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Q2 Opinion discussion

Q1 Reactive oxygen species may play an essential role in driving biological evolution: The Cambrian Explosion as an example

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The Cambrian Explosion is one of the most significant events in the history of life; essentially all easily fossilizable animal body plans first evolved during this event. Although many theories have been proposed to explain this event, its cause remains unresolved. Here, we propose that the elevated level of oxygen, in combination with the increased mobility and food intake of metazoans, led to increased cellular levels of reactive oxygen species (ROS), which drove evolution by enhancing mutation rates and providing new regulatory mechanisms. Our hypothesis may provide a unified explanation for the Cambrian Explosion as it incorporates both environmental and developmental factors and is also consistent with ecological explanations for animal radiation. Future studies should focus on testing this hypothesis, and may lead to important insights into evolution.

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Introduction

Although the first animals may have evolved during the Ediacaran Period (about 580 million years ago (mya)) or even earlier, essentially all easily fossilizable animal body plans emerged within about 35 mya in the early Cambrian (Marshall, 2006; Briggs, 2015; Valentine, 2004; Butterfield, 2015). This phenomenon is called the Cambrian Explosion, and is one of the most important evolutionary events in Earth history.

There have always been questions about the reliability of fossil evidence, because of the incompleteness of the fossil record and conflicts with molecular clock estimates. However, recent evidence strongly supports the conclusion that the Cambrian Explosion was a real evolutionary phenomenon as opposed to an artifact of taphonomy. The occurrence of trace fossils is independent of the presence of hard parts, and can provide information on soft-bodied animals that were rarely preserved. Studies have shown that trace fossils became larger and more complex throughout the Cambrian Period, which is consistent with the rapid radiation of animals (Valentine, 2004). Although earlier molecular clock analyses often conflicted with fossil data by suggesting many phyla evolved several hundred million years before the Cambrian, recent advances in molecular analyses have significantly reduced Precambrian divergence time estimates between phyla (Lee et al., 2013; Erwin et al., 2011; Rota-Stabelli et al., 2013), and current results from molecular analyses and are more or less reconcilable with the fossil record.

One explanation for the Cambrian Explosion is that the rate of animal evolution may have been much higher during that period. One simulation study has indicated that rates of evolution would have to increase by a factor of five to recreate the observed divergences that were then compressed into 35 million years (Levinton et al., 2004). Recent analyses of molecular and morphological data of arthropods have suggested that their rates of evolution indeed increased by 4- to 5.5-fold in the early Cambrian (Lee et al., 2013).

Several possible mechanisms for the Cambrian explosion have been proposed (Marshall, 2006; Valentine, 2004); some are based on environmental changes, such as increased atmospheric oxygen levels or Snowball Earth events. However, it is difficult to directly correlate environmental change with new levels of developmental and morphological organization. Another theory is that the evolution of a new genetic circuit was the primary cause. However, evidence suggests that the genes governing bilaterian development evolved at least tens of millions years before the Cambrian Explosion (Valentine, 2004). Finally, there are ecological explanations whereby predation and grazing are suggested to have been the major causes of the rapid radiation of animals. Although ecological factors are expected to play important roles in evolution, these theories fail to explain the duration and uniqueness of the Cambrian Explosion. Furthermore, none of these theories directly address why the rate of evolution increased.

It has long been established that oxygen can produce reactive oxygen species (ROS), and that the resulting oxidative stress may cause genomic damage and mutations (Schieber and Chandel, 2014; Puente et al., 2014; Cadet and Wagner, 2013). Furthermore, because ROS are also important signaling molecules, their increased abundance could also provide new regulatory mechanisms for development (Covarrubias et al., 2008). Therefore, we proposed that ROS may have been a central factor in the environmental, developmental and ecological mechanisms that caused the radiation of early bilaterians. In the following sections of this article, we will discuss this model in greater detail.

1. Increased oxygen level before the Cambrian set the stage for animal evolution

Before the Great Oxygenation Event (GOE) at about 2.45 Ga, any oxygen molecules in the atmosphere were captured by oxygen sinks such as dissolved iron and organic matter (Canfield, 2005, 1998; Holland, 2006). Between 1.8 and 0.85 Ga, the oxygen level in the atmosphere remained low, no more than 10% PAL (present atmospheric level) (Canfield, 2005, 1998; Holland, 2006; Sperling et al., 2015; Mills and Canfield, 2014). Some researchers have estimated that during much of the Proterozoic Eon, atmospheric oxygen could have been as low as 0.1% PAL (Sperling et al., 2015), in which case the oxygen content of seawater would have been exhausted as it passed from the sea surface downward to the seafloor, and thus caused the deep-ocean anoxia (Canfield, 2005). Canfield and colleagues (Canfield, 2005, 1998; Holland, 2006) have shown that the oxygen content in the atmosphere and the anoxic conditions in the deep ocean could cause the buildup of H_2S in the ocean, and form a so-called “Canfield Ocean”, which may explain why complex multicellular organisms did not evolve during this period of Earth's history (termed the “Boring Billion”).

Between 850 and 540 mya, there was a rapid increase in atmospheric oxygen content. The causes of this rise remain uncertain, although plausible explanations have been proposed, such as increased burial of organic carbon associated with continental breakup (Canfield, 2005, 1998; Holland, 2006). At the end of this period, the level of oxygen in the atmosphere was close to that of the present (Holland, 2006), which could lead to oxygenation of the deep ocean. A recent geochemical study on sedimentary rocks from the late Ediacaran revealed that these rocks formed under a more oxygenated environment than the underlying Cryogenian deposits. This finding suggests that immediately before the Cambrian Explosion, water of the deep ocean had already transitioned from anoxic to fully oxygenated (Chen et al. 2015; Johnston et al., 2012).

A high oxygen level is essential for metabolically active animals. It is also necessary for synthesizing collagen. Because collagen is essential for the formation of tissues, a minimum level of oxygen is required for the evolution of complex animals. Furthermore, because of their thick muscle layers and mesodermally derived internal organs, it is more difficult for triploblastic animals to obtain sufficient oxygen via diffusion, and their maximum body sizes should be related to oxygen availability. Therefore, the diversification of bilaterians could only take place after the oxygen level at the seafloor increased (Marshall, 2006; Valentine, 2004; Chen et al., 2015; Johnston et al., 2012; Mills et al., 2014; Knoll and

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