

Author's Statement: "This research paper dives into the theories that work to piece together the causes of the diversification of life during the Cambrian Explosion (540 million years ago). The main theory discussed in this paper relates to how oxygen levels in the ocean could have affected the diversity of life. My main goal is to argue that although oxygen played an important role in the diversification of life, higher oxygen levels wasn't the sole cause of the Cambrian Explosion."

Was Oxygen the Only Player in the Cambrian Explosion?

Introduction

Today life is diverse and full of complex structures, but it was not always this way. Before the Cambrian time period, during the Ediacaran, life was relatively simple. There were mats of unicellular bacteria that coated the ocean floor, and there were also multicellular organisms which were mainly soft-bodied organisms, like Dickinsonia (Fox, 2016). So when did life develop into the complex multicellular animals with nervous systems, skeletons, eyes, and gene regulation seen today? In the early Cambrian, around 540 million years ago, an explosion of diversity and complexity occurred, and more diverse and mobile forms of life started to appear (Wood, 2019). This event is called the Cambrian explosion, which was a punctual burst of evolution of marine animal life (Fox, 2016). Fossils from around 540 million years ago (Ma) indicate organisms with more complex behaviors that had shells, skeletons, and nervous systems. Examples of the complex behaviors exhibited by animals during the Cambrian explosion include burrowing in the sediment, swimming in the water column, and preying on other organisms (Fox, 2016).

But what caused the Cambrian explosion? Why didn't it happen earlier? There are many theories that have tried to answer these questions. One common theory states that increases in oxygen levels allowed for life to diversify and increase in complexity, but the oxygen theory has been highly debated (Wood, 2020). Over the years, studies of oxygen levels during the early Cambrian and the present day environment have led scientists to think that oxygen may have

played one of the key roles in triggering the Cambrian explosion; however, it is unlikely that oxygen was the only factor.

Oxygen

Many diverse animals—animals with skeletons, eye spots, protective shells, and the ability to move both along the seafloor and in the water column—appear in the fossil record during the Cambrian explosion. Biomineralization of protective shells, development of nervous systems, and use of specialized muscles all require a substantial amount of energy (Fox, 2016). In order for animals to power these more complex structures, they metabolize oxygen. The energy released from the metabolic process using oxygen supports the high demand of energy required to keep complex animals functioning (Fox, 2016).

All animals need oxygen to survive, even the most simple animals like sponges and Dickinsonia. Animals need oxygen for the metabolic process that occurs in a mitochondria to produce energy (Fox, 2016). In addition to the metabolic processes, animals also need oxygen because it is required in the production of steroid lipids called sterols, which are a major component of the cell membrane's structure (Runnegar, 2003; Dufourc, 2008). Sterols have been found within fossils of Dickinsonia, suggesting that Precambrian Dickinsonia were animals that were able to absorb oxygen and use it to produce sterols (Runnegar, 2003). Although the minimum oxygen level required to produce a sterol is unknown, finding sterols in Precambrian life forms supports that the use of oxygen is deeply rooted into the evolution of animals (Runnegar, 2003).



Figure 1 (left). An illustration of what the Cambrian explosion could have looked like. There are organisms swimming in the water column, burrowing under the sediment, and crawling along the seafloor. This illustration captures the diversity and the complexity of life (Fox, 2016).

Then the next question is *did the presence of oxygen enable organisms to increase in complexity?* Runnearer (2003) referenced Robinson et al. (1983) in a study about the possible relationship between metabolic rate and body size. Robinson et al. (1983) suggest that the metabolic rate and body size are generally proportional. So, when the body size is larger the metabolic rate is higher, meaning that the larger the body size, the more oxygen that is consumed by the metabolic processes (Runnearer, 2003). The fact that larger organisms require more oxygen suggests that larger, more complex Cambrian organisms could not have evolved without the presence of oxygen (Fox, 2016). If we look at modern-day environments with low oxygen levels, biodiversity in those areas is limited to soft-bodied organisms with low complexity. Modern-day environments with high oxygen levels, however, tend to have more biodiversity and complex organisms (Wood, 2019). Although it may seem simplistic to compare current day life to prehistoric life, it still is a good starting point since some organisms from the Cambrian are the ancestors of modern-day organisms (Budd, 2013).

Although animals need oxygen, it is questionable what the oxygen levels were during the Cambrian explosion. So, scientists collected rocks from sea beds formed during the Cambrian period and studied the rocks through chemical analysis. By analyzing the quantity of the different types of metals and different isotopes in the sediment, researchers were able to estimate the oxygen levels in the ocean at the time the sediment formed (Fox, 2016; Wood, 2020).

One set of indicators that can be used indirectly to estimate oxygen levels over Earth's history involves carbon and its stable isotopes (Time Scavengers, 2017). Carbon-12 (^{12}C) is the most abundant form of carbon, with six protons and six neutrons. Carbon-13 (^{13}C) is another one of carbon's isotopes, and is composed of six protons and seven neutrons. ^{13}C is significantly less common than ^{12}C (Time Scavengers, 2017). Researchers use the ratio $^{13}\text{C}/^{12}\text{C}$ to chemically compare rocks and fossils from the same and different time periods (US Department of Commerce, 2005). Since living organisms preferentially use ^{12}C for photosynthesis instead of ^{13}C , the ratio of ^{13}C to ^{12}C increases in surrounding water where photosynthesis is occurring. With this higher ratio of ^{13}C to ^{12}C in the water, organisms living in the water reflect ^{13}C to ^{12}C ratio in their skeletons. When the organisms die their skeletons are buried in the sediment and the ^{13}C to ^{12}C ratio is preserved in time (Time Scavengers, 2017). Researchers, then, are able to test

fossils from the Cambrian time period to see what the ^{13}C to ^{12}C ratio was, and compare it to the standard ^{13}C to ^{12}C ratio. When comparing the ^{13}C to ^{12}C ratio in the fossil sample to the standard ^{13}C to ^{12}C ratio, researchers produce a value called $\delta^{13}\text{C}$ (US Department of Commerce, 2005).

The value $\delta^{13}\text{C}$ in fossils is helpful in estimating oceanic oxygen levels. When the $\delta^{13}\text{C}$ value in the fossil sample is larger, that means more ^{12}C was taken up in photosynthesis to form organic matter and buried in the sediment. As a result of more ^{12}C being incorporated into organic molecules during photosynthesis, oxygen is released as a by-product of oxygenic photosynthesis. If the organic matter is buried and not oxidized, that oxygen remains in the atmosphere (He, 2019).

$$\delta = \left[\frac{\left[\frac{^{13}\text{C}}{^{12}\text{C}} \right]_{\text{sample}}}{\left[\frac{^{13}\text{C}}{^{12}\text{C}} \right]_{\text{standard}}} - 1 \right] \times 1000$$

Figure 2 (left) is the equation used to calculate the $\delta^{13}\text{C}$ value.

The numerator is the ^{13}C to ^{12}C ratio in the sample rock, and the denominator is the ^{13}C to ^{12}C ratio in the standard. After subtracting one, the value is multiplied by 1000 to make the differences between values more noticeable (US Department of Commerce, 2005).

In addition to the $\delta^{13}\text{C}$ values, $\delta^{34}\text{S}$ values were also used to help predict the oxygen production (OP). Figure 3 shows the values of $\delta^{13}\text{C}$, $\delta^{34}\text{S}$, estimated oxygen production, and the number of animal species over the Cambrian stages 2 and 3. During Cambrian stages 2 and 3, there were increases in oxygen production at around 514.3 Ma (VII OP), 515 Ma (VI OP), 516.3 Ma (V OP), 520 Ma (IV OP), and 522.5 Ma (III OP)(He, 2019). Each of these peaks in oxygen production appears to correlate with an increase in animal species (He, 2019). This correlation between oxygen production and the number of animal species does not prove, but supports, the argument that oxygen could be a potential stimulant for the Cambrian explosion. Equally as important to the peaks of oxygen production corresponding with higher numbers of animal species, is the fact that the lower points of oxygen production also correspond with lower numbers in animal species (He, 2019). Generally, then, it is unlikely that an explosion in diversity could have occurred without an increase in oxygenation.

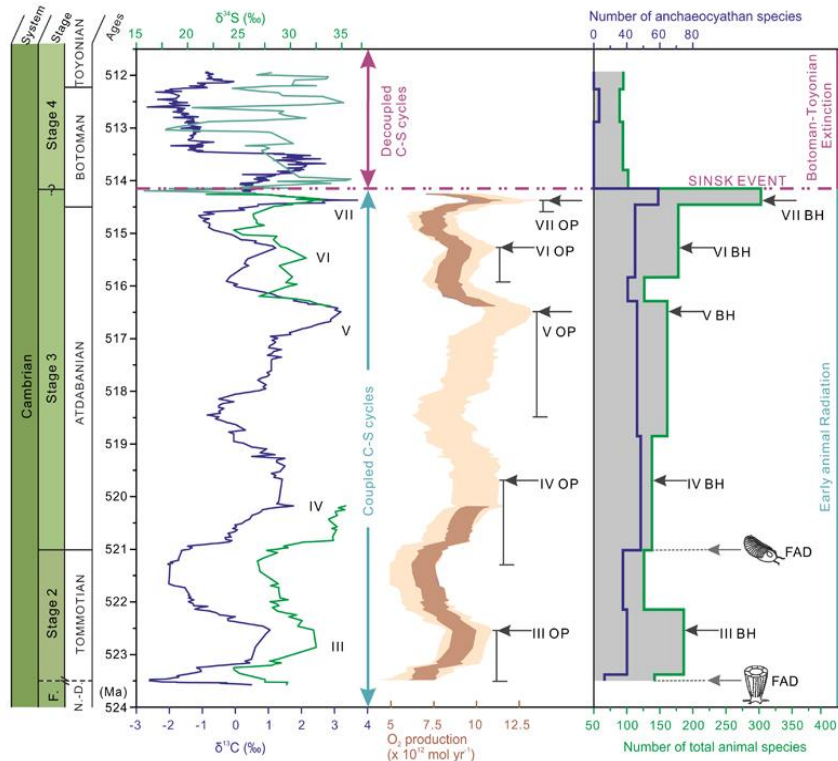


Figure 3 (above). Represents the possible association between $\delta^{13}\text{C}$ (dark blue line on the left), $\delta^{34}\text{S}$ (green line on the left), estimated oxygen production (shaded tan region in the middle), and the number of animal species (grey box on the right). Along the left hand side is the time period, Cambrian stages, and the years (by millions) (He, 2019).

Why Oxygen Was not the Only Player

In order to see if oxygen played a role during the Cambrian explosion, researchers are trying to figure out what the oxygen levels have been at different points in time. Oxygen levels during the Cambrian are continually debated because various metals and isotopes suggest slight differences in timing of oxygenation events (Fox, 2016). With variation between the different metal indicators and isotopes it is hard to tell when the oxygenation events occurred, and whether one coordinated with the Cambrian explosion or not (Wood, 2019).

Erik Sperling also conducted a study on the late Ediacaran and early Cambrian oxygen levels. It was previously thought that there was a large oxygenation event around the same time as the Ediacaran-Cambrian boundary, leading up to the Cambrian Explosion, but Erik Sperling challenged that theory. Sperling took rock samples from both the Ediacaran and Cambrian time

periods. After studying the iron levels in each of the samples, he revealed that the oxygenation event was perhaps not as significant as was originally thought (Sperling, 2015). Instead, the oxygen levels of the oceans are believed to have oscillated between oxic and anoxic states, and gradually leveled off in the Devonian period (Wood, 2019). Some scientists are puzzled by the fact that marine life continued, and potentially diversified, despite oscillating oxygen levels (Wood, 2020).

Also, in trying to identify a single oxygenation level for a time period, the variations in environments on a local scale are muted. As seen in Figure 4, locations like the Yangtze Block have zones with anoxia, but then the Nama Group has oxygenated water that supports the growth of benthic Transgressive Pinnacle reefs (Wood, 2020). There also could have been an “oxygen oasis,” which is when a bacterial mat on the seafloor produces enough oxygen to oxygenate the surrounding area. In and around oxygen oases, organisms could use the produced oxygen to survive in generally anoxic environments (Olson, 2013). Overall, the variations in oxygen levels in local environments makes it difficult to figure out whether oxygen levels were significant enough to stimulate the Cambrian explosion, leaving researchers questioning whether oxygen alone stimulated the Cambrian explosion, or if there were other factors involved (Wood, 2020).

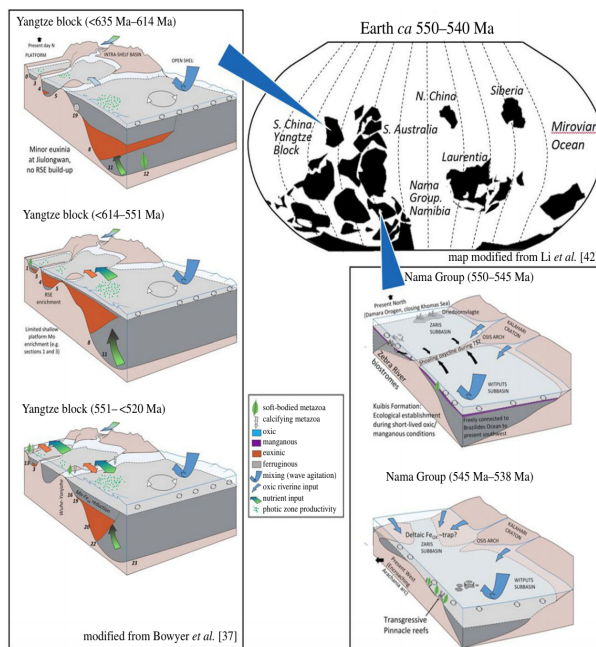


Figure 4 (Left). A diagram showing how there can be differences in local benthic marine environments. The Yangtze block (left) has a photic productivity at the surface and some shallow oxygenated zones with soft-bodied metazoa and calcifying metazoz. In the deeper regions of the Yangtze there are euxinic conditions (orange) with no oxygen and high in sulfides. The Nama Group (right) with well-mixed oxygenated waters that support reefs (Wood, 2020).

If Not Only Oxygen? Then What Else?

Since oxygen levels may have not been significant enough to be the sole cause of the Cambrian explosion (Fox, 2016), scientists have proposed theories about nutrient availability,

evolutionary innovation, and predation, which all could have helped stimulate the Cambrian explosion.

Nutrient Availability

One theory that is tied to the cause of the Cambrian Explosion is nutrient availability. In order for life to grow and develop it needs phosphorus. Phosphorus does not naturally occur in oceans, and can only enter the ocean through weathering and erosion (Planavsky, 2010). Before the Cambrian, there was an event called Snowball Earth. Snowball Earth was when all the continents and oceans were covered in ice and glaciers. When the glaciers melted, they deposited sediments and nutrients into the ocean that had been picked up as they crawled over the continent. Sediments from the glaciers could have had high concentrations of phosphorus, so when the glaciers deposited them into the oceans, it could have given the algae and cyanobacteria what they needed to grow and expand. In turn, the increase in algae and cyanobacteria could have helped oxygenate the ocean and stimulate the Cambrian explosion (Penumaka, 2011).

Evolutionary Innovation

Another one of the theories that may have allowed life to diversify and increase in complexity during the Cambrian explosion is evolutionary innovation. Evolutionary innovation or a 'Key innovation' occurs when a novel phenotype develops and helps set life up for rapid evolution (Rabosky, 2017). One example of an evolutionary innovation could be apoptosis. It is unknown for sure when apoptosis, programmed cell death, evolved. If apoptosis did evolve during the Cambrian, then the evolutionary innovation of apoptosis could have helped prevent cancer, and further set the stage for life to thrive in the Cambrian explosion (Wood, 2020).

Another evolutionary innovation was compound eyes and eye spots (Zhao, 2013). More complex eyes helped the organisms to see their environment and explore new niches (Figure 5). Because organisms could see and better detect light, not only could they see their surroundings but they could also see each other. It is thought that with the help of eye spots and compound eyes, organisms were able to improve their predation and self defense (Zhao, 2013). The question remains, however, whether the evolutionary innovation of sight was the stimulant for the chain of events that led to the Cambrian explosion.

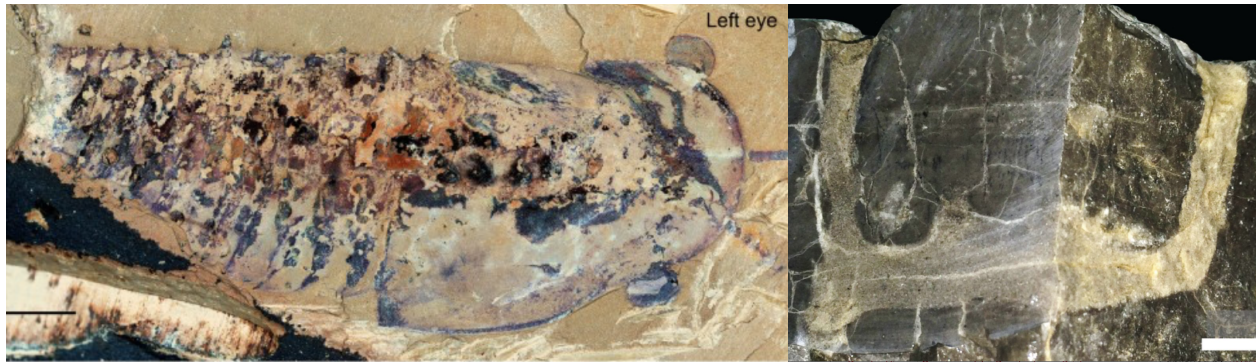


Figure 5 (above). On the left is a fossil of a Cindarella eucalla which has two complex eyes near the top of its head. On the right is a trace fossil, showing how organisms started to burrow in the sediment and starting the agronomic revolution. (Zhao, 2013; Tatsuo, 2018)

Predation

During most of the Ediacaran, organisms generally co-existed and did not prey on each other. During the Cambrian, however, some time around 550 Ma, something changed and animals shifted from coexistence to predation (Wood, 2019). As a result of predation, prey started to evolve to defend themselves, and predators evolved to hunt. Predators evolved muscles and nervous systems to increase mobility. Prey evolved to create shells; some even had spikes on their backs. Also to escape predation, prey may have started to burrow under the surface of the sediment (Figure 5), resulting in the agronomic revolution (Tatsuo, 2018).

The agronomic revolution occurred after bacterial mats started to fracture on the seafloor, allowing organisms to burrow into the ocean floor and start mixing the sediment with water and oxygen. This change in the surface sediment composition is known as the agronomic revolution. The agronomic revolution is an example of how animals were evolving to take on new niches (Tatsuo, 2018). Whether the new niches were used to the advantage of prey or predators first is unknown, but either way as the animals adapted to their new niches, they increased in diversity and complexity (Fox, 2016).

Conclusion

It is likely that the theories discussed above were not mutually exclusive. The Cambrian explosion could have been caused by a combination of oxygenation, nutrient availability, evolutionary innovation, and predation. It is optimistic, and perhaps simplistic, to say that there is just one cause of the Cambrian explosion, because in all systems of life there are many complex interactions between animals and the environment.

Due to the fact that there is variation in theories about when oxygenation events occurred based on which indicator is used, it is hard to isolate the exact cause or causes of the Cambrian explosion. In addition to the fact that it is hard to date oxygenation events, it is also debated when, exactly, the Cambrian Explosion started due to the gaps in the fossil record (Wood, 2020). Some, such as Penumaka (2011), think that the Cambrian explosion started 560 Ma, while others, such as Fox (2016), say 540 Ma; many others argue everywhere in between. Woods suggests that if all data sets of the fossil record across the globe were more integrated, it would give researchers a more precise timeline of biological and geological events (Wood, 2020). Regardless, until the fossil record is more complete and integrated with all data sets, answers to the questions of what caused the Cambrian explosion will remain theories.

Reflection

After doing research and writing this paper, it seems that the Cambrian explosion probably would not have occurred without oxygen being present in the oceans. There were oscillating oxygen levels throughout the Ediacaran and Cambrian, as stated in Fox (2016), but the Cambrian explosion needed more than just higher oxygen levels. The Cambrian explosion also needed the help of other events, such as the melting of the glaciers, evolutionary innovations, and predation. For example, animals need oxygen to grow in size (Runnegar, 2003), however, without the evolutionary innovation of vision and the start of predation, the animals may have not diversified at an explosive rate. The complex interactions between organisms, their habitats, and the environmental conditions led to the Cambrian explosion. Isolation of a single event that caused the Cambrian explosion seems too straightforward when piecing together the answer about the diversity of life.

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