambrian. This was followed by more frequent appearance of shelly fauna at the base of Cambrian. There have been numerous reports of still older animal fossils but none of them is yet confirmed (Box 5). The ediacaran fossils believed to represent the earliest metazoans are still very enigmatic. Chinese palaeontologists have recently unearthed remarkably preserved metazoan eggs and embryos (Figure 2) from the Yunnan province. These embryos dated at 570 Ma are the earliest unequivocally recognized metazoan body fossils known.

Salient Features of the Cambrian Explosion

Figure 2. Fossil embryos showing different stages of early cleavage.

(*Development*, Vol.126, pp.851-859, 1999; Reproduced with permission from The Company of Biologists Ltd.)

The animals of the Cambrian explosion represent unusual evolutionary mileposts. The explosion commenced around 530 Ma ago and ended around 520 Ma ago. The 10 Ma interval was marked by abundant mineralized hard parts (composed chiefly of CaCO_3) in the fossil record. Several phyla level organisms appeared in relatively rapid geologic succession during this



interval and when the explosion ended almost all known animal phyla were represented. Geologically speaking, 5 to 10 Ma is an exceedingly short window of time, just the blink of the eye. What is baffling is that almost all major innovations in the basic body architecture of living metazoans occurred within such a short span of time. To denote the suddenness of appearance of animal life at this time, the Cambrian explosion has also been nicknamed as *biological big bang*, *big bang of animal evolution* or *evolution's big bang* in analogy with the big bang by which the universe came into being.

The Cambrian animals encompass 2/3 of the phyla of kingdom Animalia. About 37 phyla are recognized among present day animals, and almost all of them were established by the close of the Cambrian explosion, including all shelled invertebrates like mollusca, echinodermata and arthropoda (*Figure 3*). Thus, the evolution of major life forms as represented in the fossil record is not a gradual one: there was very little diversification of basic body plan in the Precambrian, but a sudden burst at the early Cambrian.

Another remarkable feature of the Cambrian explosion is the morphological *disparity* and evolutionary *stasis* displayed by Cambrian fauna. We must differentiate between *diversity* and *disparity* among animals. Diversity refers to small-scale differences that are evident at the species level, whereas large-scale morphological differences among animals evident at taxonomically higher levels than species are generally referred to as *disparity*. Though the animals of the Cambrian explosion fall within about 37 basic body plans, each of these body plans exhibit clear morphological differences or disparity from the others. The body plans defining each phylum do not grade into one another over the course of geological history but maintain their morphological isolation or disparity from all other phyla. In addition, instead of diversity grading into disparity, disparity precedes diversity in the fossil record, which is not expected if life-forms evolved gradually from one another. They also exhibit a remarkable stability or stasis during their time on earth,



Figure 3. A typical Cambrian trilobite fossil.

(*Geology*, Vol.31, No.12, cover page, 2003; Reproduced with permission from Robert R Gaines)

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meaning that after their appearance they maintained their characteristic body architecture without any evidences of alteration.

Yet another feature of the Cambrian explosion is the quantum jump in biological complexity. The biosphere in the entire Precambrian comprised little more than unicellular cyanobacteria. Compared to the small increase in complexity that occurred between the origin of life ~ 3.85 Ga ago and the first appearance of multicellular algae (1 Ga ago), the Cambrian explosion is a huge increase in biological complexity. A rough measure of biological complexity of animals is the number of cell types they have. The early Cambrian animals had roughly 50 cell types while the sponges that appeared a little earlier had only 5.

Was the Cambrian Explosion Real?

A few biologists advocating the narrow gradualistic version of Darwinism have argued that the absence of Precambrian transitional forms merely indicates the incompleteness of the fossil record, that is, intermediate forms did exist but somehow were not fossilised. Unfortunately in spite of the earnest efforts by palaeontologists the missing ancestors of the Cambrian fossils were never found. This led several biologists to propose the artifact theory, which held that the missing ancestors existed, but for various reasons were not fossilised and preserved in the fossil record.

It is well known that animals with a shelled exoskeleton stand a better chance of fossilization than the soft-bodied animals. Advocates of the artifact theory therefore presume that the Precambrian animals lacked hard parts necessary for fossilisation. This is not always true. Soft-bodied fauna are abundant in the fossil record of the Cambrian and representatives of several phyla are exclusively soft-bodied. The lower Cambrian sediments near Chengjiang, China have preserved soft tissues and several organs such as eyes, stomachs, digestive glands, sensory organs and nerves, besides fossilized embryos. These observations shake the very foundations of the artifact theory. Others have ex-



plained the absence of transitional organisms as the result of their small shell size. However, fossils of filamentous algae (cyanobacteria) have been documented in Western Australia from rocks as old as 3.3 to 3.5 Ga. Besides, 2.7 Ga old species of single-celled algae and cells with nucleus have also been well documented in the fossil record as also embryos at different stages of cell division (*Figure 2*). The consensus among evolutionary biologists today is that the Cambrian explosion is indeed real.

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The Ediacaran Fauna

The Ediacaran fauna (565 to 548 Ma) is a distinctive group of large and soft-bodied organisms, fossils of which have been discovered from around the world suggesting that they once had global distribution during the Vendian period (650-544 Ma). They are, by and large, only fossil markings and not truly fossilised organisms. The ediacarans are enigmatic fossils that have no living representatives but appear as remains of multicellular organisms. A few biologists are of the opinion that the ediacaran fauna might represent transitional intermediates to the Cambrian animals. Seilacher (1992) considered them as an altogether different group unrelated to any extinct or extant fauna and named them as 'Vendobionta'. According to Narbonne (1998) ediacarans represent a failed experiment in the evolution of life. The ediacaran fossils appear to bear no clear relationships to any of the organisms in the Cambrian explosion. Although the soft-bodied ediacarans appear like animals, their classification is hotly debated and their metazoan status is still unclear.

Moreover, the ediacarans comprise only three or four phyla and do not represent the whole range of expected intermediate ancestors to the Cambrian fauna. Further, while the animals of the Cambrian explosion encompass at least twenty eight phyla, the ediacaran organisms represent at best four phyla that leave 90% of the Cambrian phyla with no ancestors in the Precambrian. Finally, even if the ediacaran animals are considered as harbingers of the Cambrian explosion, the total time encom-



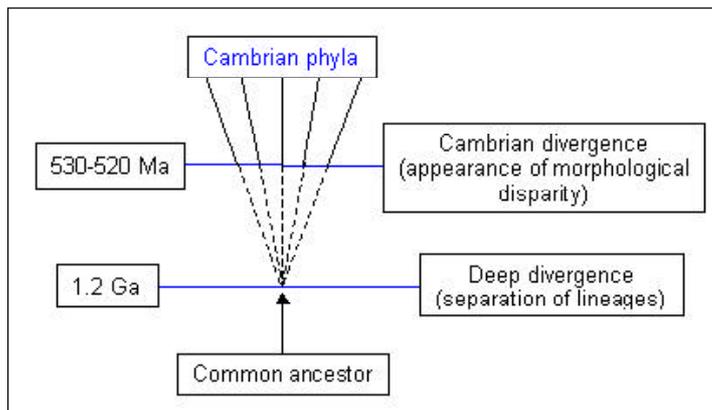


Figure 4. The deep divergence of Cambrian animals.

evolutionary history in the Precambrian, not reflected in the fossil record? Recent molecular data (Box 3; Figure 4) are in support of such a claim that questions the explosive nature of the Cambrian radiation. The protein sequencing data of Wray *et al.* (1996) provide compelling evidence for a common ancestor of the Cambrian phyla dating from 1.2 Ga ago, nearly 700 Ma before the Cambrian explosion! Wray *et al.* suggest that the metazoan phyla diverged from a common ancestor 1.2 Ga ago and underwent a cryptic evolution until the Cambrian explosion. The absence of missing ancestors is then accounted using the artifact theory.

However, the deep divergence hypothesis has several shortcomings: Firstly an extensive period of soft-bodied evolution is questionable from palaeontological point of view. Preservation of numerous soft-bodied Cambrian animals as well as Precambrian embryos and microorganisms undermines the deep divergence hypothesis. Secondly subsequent molecular estimates by Ayala and colleagues (1998) are in agreement with palaeontological evidence, questioning the deep divergence hypothesis. Further, the proteins that Wray and colleagues have analysed are not involved in the development of animal body plans and therefore they would not have played any role in the origin of new phyla. Another major problem with the deep divergence hypothesis is that the protein clock does not tick at a constant rate. Unlike radiometric clocks widely used in dating rocks, molecular clocks depend upon both biological and environmental factors. For

passed by the Vendian and Cambrian radiations together is still exceedingly brief (~ 45 Ma: from 565 to 520 Ma) and therefore would still constitute a relatively sudden event.

The Deep Divergence

Could it be possible that the metazoans had an invisible



instance, different genes in different clades evolve at different rates. Above all the molecular clock is calibrated with Phanerozoic (< 550 Ma) fossil record that may not be reliable in dating the origin of the much older (1 to 1.2 Ga old) animal phyla.

Proponents of the deep divergence hypothesis emphasize that molecular data only document the time of divergence of lineages while palaeontological data record the divergence of morphological form. Morphological and genetic changes need not necessarily be correlated over evolutionary time. The morphological expression and therefore preservation of organisms as fossils occurs millions of years after lineages diverge; there may be long gaps between separations of sister groups from a common ancestor and manifestation of their morphological disparity (*Figure 4*) as fossils.

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Mystery of the Cambrian explosion: View from Modern Genetics

Unicellular life is relatively simple; there is little division of labour and the single cell performs all functions of life. Obviously the genetic information content of unicellular organisms is relatively meagre. Multicellular life, on the other hand, requires more genetic information to carry out myriads of cellular functions as their cells are differentiated into different cell types, tissues and organs. But new cell types themselves require specialised proteins, and novel proteins arise from novel gene sequences, that is new genetic information. As the organisms that appeared in the Cambrian explosion had many more novel and specialised cell types than their prokaryotic ancestors, the amount of new genetic information that arose in the Cambrian explosion represents a large increase in biological information.

In metazoans, cell differentiation from simple to multiple cell types is controlled by genetic mechanisms. It is now understood that cells differentiate from master cells called stem cells present in embryos (embryonic stem cells). It is this cell differentiation that led to evolution of various body plan architecture in the



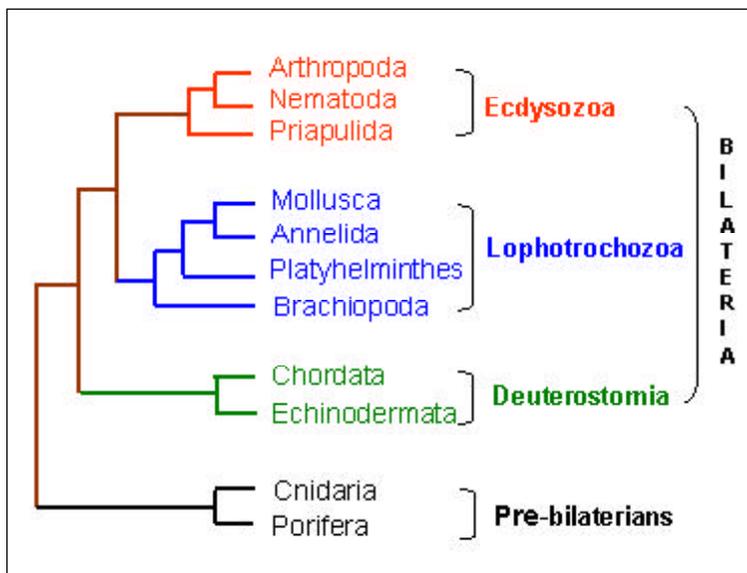
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Cambrian explosion. Now the question is were there genetic controls in early eukaryotic cells for cell differentiation. Many different classes of regulatory genes are present in metazoans that are responsible for their body architecture. A set of such regulatory genes called *Hox* genes occur in clusters in DNA segments of metazoans. These genes are best known for their roles in determining developmental patterns in model biological systems such as the fruit fly *Drosophila* and the nematode worm *Caenorhabditis*. It appears that *Hox* genes are widely and probably universally distributed in metazoan phyla. Molecular data confirm that these regulatory genes were already in place before the Cambrian explosion.

What Triggered the Cambrian Explosion?

Several factors must have collectively contributed to the Cambrian explosion. The role played by regulatory genes, like the *Hox* genes for example, are crucial. New metazoan phylogenies (Figure 5) reconstructed from gene sequencing suggest that much of the basic gene regulatory machinery required for their body plan development was in place significantly before the Cambrian explosion.

Figure 5. The metazoan evolutionary tree.



The Cambrian explosion of animals occurred soon after late Proterozoic snowball earth event (Hoffman and others 1998; also see Sukumaran, *Resonance*, December 2003) roughly 600 Ma ago. Extreme climatic events have catastrophic effect on the biosphere. All forms of eukaryotic life would have perished under the climatic stress of a global ice cover. The conge-nial habitats created on the



earth by the disappearance of global ice cover are believed to have facilitated the explosive radiation of multicellular life in the early Cambrian.

Events like the increase in molecular oxygen may also have been crucial. Giant fossil insects (dragon flies with wing spans of 70 cm) are common in coal beds deposited during the Permo-Carboniferous times (~ 300 Ma) and insect gigantism has been correlated with increase in atmospheric oxygen to 35% at that time. Geological evidence also attests to late Proterozoic increase in atmospheric oxygen levels. This event could have favoured the rise of metazoans because all metazoans require molecular oxygen for respiration as also to build the structural protein called collagen that all metazoans have.

The period from 2 Ga to 1 Ga in earth history was very sluggish in terms of organic evolution. All life that existed on earth during this time consisted largely of cyanobacteria. Molecular oxygen appeared only by 2.2 Ga and, in the absence of oxygen, the primordial ocean was oxygen-free and iron-rich; in comparison the modern ocean from about the late Precambrian is oxygen-rich and iron-poor. The ocean during the intervening period was neither like the primordial one nor like the modern. Canfield (1998) suggested that the ocean during this interval was largely oxygen-deficient below the uppermost waters. Newly oxygenated atmosphere weathered large amounts of sulphur into the sea, where it reacted with dissolved iron and precipitated as sulphides. Along with iron other nutrient metals like Mo, Cu, Zn, V and Cd were also removed. In the absence of these nutrients eukaryotic algae could not fix nitrogen to nitrates because the enzymes responsible for nitrogen fixation require iron and other metals. According to Anbar and Knoll (2002) such a situation leading to nutritional deficiency of the ocean was responsible for low ocean productivity and evolutionary hiatus during 2 Ga to 1 Ga ago. By the end of the Precambrian, however, oxygen had grown to almost present atmospheric levels, the oceans had become more ventilated with oxygen and sulphate concentration had also become more modern-like re-

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It is clear from the above account that many questions remain about this early radiation of animal groups. Why did animals suddenly develop mineralized skeletons that facilitated their preservation in the rock record? Does the Cambrian explosion really represent an evolutionary event or merely a mineralisation event? The puzzle of the Cambrian explosion poses a major challenge to evolutionary biologists. Some of the answers may come from the young field of evolutionary developmental biology (evo-devo) which seeks to understand how ontogenies themselves evolve.

Suggested Reading

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