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GR Focus Review

Triggers for the Cambrian explosion: Hypotheses and problems

Xingliang Zhang *, Degan Shu, Jian Han, Zhifei Zhang, Jianni Liu, Dongjing Fu

Early Life Institute and State Key Laboratory for Continental Dynamics, Department of Geology, Northwest University, Xian 710069, China

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ABSTRACT

Abrupt appearance of major bilaterian clades in the fossil record during the first three stages of the Cambrian Period has puzzled the scientific world since 1830s. Many proposed causes including environmental, developmental, and ecological hypotheses, are reviewed. Nutrient availability, oxygenation, and change of seawater composition are commonly supposed to be environmental triggers. The nutrient input, e.g. the enrichment of phosphorus in an environment, would cause excess primary production, but it is neither directly linked with diversity nor disparity. Fluctuating abiotic conditions during the Snowball Earth and the associated oxygenation event may have stimulated the diversification of complex multicellular organisms including diverse of macroscopic and morphologically differentiated algae in the early Ediacaran, but did not lead to the ecological success of metazoan or bilaterian lineages. Further increase of oxygen level and change of seawater composition just before and during early Cambrian are suggested by the high weathering rate of the trans-Gondwana mountains, Great Unconformity, and decline of oceanic salinity. These are potential candidates of environmental triggers for the Cambrian explosion but require future more detailed geochemical studies to confirm. The molecular phylogeny calibrated with the molecular clock data suggested that the developmental system of bilaterians was established before their divergence. This, in turn, suggests that the Cambrian explosion require environmental triggers. However, there still exists the contention between deep or shallow divergence of bilaterian clades, which remains to be solved in the future. The deep divergence model is supported by a majority of molecular clock studies, but is challenged by the paucity of bilaterian fossils before and during the Ediacaran Period. The shallow model is generally consistent with the fossil record, but has to explain the rapidity of increase in diversity, disparity, morphological complexity, acquisition of biomineralized shells, etc. Regardless of deep or shallow model, the conservation of lineage-specific kernels within the gene regulatory networks (GRNs) provides an explanation for the long-term stability of body plans after the Cambrian explosion, and continuous addition of microRNAs into the GRNs seems to correspond well to the increase in morphological complexity. As for ecological causes, some hypotheses (e.g. adaptive radiation after mass extinction, cropping, and geosphere–biosphere feedbacks) cannot explain the uniqueness of the event, some others (such as Cambrian substrate revolution, predator–prey pressure, evolution of zooplankton, and roughening of fitness landscapes) fall into the trap of chicken-and-egg problem because of considering the consequence as a cause. Expansion of ecosystem engineering in the early Cambrian might also be caused by the Cambrian explosion. However, ecosystem engineering associated with Ediacaran ecosystems is likely a pivotal ecological prerequisite for the later ecological success of bilaterian clades, particularly the engineering effect by Ediacaran sponges that ventilated seawater by sponge pumping and removing organic material from the water column. However, the ecological abundance of Ediacaran sponges needs to be further investigated. Finally, a working plan is proposed for future research. For paleontologists, searching for ancestors of early Cambrian faunas is crucial to testify the earlier divergence of bilaterian lineages. Environmentally, precise values on the oxygen level and seawater composition are required during the Ediacaran–Cambrian transition.

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* Corresponding author. Tel.: +86 29 88303200; fax: +86 29 88304789.
E-mail address: xzhang69@nwu.edu.cn (X. Zhang).

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1. Introduction

The Cambrian explosion is a long standing macroevolutionary issue, which has been puzzling paleontologists and evolutionary biologists since 1830s as Conway Morris (2000, p. 4426) stated "William Buckland knew about it, Charles Darwin characteristically agonized over it, and still we do not fully understand it." It is generally accepted that essentially all of the readily fossilizable animal body plans (about half of living animal phyla) made their first appearance in the fossil record within a few tens of millions of years during the early Cambrian (Valentine, 2002; Erwin et al., 2011). Therefore, the Cambrian explosion has been widely realized as the most significant evolutionary event in the history of life on Earth (Conway Morris, 2006; Marshall, 2006; Shu, 2008; Maruyama et al., 2013; Santosh et al., 2013).

Fossil first appearances of animal phyla are obviously diachronous, but relatively abrupt in a short time span during the late Ediacaran to the early Cambrian (Shu et al., 2014-in this issue). The fossil record of basal animals (sponges and cnidarians) is extended to a period of time significantly before the beginning of the Cambrian. Thus, the Cambrian explosion itself seems to represent the arrival of the bilaterians (Budd, 2008). Analyses of early Cambrian faunas revealed that the divergence of bilaterian clades are episodic: lophotrochozoans were diversified during the Terreneuvian Epoch, mainly the Fortunian Age; ecdysozoans become diverse at the beginning of the Cambrian Stage 3 despite the fact that their fossil first appearance can be traced back to the Terreneuvian Epoch (e.g. arthropod traces and grasping spines of chaetognaths); divergence of deuterostomes started from the middle of Cambrian Stage 3 (Shu, 2008; Shu et al., 2009; Maloof et al., 2010; Kouchinsky et al., 2012), but the appearance of remains and traces of bilaterian animals remains abrupt (Erwin et al., 2011; Shu et al., 2014-in this issue). Apparently, the Cambrian faunas show that diverse animal phyla were already established during early Cambrian and have given us plenty of information about the diversity, disparity and morphological complexity of animal life at that time (Nielsen, 2001). Unfortunately, the fossil record tells very little about the origin of animal phyla because early ancestors might be small and/or soft-bodied, with little or no preservation and/or recognizable potential. Therefore, it is likely that a period of animal evolution preceded the Cambrian explosion we see in the early Cambrian. This is also indicated by studies of molecular diversification and comparative developmental data (Wray et al., 1996; Bromham et al., 1998; Aris-Brosou and Yang, 2003; Peterson et al., 2004, 2008; Blair, 2009), evolution of oxygen transport proteins (Decker and van Holde, 2011), and phylogenic analyses of Cambrian fossils and biogeography (Fortey et al., 1996; Lieberman, 2002), all suggesting that the major animal clades diverged many tens of millions of years before their first appearance in fossil record. Any inference on earlier divergence of bilaterian phyla was unavoidably challenged by the paucity of fossils of bilaterian clades during the Ediacaran period.

Provisionally, the conundrum of the Cambrian explosion seems to be conquered by the combination of present paleontological and molecular data: the major animal clades, at least stem lineages, diverged during the late Cryogenian to early Ediacaran, and did not become ecologically important until the late Ediacaran to early Cambrian (Erwin et al., 2011). This solution still implies a long history of cryptic evolution not present in the fossil record. Therefore, the Cambrian explosion is largely an ecological phenomenon, including the increasing of body size and morphological complexity, and widespread biomineralization among animals.

However, the exact causality has not yet been established, although there are many hypotheses as to what triggered the Cambrian explosion, ranging from environmental, developmental to ecological causes. Since 2005, a joint project by Chinese and Japanese scientists have worked on paleontological and environmental issues of the Cambrian explosion, with preliminary research progress published in a special issue of *Gondwana Research* 14 (1–2) 2008 and this volume. The cooperative project will be continued in the next five years. Therefore, here we give a review on available triggering mechanisms of the Cambrian explosion, to identify the shortcomings of each hypothesis, particularly with regard to paleontological data, and finally explicate our future research on this topic.

2. Hypothetical triggers

It seems obvious that something must have changed or reached a critical level favorable for the building of large, complex bodies and the construction of hard skeletal material. The hypotheses of what such evolutionary triggers can be split into extrinsic or external environment factors (e.g. tectonic settings, climatic conditions, nutrient availability, oxygen level, oceanic salinity), intrinsic or internal biotic factors (genetical and developmental innovations), and ecological causes (Fig. 1).

2.1. Environmental triggers

Many environmental triggers have been proposed but the oxygenation and change of seawater composition are most relevant factors. Some others, e.g. tectonic background and deglaciation of the Snowball Earth, merely provide mechanisms for the rise of oxygen level and the