Gondwana Research 25 (2014) 884–895

Contents lists available at ScienceDirect

Gondwana Research

journal homepage: www.elsevier.com/locate/gr

GR Focus Review

Birth and early evolution of metazoans

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ARTICLE INFO

Article history:
Received 8 January 2013
Received in revised form 31 August 2013
Accepted 1 September 2013
Available online 7 September 2013

Keywords:
Tree of animals
Cambrian
SSF
Ediacaran
Diversification

ABSTRACT

The reconstruction of the phylogenetic tree of animals (TOA) has long been one of the central interests in biological and paleobiological sciences. We review the latest results of paleontological and stratigraphical studies on the Ediacaran–Cambrian sequences mainly from South China for revising the TOA in accordance with modern genome biology. A particular focus is given to the pattern of animal diversification based on the fossil first appearances of high-rank clades chiefly in phylum-level. The results show an abrupt divergence of lineages during the Ediacaran–Cambrian transition; however, the appearances of metazoan phyla were obviously diachronous, with three major phases recognized herein. The first phase is marked by the appearances of basal metazoan phyla in the latest Ediacaran. Very few unequivocal bilaterian clades were present at this phase. The second phase occurred in the Terreneuvian (Cambrian Stages 1–2), represented by the occurrences of many lophotrochozoan lineages. This phase also involves the appearances of calcified basal metazoan lineages, and possibly, those of contentious ecdysozoans in the latest Terreneuvian, but no deuterostome has been known from this age. The third and also the largest phase occurred in the Cambrian Stage 3, which involve all the three supraphylogenetic clades of the Eubilateria. A number of lophotrochozoan lineages, the bulk of ecdysozoans, and all deuterostome phyla, appeared for the first time in this phase. Since there is no unambiguous evidence for bilaterians in the Ediacaran, the Cambrian explosion sensu stricto was an abrupt diversification of bilateral lineages in a short time of ca. 25 million years across the Ediacaran–Cambrian boundary. Next critical issues in research include high-resolution chrono- and chemostratigraphic analyses, correlations between biotic events and environmental perturbations, physiological approach to the biological connotation of biomineralization, and exploration for the lost mid-oceanic biota and environments, which are crucial in understanding the entire picture of the Cambrian explosion.

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1342-937X/$ – see front matter
http://dx.doi.org/10.1016/j.gr.2013.09.001

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1. Introduction

The term “Cambrian” was first used by Adam Sedgwick for the “Cambrian successions” in north Wales and Cumberland, UK (in Sedgwick and Murchison, 1835). The Cambrian was officially accepted as the lowermost system of the Paleozoic at the 21st International Geological Congress (IGC) in Copenhagen, Denmark. As used today, the Cambrian applies only to a part of the Lower Cambrian as originally proposed by Sedgwick in 1852, representing the first geological period after the long-lasting Precambrian time. The beginning of the Cambrian period, ca. 541 Ma (Peng et al., 2012), marked one of the most significant changes in the history of life on Earth, i.e. the onset of the golden animal age named the Phanerozoic. This change was significant not only in driving the great diversity of animals but also in determining the entire course of the animal evolution in the Phanerozoic. In contrast to the proceeding Precambrian time, the size, variety, and complexity of animals increased dramatically in the Cambrian, and the fossil occurrences also became increasingly common from the Cambrian and overlying strata, mostly due to the acquisition of hard skeletons.

As the emergence of diverse animal lineages was once believed as if it occurred in a relatively short time, this unique event has been often called the “Cambrian explosion”. The term “Cambrian explosion” was first coined by Cloud (1948). Later, on the basis of the sophisticated series of paleontological researches on the Burgess Shale in Canada by Charles D. Walcott and the Cambridge working group (see Whittington, 1985), S.J. Gould, 1989 very much emphasized the significance of this unique event in the history of life, making the Cambrian explosion extremely popular even to general public. Nonetheless, in the 1990s–2000s, remarkable progresses were made particularly in South China, as to the early animal evolution (e.g., Shu, 2008). The latest discoveries of many fossil groups, such as tunicate, fishes, and the new phylum Vetulicolia from the Chengjiang biota (Fig. 1), filled the long-lost missing links in the early evolution of animals, in particular of Chordates.

The new results of geochronological dating definitely lead to major changes in our understanding of the overall picture of the early animal evolution (e.g., Bowring et al., 1993). At present, it becomes apparent that the emergence of animals in fossil records was indeed a long-lasting process that spanned roughly from 580 to 500 Ma rather than a single event that happened in a extremely short time interval. The major increase in both animal diversity and disparity occurred particularly during the early Cambrian between 541 and 520 Ma. In addition, the biodiversification was further accelerated in the subsequent Ordovician time, as recently recognized as the Great Ordovician Biodiversification Event (GOBE) (e.g., Droser and Finnegan, 2003; Servais et al., 2010). At any rate, we still do not fully understand what caused this big change, how long it took, and what kind of immediate biological responses were made to the environmental changes (see X.L. Zhang et al., 2014; Z.F. Zhang et al., in press).

On the other hand, the comparison with molecular analyses dramatically enhanced the resolution of the phylogenetic tree of animals (TOA) (e.g., Dunn et al., 2008; Erwin et al., 2011). Furthermore, the real history of the Cambrian explosion on our planet may provide a clue to understand the critical conditions for large animal evolution/diversification on other Earth-like planets. It becomes more frequent to discuss about extra-solar life, as we are looking for some kind of animals also on extra-solar (or exo-)planets, simply because nearly 1000 exoplanets, including many Earth-like ones, were discovered outside of our solar system (e.g., Marcy, 2009).

This article reviews the latest aspect of the unique animal diversification events during the Cambrian explosion and an updated TOA, on the basis of newly added fossil information from South China to the previous database.

2. A brief summary of recent progress

Already more than five years have passed since Shu (2008) reviewed extensively on the Cambrian explosion by scrutinizing over 450 previous relevant articles that include the classic papers by Buckland (1837) and Darwin (1859). Even in such a short elapse of time, however, great progresses have been added mainly in South China to our knowledge on the entity of the Cambrian explosion, particularly in the following five aspects; i.e. (1) advance in geochronology, (2) new paleontological discoveries (Fig. 1), (3) detailed analyses on small shelly fossils (SSFs), (4) re-evaluation of the role of mass extinction, and (5) revision of the overall history of early animal evolution (TOA). In the next two sections, we briefly introduce the first four of these aspects. The updated discussion on the uniqueness of the Cambrian explosion (5) will be discussed separately afterwards.

2.1. Geochronology

During the last decade, the stratigraphy of the Ediacaran and Cambrian systems has been extensively studied worldwide, particularly in South China as the key investigated target. New progresses have provided better time constraints on the evolution of early metazoans. Since the landmark work by Bowring et al. (1993), a large number of respectable ages have been added also in South China (e.g. Condon et al., 2005; P. Liu et al., 2009; Xiao and Laflamme, 2009; Sawaki et al., 2010; Liu et al., 2013; Zhu et al., 2013; Tahata et al., 2013; Okada et al., 2014-in this issue).

2.1.1. The Ediacaran

Two schemes of the subdivision of the Ediacaran system, one with 4 and the other with 5 stages, were recently proposed on the basis of new chemo-, bio-, and chronostratigraphical data (Narbonne et al., 2012). In the preferred scenario with 5 stages (epochs), the earlier half of the Ediacaran before the Gaskiers Glaciation is subdivided into two stages (Ediacaran 1–2), whereas the post-Gaskiers younger half into three (Ediacaran 3–5). Spiny acritarchs, Doushantuo “embryos”, and complex carbonaceous macrofossils occurred immediately above the base of the Ediacaran, whereas all the three assemblages of the soft-bodied Ediacara-type biotas, bilaterian traces, and mineralized metazoan tubes appeared in the upper Ediacaran. These two distinct sets of fossil occurrence were clearly separated by the Gaskiers glaciation (ca. 582 Ma).

2.1.2. The Cambrian

The subdivision with 4 series and 10 stages (Peng et al., 2012) has been widely accepted in the geological community. Among the currently ratified five GSSPs (Global Stratotype Sections and Points), three are located in South China (see Peng et al. (2012) and references therein). The upper two series (roughly equivalent to the traditional Middle and Upper Cambrian) have many significant levels for global correlation, each subdivided into three stages, and four of the six stages defined at these GSSPs.