



GR Focus Review

Birth and early evolution of metazoans

Degan Shu ^a, Yukio Isozaki ^{b,*}, Xingliang Zhang ^{a,*}, Jan Han ^a, Shigenori Maruyama ^c^a Early Life Institute and State Key Laboratory of Continental Dynamics, Northwest University, Xi'an 710069, PR China^b Department of Earth Science and Astronomy, University of Tokyo, Tokyo 153-8902, Japan^c Earth-Life Science Institute, Tokyo Institute of Technology, Tokyo 152-1551, Japan

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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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* Corresponding authors.

E-mail addresses: isozaki@ea.c.u-tokyo.ac.jp (Y. Isozaki), xzhang69@nwu.edu.cn (X. Zhang).

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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 preceding 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 an 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 microfossils 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.

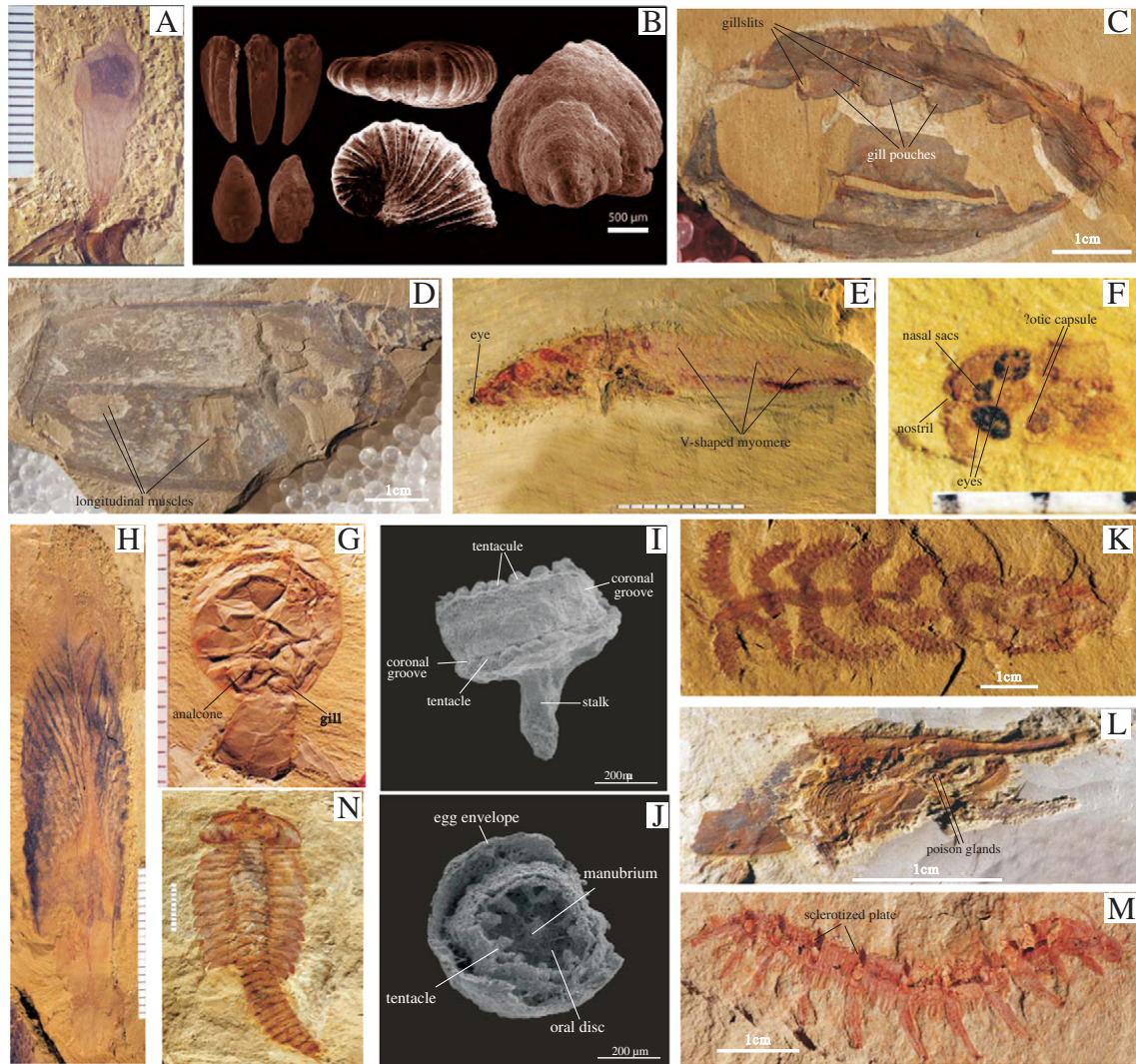


Fig. 1. Lately found some significant fossils relevant to the Cambrian explosion. One millimeter-grid for A, E–H. Scale bars: 500 µm for B; 1 cm for C, D, K–N; 200 µm for I, J. All the illustrated fossils were unearthed from Yunnan, except specimens I and J from Shaanxi, South China. Specimens of A, C–H, and K–N were from the Lower Cambrian Yu'an-shan Member (Stage 3), those of B from the Lower Cambrian Zhongyicun Member (Stage 2) in Yunnan, and those of I and J were from the Kuanchuanpu Formation (Stage 1) in Shaanxi. A: the oldest tunicate fossil (*Cheungkongella ancestralis*) from Ercai near Haikou (Shu et al., 2001a), B: various SSFs from Hongjiachon near Chengjiang (Sato et al., 2014-in this issue), C, D: two new vetulicolian specimens from Erjie near Jinning (Ou et al., 2012a, 2012b), E: the oldest fish (*Haikouichthys ercaicunensis*) from Jianshan near Haikou (Shu et al., 2003), F: the enlarged head part of *Haikouichthys*, G: the ancestral soft-bodied echinoderm (*Vetulocystis catenata*) from Jianshan (Shu et al., 2004), H: the tectonophore-like vendobiont (*Stromatoveris psymoglena*) from Erjie (Shu et al., 2006), I, J: ancestral polypoid cnidarian *Eolympia* (I) and unnamed cubozoan (J) from Ningqiang, Shaanxi (Han et al., 2010, 2013), K: "walking cactus" lobopodian (*Diania cactiformis*) from Ercai (Liu et al., 2011), L: bivalved arthropod with venomous glands (*Isoxys*) from Ercai (Fu et al., 2011), M: *Onychodictyon ferox* as a stem-group panarthropod from Erjie (Ou et al., 2012a, 2012b), and N: a stem-group arthropod with tripartite brain (*Fuxianhuia protensa*) from Erjie (Ma et al., 2012).

The lower two series (approximately equivalent to the traditional Lower Cambrian) represent the critical interval for the Cambrian explosion, during which world oceans experienced a rapid diversification of metazoans. The Lower Cambrian consists of 2 series, i.e., Terreneuvian and Series 2 in ascending order. The former is subdivided into Fortunian (Stage 1) and Stage 2, whereas the latter into Stage 3 and Stage 4 (names for the latter 3 will be given hopefully in near future). Because of the strong faunal provincialism and fewer correlative levels of GSSP quality in the earlier part of the Cambrian Period, each of these lower two series may be subdivided into two stages, only the base of the Cambrian being defined by the GSSP. However, there are still a few levels that have potential utility for global or intercontinental correlation (Steiner et al., 2007; Peng et al., 2012). This new chronological framework of the Cambrian is crucial for understanding the episodic nature of the Cambrian explosion, and for constraining the duration of this event.

2.2. Paleontological discoveries from exceptionally preserved Lagerstätten

The Ediacaran–Cambrian sequences of South China have incessantly been a favorite among paleontologists. Dozens of exceptionally well-preserved biotas in sequence have been found, which almost completely recorded the biological communities in marine habitats during the Ediacaran–Cambrian transition. New animal taxa continue to be found in old and new fossil localities, e.g., as added in various contributions in this special issue, thus give us an unrivaled insight into the Cambrian explosion.

On the basis of the fossil-bearing rock types and their mode of occurrence, the Ediacaran–Cambrian Lagerstätten biotas can be categorized into two distinct types of preservation, i.e., Orsten-type (phosphatization of soft-bodied organisms) and Burgess Shale-type (soft-tissue preservation in fine-grained siliciclastic rocks). The former was named after the Upper Cambrian Orsten bed in Sweden, while the latter after the

Middle Cambrian Burgess Shale in western Canada. Accordingly, we here present an update review on recent discoveries from the two types of biotas in South China, each arranged in a chronological sequence.

2.2.1. Orsten-type biota

The Ediacaran phosphatized Weng'an biota, that pre-date (Xiao and Laflamme, 2009) or post-date (Zhu et al., 2007) the Gaskiers glaciation, contains globular fossils showing palintomic cleavage. These have been interpreted as embryos of some of the earliest animals (e.g., Xiao et al., 1998) or alternatively as giant bacteria (Bailey et al., 2007). More recent study conservatively assigned these fossils within the total-group Holozoa, but outside the crown-group Metazoa, largely because the endless cell division does not generate metazoan synapomorphies, tissue differentiation, and/or association of juvenile/adult forms (Butterfield, 2011; Hultgren et al., 2011). Other putative metazoan adults include sponges (Li et al., 1998), cnidarians (e.g., Xiao et al., 2000; Liu et al., 2006), and even bilaterians (Chen et al., 2004). However, nearly all of these fossils are still regarded controversial (Budd, 2008). Up to the present, therefore, no unequivocal animal remains have been recovered from this biota.

In contrast, phosphatized biotas of Cambrian yield diverse of metazoan fossils, exemplified by many occurrences of SSF faunas. Three Orsten-type faunas are known from the Cambrian strata in South China. The Fortunian Kuanchuanpu fauna contains abundant embryos, larva, and adults of cnidarians, e.g., *Punctatus*, allowing the more complete reconstruction of their developmental sequence (Y.H. Liu et al., 2009; Yao et al., 2011). More recently a tiny sea anemone and some ancestral cubozoans with unequivocal internal anatomical structures were described from this fauna (Han et al., 2010, 2013). The limestone nodules of Cambrian Stage 3 in the Heilinpu Formation in Yunnan also contain phosphatized crustaceans showing nicely preserved soft-tissues (Zhang et al., 2007, 2010; Zhang and Pratt, 2012), which provide valuable data for the evaluation of the early evolutionary development and phylogenetics of the Crustacea and other related euarthropods. Additionally, phosphatized embryos of priapulids were also described from the Guzhangian–Paibian limestones of Hunan Province (Dong et al., 2004).

2.2.2. Burgess Shale-type biota

This type of Lagerstätten occurs widely in Cambrian fine-grained siliciclastic strata in South China, and range from lower Ediacaran to the Furongian (Cambrian Series 4). The early Ediacaran Lantian biota is dominated by macroscopic and morphologically complex algae along with problematic fossil informally compared with cnidarians and simple bilaterian (Yuan et al., 2011). Several Lantian macroscopic algae also range into the younger Miaohu biota, which is late Ediacaran epoch 5 in age, approximately 551 Ma, and contain a large diversity of megascopic algae. The eight-armed spiral body fossil *Eoandromeda* from the Miaohu biota of South China, and also from the Ediacara biota of South Australia, was favorably interpreted as a diploblastic-grade animal, belonging to either cnidarians or stem-group ctenophores (Zhu et al., 2008; Tang et al., 2011). The latest Ediacaran Gaojiashan biota from the silty mudstone in the middle part of the Dengying Formation is characterized by megascopic tubular fossils, including *Cloudina*, *Conotubus Gaojiashania*, and *Shaanxilithes*. These fossils are accustomedly considered as metazoan tubes, although metazoan synapomorphies have not been perfectly recognized. Re-description based on a large number of specimens reveals some details of these organisms, suggesting possible reconstruction of their life mode (Cai et al., 2010, 2011, 2012, 2013).

In Cambrian, Burgess Shale-type biotas have been found in vast area throughout South China, straddling both shallow and deep shelf facies, but concentrated in Cambrian Stage 3 to Stage 5. This type of biota from the sub-trilobitic Lower Cambrian (Terreneuvian) appears conceivably more important but has not been documented yet. In the past

five years, new animals and fantastically informative specimens have continuously been excavated from these biotas.

In particular, the Chengjiang biota from Stage 3 provides a unique window to look into the evolution of earliest deuterostomes (Shu et al., 2010), from which the oldest pterobranch hemichordate, morphologically similarity to extant representatives, was described (Hou et al., 2011), and new evidence on the structure of the lateral gills of vetulicolians strengthens their deuterostome relationships (Ou et al., 2012a, 2012b; Smith, 2012; Fig. 1C, D). Many more findings come out within the protostome clade. New material indicates that brachiopods are not only morphologically diversified but also ecologically expanded during the second epoch of the Cambrian period (Zhang et al., 2011a, 2011b, 2011c; Wang et al., 2012). Lobopodians, resembling worms with legs, have long attracted much attention because they may have given rise to both Onychophora and Tardigrada, as well as to arthropods in general. They are especially diverse in the Cambrian of South China, from where three more taxa were described (Liu et al., 2011; Ou et al., 2011; Steiner et al., 2012). Intriguingly, the lobopodian *Diania cactiformis* (Fig. 1K) possesses sclerotized and jointed appendages, and thus may represent transitional form from lobopodians to arthropods, implying that arthropodization (sclerotization of the limbs) preceded arthroization (sclerotization of the body) (Liu et al., 2011).

Arthropods are by far the most diversified and the most abundant fossil group in Cambrian. Each year, many new or old taxa are steadily described or redescribed from the Chengjiang and other biotas (e.g., Fu and Zhang, 2011; X.L. Zhang et al., 2014; Zhang et al., 2013). There are also some interesting points. The predatory arthropod *Isoxys curvirostratus* (Fig. 1L) probably has venomous glands at the base of its fang-like appendages, suggesting that venomous predation evolved as early as Cambrian Epoch 2 (Fu et al., 2011). In addition, tripartite brain was documented in the stem-group arthropod *Fuxianhuia protensa* (Fig. 1N), suggesting that the arthropod nervous system acquired significant complexity by the early Cambrian (Ma et al., 2012). Also noteworthy is the occurrence of the Burgess Shale-type Lagerstätten from the Ordovician in Morocco (Van Roy et al., 2010); however, non-such example was reported from the Ordovician in China.

2.3. SSFs (small shelly fossils)

The diversification of SSFs constitutes an important episode of the Cambrian explosion because they record the onset of widespread biomineralization among animals. The Lower Cambrian (equivalent to Series 1 and 2) contains abundant and taxonomically diverse SSFs (Fig. 1B). The abundant SSF data from South China were summarized in the book by Qian (1999). During the past decade, the increase in number of re-described taxa, using new material, was not so large (e.g. Na and Li, 2011); however, much attention was paid to their biozonation, mineralogy, and pattern of diversification of SSFs.

The fossil first appearance of SSFs is some 400 m above the base of Cambrian at the GSSP in Newfoundland, Canada. In South China, on the other hand, the base of Cambrian is not formally defined. Steiner et al. (2007) provided an updated SSF-zonation in South China, which consists of five biozones in the sub-trilobitic Lower Cambrian (Terreneuvian) and one biozone in the Cambrian Stage 3; i.e., 1) *Anabarites trisulcatus*–*Protohertzina anabarica* Assemblage Zone (correlated to middle Stage 1 = Fortunian), 2) *Paragloborilus subglobosus*–*Purella squamulosa* Assemblage Zone (upper Stage 1), 3) *Watsonella crosbyi* Assemblage Zone (lower Stage 2), 4) poorly fossiliferous interzone (middle Stage 2), 5) *Sinosachites flabelliformis*–*Tannuolina zhangwentangi* Assemblage Zone (upper Stage 2), and 6) *Pelagiella subangulata* Taxon-range Zone (Stage 3) in ascending order.

According to the SSF dataset of Li et al. (2007), 19 genera occur in the first biozone, whereas 140 in the second to fourth biozones, and 50 in the fifth biozone. Thus, the highest diversity of SSF on genus level obviously occurred at the Fortunian (Stage 1)–Stage 2 transition, within the second and third SSF assemblage zones (Li et al., 2007). When numbers

of new genera were calculated in every 2 million years, fossil first appearances of SSFs in China are clustered in two pulses; i.e., a major pulse in the late Stage 1 and a minor one in the upper Stage 2. These two pulses are separated by a barren interval (Maloof et al., 2010). This pattern is slightly different from the global dataset with three pulses, which also includes an additional smaller pulse in the lower Fortunian (see Maloof et al., 2010, Fig. 7).

As for mineralogy of SSFs, it is difficult to determine the primary minerals of these skeletal fossils because of diagenetic alterations, but a number of well-accepted criteria can be used to infer primary mineralogy of ancient skeletons (see Porter, 2007). Three principal classes of minerals are widely exploited by animals to build skeletons. They are calcium carbonate minerals (aragonite and calcite), calcium phosphate minerals (e.g., apatite), and silica minerals (opal-A), all of which have been recognized in SSFs (Li et al., 2007, 2011; Kouchinsky et al., 2012). Silica mineral in fossil is only known in the Ediacaran sponges before the first fossil appearance of radiolaria from Stage 5 of Series 3 (Maletz, 2011). Carbonate minerals and phosphate minerals are most common biominerals and have equal importance in diverse of SSFs. Within the carbonate skeletons, aragonitic taxa systematically appeared earlier, followed by calcitic taxa, which began mineralizing in the end of Terreneuvian (Porter, 2007; Kouchinsky et al., 2012). This mineralogical shift likely corresponds to a change of seawater chemistry (Mg^{2+}/Ca^{2+} ratio) from aragonitic sea to calcitic sea. Wood and Zhuravlev (2012) recently discuss further that changes in seawater chemistry and predation pressure had determined the pattern of the Cambrian biomineralization from the viewpoint of cost–benefit ratio.

2.4. Multiple mass extinctions

The early Cambrian (roughly corresponding to Terreneuvian and Epoch 2) is a period characterized by a dramatic increase of disparity (measured by the number of high ranking lineages in phylum or class level) (Marshall, 2006; Erwin et al., 2011), which is generally referred to the Cambrian explosion. In contrast, high-level morphological innovation occurred scarcely during the following 500 million years. Under the big shadow of this image of overall explosive increase in biodiversity (e.g., Gould, 1989), an important aspect might be overlooked; that is the involvement of multiple mass extinction events.

The diversity pattern measured in generic level is fundamentally different from the disparity pattern. The diversity curve does not steadily rise throughout the early Cambrian but is interrupted by several drops (Zhuravlev and Riding, 2001; Li et al., 2007). The rapid change of diversity is attributed not only to new origination but also to extinction events during the Cambrian. Bambach (2006) illustrated 3 major extinctions within the Cambrian. For example, at the end of early Cambrian, a mass extinction totally eliminated redlichiid trilobites and nearly all archaeocyathids.

On the basis of detailed compilation of Ediacaran–Cambrian fossil records and C-isotope data mostly from South China, Zhu et al. (2007) pointed out that multiple extinction episodes, at least 7 times, might have occurred during the Ediacaran–Cambrian time. In other words, The Ediacaran–Cambrian time was characterized not merely by the widely-believed, one-sided origination of new taxa but also by frequent termination/replacement of pre-existing taxa. This aspect requires a drastic change in our understandings, as the so-called Cambrian explosion has been long emphasized as a single big/rapid episode of the appearance of various new animals (e.g., Gould, 1989).

Owing to the scarceness of fossil records, no reasonable statistics have not yet been hitherto available unfortunately; however, each of the above-mentioned 7 distinct extinctions may possibly correspond in magnitude to the biggest mass extinction of the Phanerozoic across the Paleozoic/Mesozoic (or Permo-Triassic) boundary (e.g., Jin et al., 2000; Erwin, 2006), because the extinctions during the Ediacaran–Cambrian time involved the terminations of various animal phyla, and also because extremely large perturbations in surface environments

were suggested by the nicely-documented C-isotope secular changes for each events (Zhu et al., 2007). The Cambrian world was much wilder than previously imagined. The possible link between the neighboring extinction and radiation events should be tested in future study.

3. Current knowledge of the Ediacaran–Cambrian animal evolution

From paleontological point of view, the essential of the Cambrian explosion is no doubt the abrupt appearances of diverse animal phyla in a relatively short period during the Ediacaran–Cambrian transition. To elucidate the process of this macroevolutionary event, we need to check the sequences of the first occurrences of 38 extant animal phyla (Nielsen, 2012), together with those of some extinct phylum-level clades (e.g., Archaeocyatha and Vetulicolia), in the context of updated molecular-based animal phylogeny. On the other hand, patterns of adding taxon in class- and genus-level should be checked on the basis of available datasets of “real” fossil records. In the following discussion, the Ediacaran–Cambrian fossil first occurrence of each phylum is assigned to an appropriate geological stage, according to the new stratigraphic framework with five stages in Ediacaran and 10 stages in Cambrian (Narbonne et al., 2012; Peng et al., 2012), as summarized in Fig. 2.

3.1. Fossil first appearance of animal phyla through geological periods

Porifera, classically comprising extant phyla Silicea, Calcarea and Homoscleromorpha, and the extinct phylum Archaeocyatha, is proved to be a paraphyletic group. The molecular record of the Silicea (Demospongiae + Hexactinellida) may have extended back to the Cryogenian (Love et al., 2009), but bona fide fossil spicules of domosponge affinities first appeared in the *Cloudina* reefs of Namibia (Reitner and Wörheide, 2002), which is correlated to the Ediacaran Stage 5 (Fig. 2). Spicules of hexactinellids first occurred in the upper Tsagan Oolom Formation (Brasier et al., 1997), but the age of this fossil horizon was not well constrained; probably in latest Ediacaran or earliest Cambrian. There were many other occurrences of sponge-like spicules or sponge-grade metazoans from older rocks (e.g. Gehling and Rigby, 1996), but all their identities are questionable (see Kouchinsky et al. (2012) for discussion). Both Calcarea and Archaeocyatha first occurred in the upper Stage 2 of the Cambrian (Reitner, 1992; Rowland and Hicks, 2004). The fossil record of Homoscleromorpha is somewhat uncertain, and the earliest forms were obtained from no earlier than Carboniferous (Reitner and Wörheide, 2002).

Within the basal eumetazoans, the basal-most phylum Placozoa virtually does not have fossil record, but the fossil *Dickinsonia* (Ediacaran 4) has recently been interpreted as a placozoan (Sperling and Vinther, 2010). *Dickinsonia* may be the most controversial fossils hitherto known, which has been assigned to many phyla, ranging from lichens, Cnidaria, Ctenophora, Platyhelminthes, Annelida, and a phylum of its own to a non-metazoan kingdom (see Zhang and Reitner (2006) and references therein). If it was an animal, *Dickinsonia*, together with many other “bilaterally” and non-bilaterally symmetrical fossils from the Ediacara-type biotas (ranging in the Ediacaran epochs 3 to 5), is likely within the variety of cnidarian-grade organisms, or more safely belongs to clades below the protostome/deuterostome split (Erwin, 2009). Moreover, many early tubular fossils are frequently compared to cnidarians. A couple of microtubes from the Weng’an biota (Ediacaran 3) are considered to be cnidarian affinities (Xiao et al., 2000; Chen, 2004). Tubular fossils like *Cloudina* and others from the Nama Group in Namibia and the Gaojiashan biota in South China, both of which are of the Ediacaran epoch 5 in age, are usually considered as cnidariomorphs (Kouchinsky et al., 2012). There are also a number of calcified cnidariomorphs, e.g., corallomorphs, anabaritids, and protoconulariids, and their lowermost occurrence is documented from the Fortunian. Although there are many possible cnidarians in the Ediacaran, the oldest fossils that can be unequivocally assigned into the

Cryogenian	Ediac 4	Ediac 5	Camb 1	Camb 2	Camb 3	Camb 5	Camb 9	Post-Cambrian	No fossil record	
this study										
?Silicea	?Cnidaria	Silicea	Cnidaria	Calcarea	Vertebrata	Annelida	Tardigrada	Bryozoa	Homoscleromorpha (C)	Acoela
	?Ctenophora	?Annelida	Ctenophora	Archaeocyatha	Urochordata	Sipuncula			Nemertini (C)	Nemertodermatida
	?Placozoa		Mollusca	Brachiopoda	Cephalochordata	?Phoronida			Platyhelminthes (Pa)	Xenoturbellida
	?Mollusca		Cambroclavids	Tianzhushanelids	Pterobranchia	?Entoprocta			Rotifera (Eo)	Gastrotricha
			Chaetognatha	Stenothecoids	?Enteropneusta	Loricifera			Entoprocta (J)	Gnathostomulida
				Mobergellids	Echinodermata	Priapula			Nematoda (D)	Micrognothozoa
				?Priapula	Vetulicolia	Arthropoda			Nematomorpha (K)	Cycliophora
				?Arthropoda		Lobopodia				Phornida
						Onychophora				Kinorhyncha
Erwin et al. (2011)										
			Cnidaria	Calcarea	Vertebrata	Ctenophora	Tardigrada	Bryozoa	Homoscleromorpha (C)	
			Chaetognatha	Archaeocyatha	Urochordata	Annelida			Rotifera (Eo)	
			Phoronida	Demospongiae	Cephalochordata	Sipuncula			Platyhelminthes (Pa)	
			Brachiopoda	Hexactinellida	Hemichordata	Nematomorpha			Entoprocta (J)	
			Hyalolitha	Priapula	Echinodermata	Loricifera			Nemertini (C)	
			Mollusca		Vetulicolia	Lobopodia			Nematoda (K)	
			Coeloscleritophora		Cambroernids	<i>Rusophycus</i>				
						Arthropoda				

Fig. 2. List of fossil first occurrence of animal phyla in geologic records. On the basis of the latest information, the fossil first occurrences of the Ediacaran and Cambrian animal phyla are categorized according to the geologic stages (upper). The non-listed stages, such as Ediacaran Stages 1–3 and Cambrian Stages 4, 6–8, and 10, are omitted for no occurrence of new phylum. For the post-Cambrian cases, the ages of the fossil first occurrences are shown in abbreviation; i.e., D: Devonian, C: Carboniferous, J: Jurassic, K: Cretaceous, Pa: Paleocene, and Eo: Eocene, respectively. For comparison, a similar list by Erwin et al. (2011) is shown below. Animal phyla in bold letters are those assigned differently from the Erwin’s scheme. Note that the majority of animal phyla appeared in fossil records in the first 3 stages of Cambrian, although some precursors appeared already in the latest Ediacaran. In contrast, 8 phyla were confirmed merely in the post-Cambrian strata, and 9 extant phyla have not yet been identified in fossil records.

Cnidaria are the soft-bodied microfossils *Eolympia pediculata* and some cubozoans from the Fortunian Kuanchuanpu fauna (Han et al., 2010, 2013; Fig. 11–L). Fossils with possible Ctenophora affinities were reported from the Miaohu biota in China (Tang et al., 2011) and the White Sea assemblage (Zhang and Reitner, 2006), both being of the Ediacaran epoch 4 in age. However, unambiguous ctenophores first occurred as embryo fossils in the Kuanchuanpu fauna (Chen et al., 2007), and adults from the Chengjiang fauna (Chen and Zhou, 1997). It is very interesting that a ctenophore-like vendobiont also appeared from the Chengjiang fauna (Shu et al., 2006; Fig. 1H).

Acoelomorpha is favorably placed at the basal position of the Bilateria (Edgecombe et al., 2011; Nielsen, 2012), which contains three small phyla, i.e. Acoela, Nemertodermatida, and Xenoturbellida, all escaping the fossil record. Alternatively, some workers place the acoelomorphs as the sister group of the ambulacrarians (Philippe et al., 2009). Eubilateria is traditionally divided into Protostomia and Deuterostomia. The lineages of the Protostomia are further grouped into two supraphyletic clades (Ecdysozoa and Lophotrochozoa), as this is supported by latest molecular phylogenies. The phylogenetic position of the Chaetognatha is highly controversial, which has variously been considered as a sister group or an ingroup of these supraphyletic clades: Protostomia, Lophotrochozoa, and Ecdysozoa. Edgecombe et al. (2011) and Nielsen (2012), however, place the Chaetognatha at the base of the Protostomia. The consensus lies in that the Chaetognatha is located somewhere within the Protostomia. Therefore, its phylogenetic position remains open. Unquestionable chaetognathan fossils preserved with anatomical details have been described from the Chengjiang biota (Chen and Huang, 2002; Hu et al., 2007). Since protoconodonts like *Protoherztzina* is believed to be grasping spines of chaetognathans (Szaniawski, 2002), the lowermost occurrence of this phylum extends down to the Fortunian (Fig. 2).

The Lophotrochozoa comprises 14 extant phyla, but 4 phyla (Gastrotricha, Gnathostomulida, Micrognothozoa, and Cycliophora) lack fossil record, and additional 3 phyla first appeared in post-Cambrian, Nemertini in the Carboniferous, Platyhelminthes in the Paleocene, and Rotifera in the Eocene (see references in Erwin et al., 2011; Fig. 2). The reliable fossil of the Entoprocta is known from the Jurassic (Todd and Taylor, 1992), but possible stem group entoproct may range down to the Cambrian Stage 3 (Zhang and Pratt, 2012). *Kimberella*, a possible soft-bodied mollusk, occurred in the Ediacaran epoch 4 (Fedonkin and Waggoner, 1997). Mollusca with complete hard shell (not composed of sclerites), as well as shelly fossils showing mollusk affinities (e.g., hyoliths, halwaxiids and cancelloriids), first occurred in the mid-Fortunian (Kouchinsky et al., 2012). The lowermost occurrence of the phylum Brachiopoda that includes the stem-group tommotiids (Holmer et al., 2011) is documented from the Cambrian Stage 2 (Kouchinsky et al., 2012). *Cloudina* and a number of tubular fossils from the Gaojiashan biota (Ediacaran 5) are morphologically compared with annelid tubes (Hua et al., 2005; Cai et al., 2014-in this issue), but they are alternatively considered as cnidariomorphs (Kouchinsky et al., 2012). The earliest unquestionable annelid fossil appears to be *Phragmochaeta* from the Sirius Passet fauna (Conway Morris and Peel, 2008) of the Cambrian Epoch 3. Phoronida has no reliable fossil but *Eccentrotheca* from the Wilkawillina and Ajax limestones of South Australia was putatively placed in the stem-group of phoronids (Skovsted et al., 2011). The fossil horizon is corresponding to Cambrian Stage 3. A number of sipunculan fossils strikingly resembling extant forms have been described from the Chengjiang biota (Huang et al., 2004), representing the lowermost occurrence of the phylum Sipuncula. The appearance of the Bryozoa was long regarded to have occurred in the Ordovician; however, their occurrence from the Jiangshanian (Cambrian Stage 9) was lately confirmed (Landing et al., 2010), albeit it has calcified skeletons.

In the SSFs, there are also a number of fossil groups with uncertain high-rank taxonomy (Fig. 1B). Cambroclavids first occurred in the upper Fortunian, and the first appearances tianzhushanellids, stenothecoids and mobergellids are in the upper part of the Cambrian Stage 2 (Fig. 2). Since they are frequently compared with brachiopods, mollusks, we place these four groups within the Lophotrochozoa, in agreement with the solution by Kouchinsky et al. (2012).

The Ecdysozoa contains eight living phyla. The fossil first appearance of the Nematoda was in the Devonian, and that of the Nematomorpha was in the Cretaceous (Poinar et al., 2008; Poinar and Buckley, 2006; Fig. 2). Within the Scalidophora (Kinorhyncha + Loricifera + Priapulida), the Kinorhyncha is unknown in the fossil record, an ancestral loriciferan was described from the Sirius Passet fauna (Peel, 2010), and many priapulid fossils have found in deposits as low as Cambrian Stage 3 (Chen, 2004; Hou et al., 2004). The embryo fossil *Markuelia* is worth mentioning here. It first appears in the Cambrian Stage 2, and is phylogenetically assigned to the scalidophoran total group (Dong et al., 2010). The Panarthropoda embraces three living phyla: Tardigrada, Onychophora, and Arthropoda. Lobopodians that have generally been considered as the (marine) stem-group of the modern (terrestrial) onychophorans, first occurred in Cambrian Stage 3 (Liu et al., 2007, 2011), the earliest terrestrial onychophoran fossil has been found from Cretaceous amber (Grimaldi et al., 2002). Trace fossils such as *Rusophycus* that are likely made by arthropods have been found in Cambrian stage 2; however, no arthropod body fossils occurred until the lowermost part of the Cambrian Stage 3. Tardigrad fossils are rarely known. A fossil form described from the Cambrian Stage 5 of Siberia strongly resembles living tardigrades, but has only three pairs of appendages (Müller et al., 1995).

The monophyly of the Deuterostomia is now accepted by both morphological and molecular studies. It falls into two well-defined supraphyletic clades, Ambulacraria and Chordata, each comprising three living phyla (Nielsen, 2012). In addition, the Vetulicolia is also established as a phylum-rank deuterostome clade (Shu et al., 2001b; Fig. 1C, D). Cambroernids might be in this case, too. Both clades first occur in the Chengjiang biota and extend to Cambrian Stage 5 (Fig. 2), with vetulicolians being placed at base of the Deuterostomia (Ou et al., 2012a, 2012b) and cambroernids at the base of Ambulacraria (Caron et al., 2010). Within the Hemichordata, the earliest fossil of the Pterobranchia was recently documented from the Chengjiang biota (Hou et al., 2011), but no reliable fossil of the Enteropneusta has been reported except for *Yunnanozoon* and *Haihouella* from the Chengjiang biota, which were controversially interpreted as enteropneusts, cephalochordates, basal deuterostomes or uncertain affinities (see Shu et al., 2010). Vetulocystids from the Chengjiang biota were described as ancestral soft-bodied echinoderms (Shu et al., 2004; Fig. 1G), and the earliest mineralized echinoderm plates were reported from the Cambrian Stage 3 of Siberia (Kouchinsky et al., 2012), both indicating the fossil first appearance of the Echinodermata at this time. As for the Chordata, all the three living phyla, i.e. Cephalochordata, Urochordata, and Vertebrata, have been documented from the Chengjiang biota (Shu et al., 1999, 2001a; Fig. 1A, E, F), no fossil earlier than this age has ever been found (Shu et al., 2010).

3.2. Patterns of new addition in phylum-, class-, and genus-level

Since very few fossil of the Ediacaran can be safely assigned to bona fide metazoan, the following discussion will mainly focus on the Cambrian fossil record. Erwin et al. (2011) prepared an updated database on the appearances of phyla and classes throughout the geological periods. Fig. 3 illustrates the adding pattern of phylum on the basis of the latest data, which is slightly different from that by Erwin et al. (2011). The following discussion on the appearances of new classes is based essentially on the dataset in Erwin et al. (2011), together with new genera added according to Maloof et al. (2010) and Li et al. (2007).

The new pattern (Fig. 3) confirms the previous suggestions that the diversification of animal phyla abruptly occurred in the fossil record during the first three stages of the Cambrian period (Shu et al., 2009). Only two bona fide metazoan phyla (Silicea and probable Cnidaria) appeared in the late Ediacaran, followed by the dramatic rise in novel phyla in the Terreneuvian, and by the later burst in the Cambrian Stage 3. This burst of phyla may be, at least partly, due to the intensive excavation in the exceptionally well-preserved fossil Lagerstätten, such as the Chengjiang biota and the Sirius Passet biota. Out of extant 38 phyla, 20 living phyla appeared by the Cambrian Stage 3 (Fig. 2). As to the rest, 9 phyla were continuously added to the fossil record in the later geological periods, and 9 phyla have not been known in the fossil record. As the most advanced members in both prostomes and deuterostomes, e.g., true arthropods and vertebrates, already appeared in the Chengjiang fauna, evolutionally and logically these late-coming “lower” phyla must have been present much earlier, to say in the early Cambrian. Most of those “new faces” except for the Bryozoa might escape from fossilization owing to little or no preservation potential; e.g., soft-bodied. In other words, their later fossil first appearances are largely artifact. Addition of new classes also exhibits this dramatic rise in first occurrences beginning in the Fortunian, soaring in the Cambrian Stage 3, and continuing into the Ordovician (e.g., Servais et al., 2010). From the early Paleozoic onward, there was very little addition of new classes, and again, many of these later class appearances are restricted to soft-bodied ones with poor preservation potential, suggesting earlier cryptic originations (Erwin et al., 2011).

The first fossil appearances of animal genera during the Terreneuvian occurred in three pulses; a small pulse in the early Fortunian, a large one in the late Fortunian, and the moderate in the Cambrian Stage 2 (Maloof et al., 2010; Fig. 2). Global data in the later geological periods are currently not yet available, but a much bigger pulse can be predicted in the Cambrian Stage 3 based on the data also from South China (Li et al., 2007).

3.3. Summary on the Cambrian explosion

In short, basal metazoans were no doubt present in the late Ediacaran, with calcified clades in succession added in the early Cambrian (Figs. 2, 3). On the other hand, there is no unambiguous evidence for the existence of bilaterians in the Ediacaran period, although controversial candidates are continuously emerging. The pattern of the fossil first occurrences of classes mirrors the pattern of phyla, both showing a dramatic rise during the first three stages of the Cambrian with little addition thereafter. Thus the Cambrian explosion *sensu stricto* was surely a unique event of an abrupt diversification of bilateral lineages in a short time span during the first 20 million years of the Early Cambrian period. The appearances of lophotrochozoan lineages were somewhat gradual and relatively long lasting, which began in the latest Ediacaran or the earliest Cambrian, followed by continuous addition of new clades in stages of the Early Cambrian. On the contrary, many ecdysozoan and all deuterostome lineages seem to have appeared suddenly in the Cambrian Stage 3.

Here we emphasize that the fossil first appearances of metazoan phyla (the Cambrian explosion *sensu lato*) occur in distinct three phases during the Ediacaran–Cambrian transition (Fig. 4). The first phase recognized herein is marked by a set of the first appearances of basal metazoan phyla in the latest Ediacaran (Fig. 2). It is noteworthy that no unequivocal bilaterian clade was present at this phase except *Kimberella*, a possible stem lophotrochozoan. The second phase, roughly equivalent to the first biomineralization phase recognized by Kouchinsky et al. (2012), occurred in the Terreneuvian, as evidenced by the occurrences of many lineages in the SSFs (Fig. 1B) that can be placed within the total group Lophotrochozoa. This phase was also characterized by the occurrences of calcified basal metazoan lineages (e.g., Calcareaea and Archaeocyatha), and possibly, by the appearances of contentious ecdysozoans in the latest Terreneuvian; however, no deuterostome has been known from the Terreneuvian. The third phase that

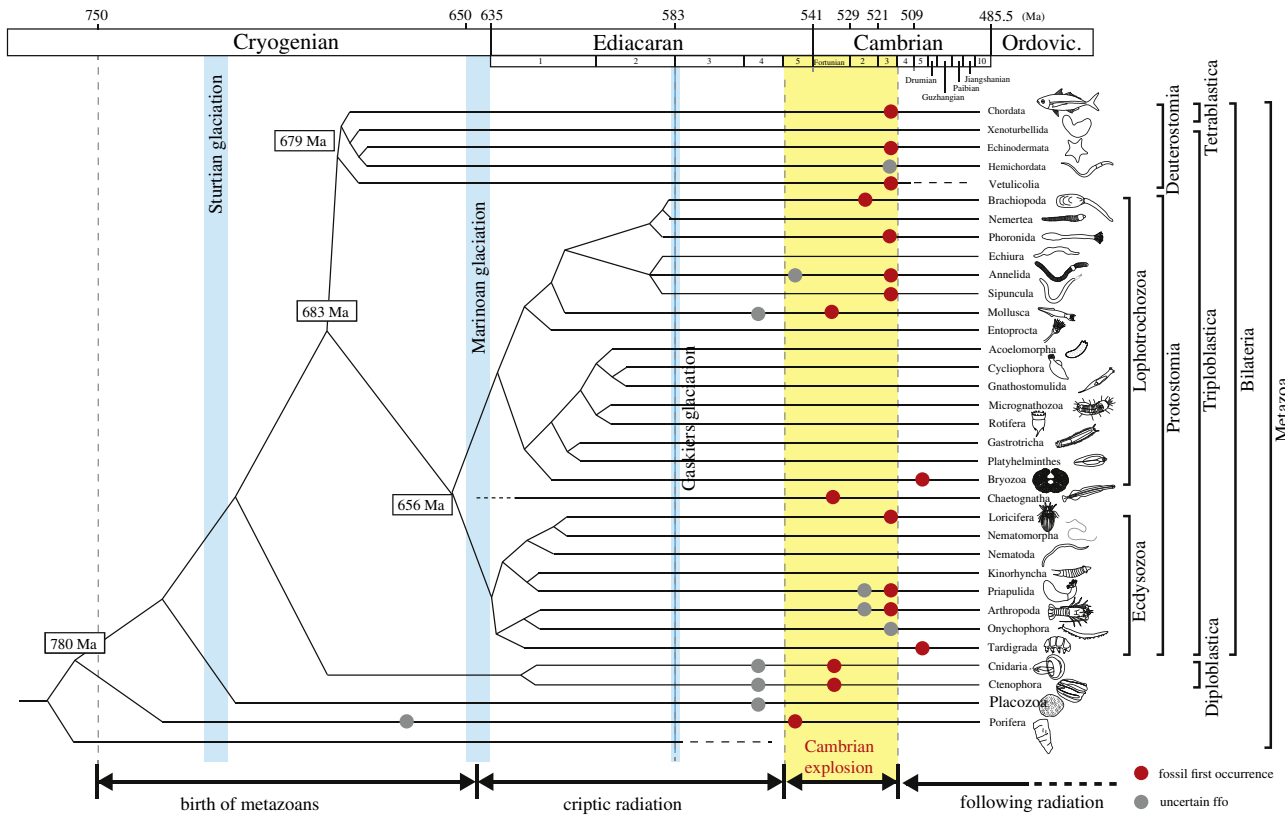


Fig. 3. Phylogeny and fossil first appearances of animal phyla during the Late Neoproterozoic to Cambrian (modified from Erwin et al., 2011). Ages of major lineage-branching and the Neoproterozoic glaciations were after molecular dating in Erwin et al. (2011) and after the latest chronological summary by Narbonne et al. (2012). The subdivision of the Ediacaran and Cambrian is after Narbonne et al. (2012) and Peng et al. (2012). All the estimates for branching ages based on molecular data are always older than the real fossil records, as previously known. In general, the appearance of phenotypes might become significantly later than the innovation on genome level. In addition, the fossil preservation bias, in particular for soft-bodied animals, likely might widen the time gap. Nonetheless the Cambrian explosion surely occurred in ca. 25 million years across the Ediacaran–Cambrian boundary. In particular, the first 3 stages of the Cambrian are highlighted with the concentrated fossil first occurrences of various animal phyla.

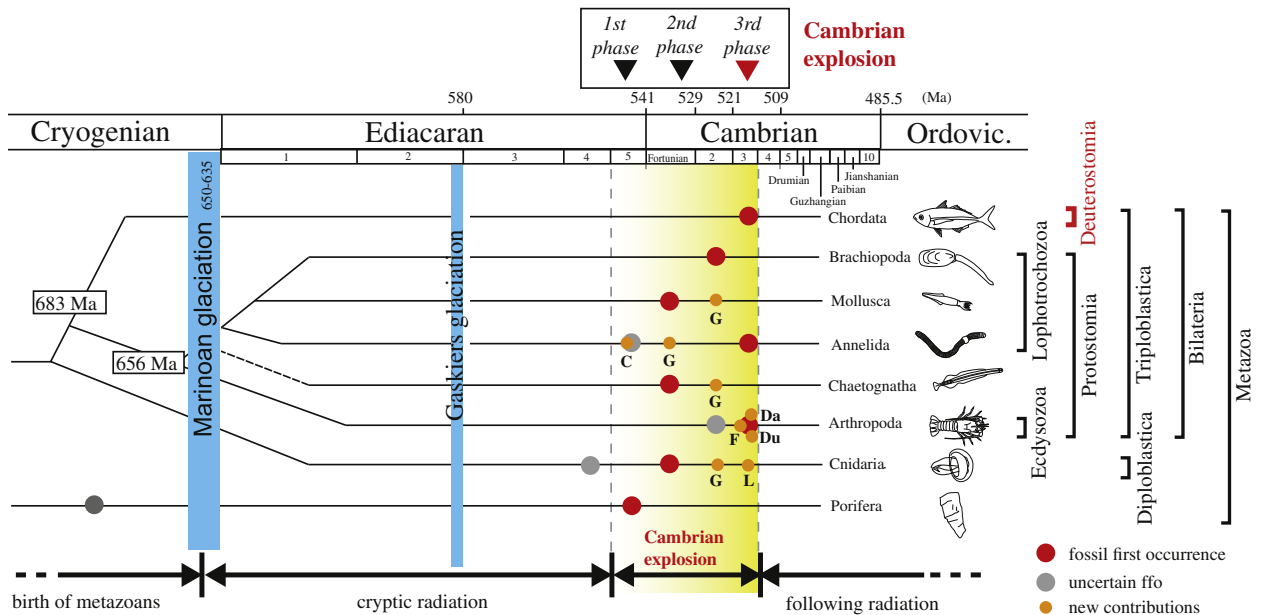


Fig. 4. The Cambrian explosion with 3 distinct appearance phases of new animal phyla. The subdivision of the Ediacaran and Cambrian is after Narbonne et al. (2012) and Peng et al. (2012). The fossil first appearance of each clade is shown as solid circle (see text and Figs. 2, 3). Note the 3 phases of appearance in representative animal phyla; the first phase in the latest Ediacaran, the second in the Terreneuvian (Cambrian Stages 1–2), and the third in Stage 3. New addition of animal phyla/classes occurred restrictedly during the first 3 stages of the Cambrian period, and became significantly rare afterwards. The concentrated appearances particularly in Stage 3 marked the apex of the “Cambrian explosion”, from which the large-bodied and highly complicated animals of Chordata and other phyla first appeared. New paleontological contributions from South China reported in this special issue are shown in orange dots (C: Cai et al., G: Guo et al., 2014-in this issue, F: Fu and Zhang, Da: Dai and Zhang, 2014-in this issue, Du: Duan et al., 2014-in this issue, L: Lei et al., 2014-in this issue).

occurred in the Cambrian Stage 3 was the largest, with the appearance of all the three supraphylogenetic clades (Figs. 2–4). A number of lophotrochozoan lineages, the bulk of ecdysozoans, and all deuterostome phyla, first appeared in this phase and this virtually marked the apex and the end of the Cambrian explosion.

4. Phylogenetic tree of animals (TOA)

To date numerous attempts have been made for establishing the TOA. In terms of the methodology and dataset employed, these attempts can be categorized into the following four groups; i.e., 1) the traditional approach based on morphological data since Haeckel (1866), 2) approach based on fossil data coupled with the check in development biology of extant animals (e.g., Margulis and Schwatz, 1982; Shu, 2008), 3) approach from molecular biology utilizing genome comparison for extant animals (e.g., Dunn et al., 2008), and 4) synthesized approach on the basis of fossil records and molecular phylogeny (e.g., Carroll, 2008; Carroll et al., 2001). During the second half of the 20th century, the third approach was regarded as a perfect shortcut to finalize the entire picture of TOA. Nonetheless, the recognition of gene lateral transfer poses some ambiguity, although the “animal kingdom” was unlikely affected too much. At any rate, as long as we deal with one and only history developed, it seems fair to take the last approach to check what really happened in the past, rather than theory-driven understanding.

By virtue of more new data from the paleontological/geological researches during the last two decades (Fig. 1), we can reconstruct more sophisticated TOA in the Ediacaran–Cambrian transition, as shown in Figs. 3, 4 that were compiled based on numerous previous works from all fields. As clearly demonstrated in Figs. 2–4, the major diversification of animals mirroring morphological innovations took place during the early Cambrian. SSFs, and exceptionally preserved fossil Lagerstätten in the Early Cambrian have been and will be constituting the major information source for understanding the Cambrian explosion.

5. Next critical issues to be solved

As discussed above, the stratigraphical and paleontological achievements from South China provided the best clue to date for understanding the essential of the Cambrian explosion. On the basis of the latest knowledge, we summarized the current aspects of early animal evolution during the Ediacaran–Cambrian transition. Nonetheless we still need more data to fully clarify the ultimate cause and processes of the biggest biological event during the last 600 million years. The main aspects that should be tested and/or clarified are listed below.

- 1) The Cambrian chronostratigraphy has made a lot of new progresses during the last two decades; however, we still need more high-resolution measurements of several significant boundaries because most stage boundaries have not yet been directly constrained by numerical dating (e.g., Peng et al., 2012).
- 2) Recent progresses in geological researches relevant to the Ediacaran–Cambrian periods are opening new windows to decipher the co-evolution of animals and background environments. Chemostratigraphic correlations of various proxies can check the global nature of environmental changes including seawater chemistry. Moreover, the close association of SSF occurrences with the peculiar deposition of huge phosphorites drives us to have a better understanding on the cause–effect links between the animal diversification/biomineralization and environmental perturbations, as previously pointed out by Cook and Shergold (1984). The unique Lower Cambrian phosphorite beds hosting abundant SSFs, particularly in southwestern South China, indicate that a peculiar environmental condition may have appeared in extremely shallow marine settings along a mantle plume-related continental rift zone in South China and have started the very first SSF diversification (Sato et al., 2014-in this issue). This

is against the conventional explanation for the supply of excess phosphorous by coastal upwelling, and invites further investigation and discussion.

- 3) Many metazoan lineages likely escaped from fossilization probably because of the lack of biomineralized hard parts. Our knowledge on the earlier appearances of many non-skeletonized animals in the early Cambrian is largely due to the intensive excavations of numerous exceptionally well-preserved Lagerstätten. This means that the actual appearances of many non-skeletonized phyla might precede their first fossil occurrences currently known, and that the above-discussed pattern of animal diversification may vary significantly with new discoveries, in particular, those from possible Lagerstätten older than the Chengjiang biota. Future test, therefore, is inevitable.
- 4) The evolution of biomineralization itself needs more attention not only from conventional paleontological viewpoints but also from more biological, i.e., physiological approaches based on modern analogs. The acquisition of sensory organs, in particular eyes (e.g., Parker, 2003), definitely had an intimate link to the early biomineralization. Molecular analyses and their comparison with real fossil records will become more necessary.
- 5) On the basis of the standard stratigraphy in South China, the global correlation is definitely needed to check the surface environmental changes during the Ediacaran–Cambrian interval. As South China was located in the mid-latitude of the southern hemisphere during the Cambrian (e.g., Rino et al., 2004), the coeval strata in the low-latitude areas and high to mid-latitude domains of the northern hemisphere will provide vital pieces of information for documenting the animal evolution/radiation pattern on a global context. Following the successfully performed studies for the Permo-Triassic boundary event (e.g., Isozaki, 1997; Isozaki and Ota, 2001; Isozaki et al., 2007; Kani et al., 2013), we need to check and to hunt fossils from unexplored mid-oceanic strata; i.e., deep-sea cherts and shallow marine paleo-atoll carbonates on seamounts from the Ediacaran–Cambrian mid-oceans (e.g., Ota et al., 2007; Uchio et al., 2008; Kawai et al., 2008; Nohda et al., 2013).

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References

- Bailey, J.V., Joye, S.B., Kalanetra, K.M., Flood, B.E., Corsetti, F.A., 2007. Evidence of giant sulphur bacteria in Neoproterozoic phosphorites. *Nature* 445, 198–201.
- Bambach, R.K., 2006. Phanerozoic biodiversity mass extinctions. *Annual Review of Earth Sciences* 34, 127–155.
- Bowring, S.A., Grotzinger, J.P., Isachsen, C.E., Knoll, A.H., Pelechaty, S.M., Kolosov, P., 1993. Calibrating rates of early Cambrian evolution. *Science* 261, 1293–1298.
- Brasier, M.D., Green, O., Shields, G., 1997. Ediacaran sponge spicule clusters from southwestern Mongolia and the origins of the Cambrian fauna. *Geology* 25, 303–306.
- Buckland, W., 1837. *Geology and Mineralogy Considered with Reference to Natural Theology*. William Pickering, London.
- Budd, G.E., 2008. The earliest fossil record of the animals and its significance. *Philosophical Transactions of the Royal Society B* 363, 1425–1434.
- Butterfield, N.J., 2011. Terminal developments in Ediacaran embryology. *Science* 334, 1655–1656.
- Cai, Y., Hua, H., Xiao, S., Schiffbauer, J.D., Li, P., 2010. Biostratigraphy of the late Ediacaran pyritized Gaojiashan Lagerstätte from southern Shaanxi, South China: importance of event deposits. *Palaios* 25, 487–506.

- Cai, Y., Schiffbauer, J.D., Hua, H., Xiao, S., 2011. Morphology and paleoecology of the late Ediacaran tubular fossil *Conotubus hemiannulatus* from the Gaojiashan Lagerstätten of southern Shaanxi Province, South China. *Precambrian Research* 191, 46–57.
- Cai, Y., Schiffbauer, J.D., Hua, H., Xiao, S., 2012. Preservation modes in the Ediacaran Gaojiashan Lagerstätte: pyritization, aluminosilicification, and carbonaceous compression. *Palaeogeography, Palaeoclimatology, Palaeoecology* 326–328, 109–117.
- Cai, Y.P., Hua, H., Zhang, X.L., 2013. Tube construction and life mode of the late Ediacaran tubular fossil *Gaojiashania cyclus* from the Gaojiashan Lagerstätte. *Precambrian Research* 224, 255–267.
- Cai, Y.P., Hua, H., Schiffbauer, J.D., Sun, B., Yuan, X., 2014. Tube growth patterns and microbial mat-related lifestyles in the Ediacaran fossil *Cloudina*, Gaojiashan Lagerstätte, South China. *Gondwana Research* 25, 1008–1018 (in this issue).
- Caron, J., Conway Morris, S., Shu, D.G., Soares, D., 2010. Tentaculate fossils from the Cambrian of Canada (British Columbia) and China (Yunnan) interpreted as primitive deuterostomes. *PLoS One* 5 (3), e9586.
- Carroll, S.B., 2008. Evo-devo and an expanding evolutionary synthesis: A Genetic theory of morphological evolution. *Cell* 134, 25–36.
- Carroll, S.B., Grenier, J.K., Weather, S.D., 2001. From DNA to Diversity: Molecular genetics and the evolution of animal design. Blackwell, Oxford.
- Chen, J.Y., 2004. The Dawn of Animal World. Jiangsu Science and Technology Press, Nanjing (366 pp., in Chinese).
- Chen, J.Y., Huang, D.Y., 2002. A possible Lower Cambrian chaetognath (arrow worm). *Science* 298, 187.
- Chen, J.Y., Zhou, G.Q., 1997. Biology of the Chengjiang fauna. *Bulletin of National Museum of Natural Science, Taichung Taiwan* 10, 11–105.
- Chen, J.Y., Bottjer, D.J., Oliveri, P., Dornbos, S.Q., Gao, F., Ruffins, S., Chi, H.M., Li, C.W., Davidson, E.H., 2004. Small bilaterian fossils from 40 to 55 million years before the Cambrian. *Science* 305, 219–222.
- Chen, J.Y., Schopf, J.W., Bottjer, D.J., Zhang, C.Y., Kudryavtsev, A.B., Tripathi, A.B., Wang, X.Q., Yang, Y.H., Gao, X., Yang, Y., 2007. Raman spectra of a Lower Cambrian ctenophore embryo from southwestern Shaanxi, China. *Proceedings of the National Academy of Sciences USA* 104, 6289–6293.
- Cloud Jr., P.E., 1948. Some problems and patterns of evolution exemplified by fossil invertebrates. *Evolution* 2, 322–350.
- Condon, D., Zhu, M.Y., Bowring, S., Wang, W., Yang, A., Jin, Y., 2005. U–Pb ages from the Neoproterozoic Doushantuo Formation, China. *Science* 308, 95–98.
- Conway Morris, S., Peel, J.S., 2008. The earliest annelids: Lower Cambrian polychaetes from the Sirius Passet Lagerstätte, Peary Land, North Greenland. *Acta Palaeontologica Polonica* 53, 137–148.
- Cook, P.J., Shergold, J.H., 1984. Phosphorus, phosphorites and skeletal evolution at the Precambrian–Cambrian boundary. *Nature* 308, 231–236.
- Dai, T., Zhang, X.L., Peng, S., 2014. Morphology and ontogeny of *Hunanocephalus ovalis* (trilobite) from the Cambrian of South China. *Gondwana Research* 25, 991–998 (in this issue).
- Darwin, C., 1859. On the Origin of Species by Means of Natural Selection. John Murray, London.
- Dong, X.P., Donoghue, P.C.J., Cheng, H., Liu, J.P., 2004. Fossil embryos from middle and late Cambrian period of Hunan, South China. *Nature* 427, 237–240.
- Dong, X.P., Bengtson, S., Gostling, N.J., Cunningham, J.A., Harvey, T.H.P., Kouchinsky, A., Val'kov, A.K., Repetski, J.E., Repetski, J.E., Stampanoni, M., Marone, F., Donoghue, P.C.J., 2010. The anatomy, taphonomy, taxonomy and systematic affinity of *Markuelia*: Early Cambrian to Early Ordovician scolidophorans. *Palaeontology* 53, 1291–1314.
- Droser, M.L., Finnegan, S., 2003. The Ordovician radiation: a followup to the Cambrian explosion. *Integrative and Comparative Biology* 43, 178–184.
- Duan, Y.H., Han, J., Fu, D.J., Zhang, X.L., Yang, X.G., Komiya, T., 2014. The reproductive strategy of bradoriid arthropod *Kumingella douvillei* from the Lower Cambrian Chengjiang Lagerstätte, South China. *Gondwana Research* 25, 983–990 (in this issue).
- Dunn, C.W., Hejnol, A., Matus, D.Q., Pang, K., Browne, W.E., Smith, S.A., et al., 2008. Broad phylogenomic sampling improves resolution of the animal tree of life. *Nature* 452, 745–749.
- Edgecombe, G.D., Giribet, G., Dunn, C.W., Hejnol, A., Kristensen, R.M., Neves, R.C., Rouse, G.W., Worsaae, K., Sorensen, M.V., 2011. Higher-level metazoan relationships: recent progress and remaining questions. *Organisms, Diversity and Evolution* 11, 151–172.
- Erwin, D.H., 2006. Extinction: How life on Earth nearly ended 250 million years ago. Princeton University Press, Princeton.
- Erwin, D.H., 2009. Early origin of the bilaterian developmental toolkit. *Philosophy Transactions of the Royal Society London B* 364, 2253–2261.
- Erwin, D.H., Laflamme, M., Tweedt, S.M., Sperling, E.A., Pisani, D., Peterson, K.J., 2011. The Cambrian conundrum: early divergence and later ecological success in the early history of animals. *Science* 334, 1901–1907.
- Fedonkin, M.A., Waggoner, B.M., 1997. The late Precambrian fossil *Kimberella* is a mollusc-like bilaterian organism. *Nature* 388, 868–871.
- Fu, D.J., Zhang, X.L., 2011. A new arthropod *Jugataccaris agilis* n. gen. n. sp. from the Early Cambrian Chengjiang biota, South China. *Journal of Paleontology* 85, 567–586.
- Fu, D.J., Zhang, X.L., Shu, D.G., 2011. A venomous arthropod in the early Cambrian sea. *Chinese Science Bulletin* 56, 1532–1534.
- Gehling, J., Rigby, J.K., 1996. Long expected sponges from the Neoproterozoic Ediacara fauna of South Australia. *Journal of Paleontology* 70, 185–195.
- Gould, S.J., 1989. Wonderful Life: The Burgess Shale and the Nature of History. Norton, New York.
- Grimaldi, D.A., Engel, M.S., Nascibene, P.C., 2002. Fossiliferous Cretaceous Amber from Myanmar (Burma): Its Rediscovery, Biotic Diversity, and Paleontological Significance, 3361. *American Museum of Natural History*, pp. 1–71.
- Guo, J., Li, Y., Li, G., 2014. Small shelly fossils from the early Cambrian Yanjiahe Formation, Yichang, Hubei, China. *Gondwana Research* 25, 999–1007 (in this issue).
- Haecckel, E., 1866. Generelle Morphologie der Organismen II. Allgemeine Entwicklungsgeschichte Organismen, Berlin.
- Han, J., Kubota, S., Uchida, H., Stanley, G.D.J., Yao, X.-Y., Shu, D.-G., Li, Y., Yasui, K., 2010. Tiny sea anemone from the Lower Cambrian of China. *PLoS One* 5 (10), e13276. <http://dx.doi.org/10.1371/journal.pone.0013276>.
- Han, J., Kubota, S., Li, G., Yao, X.Y., Yang, X., Shu, D.G., Li, Y., Kinoshita, S., Sasaki, O., Komiya, T., Yan, G., 2013. Early Cambrian pentamerous cubozoan embryos from South China. *PLoS One* 8, e70741.
- Holmer, L., Skovsted, C.B., Larsson, C., Brock, G.A., Zhang, 2011. First record of a bivalved larval shell in Early Cambrian tomotoids and its phylogenetic significance. *Palaeontology* 54, 235–239.
- Hou, X.G., Aldridge, R.J., Bergstrom, J., Siveter, David J., Siveter, Derek J., Feng, X.H., 2004. The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life. Blackwell, Oxford (233 pp.).
- Hou, X.G., Aldridge, R.J., Siveter, David J., Siveter, Derek J., Williams, M., Zalasiewicz, J., Ma, X.Y., 2011. An early Cambrian hemichordate zooid. *Current Biology* 21, 612–616.
- Hu, S.X., Steiner, M., Zhu, M.Y., Erdtmann, B.D., Luo, H.L., Chen, L.Z., 2007. Diverse pelagic predators from the Chengjiang Lagerstätte and the establishment of modern-style pelagic ecosystems in the early Cambrian. *Palaeogeography, Palaeoclimatology, Palaeoecology* 254, 307–316.
- Hua, H., Chen, Z., Yuan, X.L., Zhang, L.Y., Xiao, S.H., 2005. Skeletogenesis and asexual reproduction in the earliest biomineralizing animal *Cloudina*. *Geology* 33, 277–280.
- Huang, D.Y., Chen, J.Y., Vannier, J., Saiz Salinas, J.L., 2004. Early Cambrian sipuncular worms from southwest China. *Philosophical Transaction of Royal Society of London, B Biol. Sci.* 271, 1671–1676.
- Huldgren, T., Cunningham, J.A., Yin, C.Y., Stampanoni, M., Marone, F., Donoghue, P.C.J., Bengtson, S., 2011. Fossilized nuclei and germination structures identify Ediacaran “animal embryos” as encysting protists. *Science* 334, 1696–1699.
- Isozaki, Y., 1997. Permo-Triassic boundary Superanoxia and stratified superocean: records from lost deep-sea. *Science* 276, 235–238.
- Isozaki, Y., Ota, A., 2001. Middle/Upper Permian (Maokouan/Wuchapingian) boundary in mid-oceanic paleo-atoll limestone in Kamura and Akasaka, Japan. *Proceedings of Japan Academy* 77B, 104–109.
- Isozaki, Y., Kawahata, H., Ota, A., 2007. A unique carbon isotope record across the Guadalupian–Lopingian (Middle–Upper Permian) boundary in mid-oceanic paleoatoll carbonates: the high-productivity “Kamura event” and its collapse in Panthalassa. *Global and Planetary Change* 55, 21–38.
- Jin, Y.G., Wang, Y., Wang, W., Shang, Q.H., Cao, C.Q., Erwin, D.H., 2000. Pattern of marine mass extinction near the Permian–Triassic boundary in south China. *Science* 289, 432–436.
- Kani, T., Hisanabe, C., Isozaki, Y., 2013. The Capitanian minimum of $^{87}\text{Sr}/^{86}\text{Sr}$ ratio in the Permian mid-Panthalassan paleo-atoll carbonates and its demise by the deglaciation and continental doming. *Gondwana Research* 24, 212–221.
- Kawai, T., Windley, B.F., Terabayashi, M., Yamamoto, H., Isozaki, Y., Maruyama, S., 2008. Neoproterozoic glaciation in the mid-oceanic realm: an example from hemi-pelagic mudstones on Llanddwyn Island, Anglesey, UK. *Gondwana Research* 14, 105–114.
- Kouchinsky, A., Bengtson, S., Runnegar, B., Skovsted, C., Steiner, M., Vendrasco, M., 2012. Chronology of early Cambrian biomineralization. *Geological Magazine* 149, 221–251.
- Landing, E., English, A., Keppie, J.D., 2010. Cambrian origin of all skeletonized metazoan phyla – discovery of Earth's oldest bryozoans (Upper Cambrian, southern Mexico). *Geology* 38, 347–350.
- Lei, Q.P., Han, J., Ou, Q., Wan, X.Q., 2014. Sedentary habits of anthozoa-like animals in the Chengjiang Lagerstätte: Adaptive strategies for Phanerozoic-style soft substrates. *Gondwana Research* 25, 966–974 (in this issue).
- Li, C.W., Chen, J.Y., Tzzen, H., 1998. Precambrian sponges with cellular structures. *Science* 279, 879–882.
- Li, G.X., Steiner, M., Zhu, X.J., Yang, A.H., Wang, H.F., Erdtmann, B.D., 2007. Early Cambrian metazoan fossil record of South China: generic diversity and radiation patterns. *Palaeogeography, Palaeoclimatology, Palaeoecology* 254, 229–249.
- Li, G.X., Zhu, M.Y., Chen, Z., 2011. Animal skeletons, advent. In: Reitner, J., Thiel, V. (Eds.), *Encyclopedia of Geobiology*. Springer, Berlin, pp. 58–64.
- Liu, P.J., Yin, C.Y., Tang, F., 2006. Microtubular metazoan fossils with multi-branches in Weng'an biota. *Chinese Science Bulletin* 51, 630–632.
- Liu, J.N., Shu, D.G., Han, J., Zhang, Z.F., Zhang, X.L., 2007. Origin, diversification, and relationships of Cambrian lobopods. *Gondwana Research* 14, 277–283.
- Liu, P., Yin, C., Gao, L., Tang, F., Chen, S., 2009a. New material of microfossils from the Ediacaran Doushantuo Formation in the Zhangcunping area, Yichang, Hubei Province and its zircon SHRIMP U–Pb age. *Chinese Science Bulletin* 54, 1058–1064.
- Liu, Y.H., Li, Y., Gong, H.J., Zhang, Z.G., Ma, Q.H., Lu, X.Q., Chen, J., Yan, T.T., 2009b. New data on *Quadrapyrgites* from the earliest Cambrian of South China. *Acta Palaeontologica Sinica* 48, 688–694.
- Liu, J.N., Steiner, M., Dunlop, J.A., Keupp, H., Shu, D.G., Ou, Q., Han, J., Zhang, Z.F., Zhang, X.L., 2011. An armoured Cambrian lobopodian from China with arthropod-like appendages. *Nature* 470, 526–530.
- Liu, P.J., Yin, C.Y., Chen, S.M., Tang, F., Gao, L.Z., 2013. The biostratigraphic succession of acanthomorphic acritarchs of the Ediacaran Doushantuo Formation in the Yangtze Gorges area, South China and its biostratigraphic correlation with Australia. *Precambrian Research* 176. <http://dx.doi.org/10.1016/j.precamres.2011.07.009> (in press, online:).
- Love, G.D., Grosjean, E., Stalvies, C., Fike, D.A., Grotzinger, J.P., Bradley, A.S., Kelly, A.E., Bhatia, M., Meredith, W., Snape, C.E., Bowring, S.A., Condon, D.J., Summons, R.E., 2009. Fossil steroids record the appearance of Demospongiae during the Cryogenian period. *Nature* 457, 718–721.
- Ma, X.Y., Hou, X.G., Edgecombe, G.D., Strausfeld, N.J., 2012. Complex brain and optic lobes in an early Cambrian arthropod. *Nature* 490, 258–261.

- Maletz, J., 2011. Radiolarian skeletal structures and biostratigraphy in the early Paleozoic (Cambrian–Ordovician). *Palaeoworld* 20, 116–133.
- Maloo, A., Porter, S.M., Moores, J.L., Dudas, F.O., Bowring, S.A., Higgins, J.A., Fike, D.A., Eddy, M.P., 2010. The earliest Cambrian record of animals and ocean geochemical change. *Geological Society of America Bulletin* 122, 1731–1774.
- Marcy, G., 2009. Water world larger than Earth. *Nature* 462, 853–854.
- Margulis, L., Schwartz, K.V., 1982. Five Kingdoms: Illustrated Guide to the Phyla of Life on Earth. W.H. Freeman.
- Marshall, C.R., 2006. Explaining the Cambrian “explosion” of animals. *Annual Review of Earth and Planetary Sciences* 34, 355–384.
- Müller, K.J., Waloszek, D., Zakharov, A., 1995. Orsten type phosphatized soft-integument preservation and a new record from the Middle Cambrian Kuonamka Formation in Siberia. *Neues Jahrbuch für Geologie und Paläontologie* 197, 101–118.
- Na, L., Li, G.X., 2011. Nail-shaped sclerite fossils from the lower Cambrian Xihaoping Member of Fangxian, Hubei Province. *Acta Micropalaeontologica Sinica* 28, 284–300 (in Chinese with English abstract).
- Narbonne, G.M., Xiao, S.H., Shields, G.A., 2012. The Ediacaran period. In: Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), *The Geologic Time Scale 2012*. Elsevier, Amsterdam, pp. 413–435.
- Nielsen, C., 2012. *Animal Evolution: Interrelationships of the Living Phyla*, 3rd edition. Oxford University Press, Oxford (402 pp.).
- Nohda, S., Wang, B.S., You, C.F., Isozaki, Y., Uchio, Y., Buslov, M.M., Maruyama, S., 2013. The oldest (Early Ediacaran) Sr isotope record of mid-ocean surface seawater: chemostratigraphic correlation of a paleo-atoll limestone in southern Siberia. *Journal of Asian Earth Sciences* 77, 66–76.
- Okada, Y., Sawaki, Y., Komiya, T., Hirata, T., Takahata, N., Sano, Y., Han, J., Maruyama, S., 2014. New chronological constraints for Cryogenian to Cambrian rocks in the Three Gorges, Weng’an and Chengjiang areas, South China. *Gondwana Research* 25, 1027–1044 (in this issue).
- Ota, T., Utsunomiya, A., Uchio, Y., Isozaki, Y., Buslov, M.M., Ishikawa, A., Maruyama, S., Kitajima, K., Kaneko, Y., Yamamoto, H., Katayama, I., 2007. Geology of the Gorny Altai subduction-accretion complex, southern Siberia: tectonic evolution of an Ediacaran–Cambrian intra-oceanic arc–trench system. *Journal of Asian Earth Sciences* 30, 666–695.
- Ou, Q., Conway Morris, S., Han, J., Zhang, Z.F., Liu, J.N., Chen, A.L., Zhang, X.L., Shu, D.G., 2012a. Evidence for gill slits and a pharynx in Cambrian vetulicolians: implications for the early evolution of deuterostomes. *BMC Biology* 10, 81.
- Ou, Q., Shu, D., Mayer, G., 2012b. Cambrian lobopodians and extant onychophorans provide new insights into early cephalization in Panarthropoda. *Nature Communications* 3, 1261.
- Ou, Q., Liu, J.N., Shu, D.G., Han, J., Zhang, Z.F., Wan, X.Q., Lei, Q.P., 2011. A rare onychophoran-like lobopodian from the lower Cambrian Chengjiang Lagerstätte, Southwestern China, and its phylogenetic implications. *Journal of Paleontology* 85, 587–594.
- Parker, A., 2003. *In the Blink of an Eye*. Perseus, Cambridge (316 pp.).
- Peel, J.S., 2010. A corset-like fossil from the Cambrian Sirius Passet Lagerstätte of North Greenland and its implications for cycloneuralian evolution. *Journal of Paleontology* 84, 332–340.
- Peng, S.C., Babcock, L.E., Cooper, R.A., 2012. The Cambrian period. In: Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), *The Geologic Time Scale*. Elsevier, Amsterdam, pp. 437–488.
- Philippe, H., Derelle, R., Lopez, P., et al., 2009. Phylogenomics revives traditional views on deep animal relationships. *Current Biology* 19, 706–712.
- Poinar, G.J., Buckley, R., 2006. Nematode (Nematoda: Mermithidae) and hairworm (Nematomorpha: Chordolidae) parasites in the early Cretaceous amber. *Journal of Invertebrate Pathology* 93, 36–41.
- Poinar, G.J., Kerp, H., Hass, H., 2008. *Palaeonema phyticum* gen. n., sp. n. (Nematoda: Palaeonematidae fam. n.), a Devonian nematode associated with early land plants. *Nematology* 10, 9–14.
- Porter, S.M., 2007. Seawater chemistry and early carbonate biomineralization. *Science* 316, 1302.
- Qian, Y. (Ed.), 1999. *Taxonomy and Biostratigraphy of Small Shelly Fossils in China*. Beijing, Science Press (247 pp.).
- Reitner, J., 1992. Coralline spongiens: Der versuch einer phylogenetisch-taxonomischen analyse. *Berliner Geowissenschaftliche Abhandlung Reihe E (Paläobiologie)* 1, 1–352.
- Reitner, J., Wörheide, G., 2002. A guide to the classification of sponges. In: Hooper, J.N.A., Van Soest, R.W.M. (Eds.), *Systema Porifera*. Kluwer Academic/Plenum, New York, pp. 52–68.
- Rino, S., Komiya, T., Windley, B.F., Katayama, I., Motoki, A., Hirata, T., 2004. Major episodic increases of continental crustal growth determined from zircon ages of river sands; implications for mantle overturns in the Early Precambrian. *Physics of the Earth and Planetary Interiors* 146, 369–394.
- Rowland, S.M., Hicks, M., 2004. The early Cambrian experiment in reef-building by metazoans. In: Lipps, J.H., Waggoner, B.M. (Eds.), *Neoproterozoic–Cambrian Biological Revolutions*. The Paleontological Society Papers, 10, pp. 107–124.
- Sato, T., Isozaki, Y., Hitachi, T., Shu, D.G., 2014. A unique condition for early diversification of small shelly fossils in the lowermost Cambrian in Chengjiang, South China: Enrichment of phosphorus in restricted embayments. *Gondwana Research* 25, 1139–1152 (in this issue).
- Sawaki, Y., Ohno, T., Tahata, M., Komiya, T., Hirata, T., Maruyama, S., Windley, B.F., Han, J., Shu, D.G., Li, Y., 2010. The Ediacaran radiogenic Sr isotope excursion in the Doushantuo Formation in the three gorges area, South China. *Precambrian Research* 176, 46–64.
- Sedgwick, A., 1852. On the classification and nomenclature of the Lower Paleozoic rocks of England and Wales. *Quarterly Journal of the Geological Society* 8, 136–168.
- Sedgwick, A., Murchison, R.I., 1835. On the Silurian and Cambrian Systems, exhibiting the order in which the older sedimentary strata succeed each other in England and Wales. *The London and Edinburgh Philosophical Magazine and Journal of Science* 7, 483–535.
- Servais, T., Owen, A.W., Harper, D.A.T., Kröger, B., Munnecke, A., 2010. The Great Ordovician Biodiversification Event (GOBE): the palaeoecological dimension. *Palaeogeography, Palaeoclimatology, Palaeoecology* 294, 99–119.
- Shu, D., 2008. Cambrian explosion: birth of tree of animals. *Gondwana Research* 14, 219–240.
- Shu, D.G., Luo, H.L., Conway Morris, S., Zhang, X.L., Hu, S.X., Chen, L., Han, J., Zhu, M., Li, Y., Chen, I.Z., 1999. Lower Cambrian vertebrates from South China. *Nature* 402, 42–46.
- Shu, D.G., Chen, L., Han, J., Zhang, X.L., 2001a. An Early Cambrian tunicate from China. *Nature* 411, 472–473.
- Shu, D.G., Conway Morris, S., Han, J., Chen, L., Zhang, X.L., Zhang, Z.F., Liu, H.Q., Li, Y., Liu, J.N., 2001b. Primitive deuterostomes from the Chengjiang Lagerstätte (Lower Cambrian, south China). *Nature* 414, 419–424.
- Shu, D.G., Conway Morris, S., Han, J., Zhang, Z.F., Yasui, K., Janvier, P., Chen, L., Zhang, X.L., Liu, J.N., Li, Y., Liu, H.Q., 2003. Head and backbone of the Early Cambrian vertebrate *Haikouichthys*. *Nature* 421, 526–529.
- Shu, D.G., Conway Morris, S., Han, J., Zhang, Z.F., Liu, J.N., 2004. Ancestral echinoderms from the Chengjiang deposits of China. *Nature* 430, 422–428.
- Shu, D., Conway Morris, S., Han, J., Li, Y., Zhang, X., Hua, H., Zhang, Z., 2006. Lower Cambrian vendobionts from China and early diploblast evolution. *Science* 312, 731–734.
- Shu, D.G., Zhang, X.L., Han, J., Zhang, Z.F., Liu, J.N., 2009. Restudy of Cambrian explosion and formation of animal tree. *Acta Palaeontologica Sinica* 48, 414–427 (in Chinese with English abstract).
- Shu, D.G., Conway Morris, S., Zhang, Z.F., Han, J., 2010. The earliest history of the deuterostomes, the importance of the Chengjiang Fossil-Lagerstätte. *Proceedings of the Royal Society Series B* 277, 165–174.
- Skovsted, C.B., Brock, G.A., Topper, T.P., Paterson, J.R., Holmer, L.E., 2011. Scleritome construction, biofacies, biostratigraphy and systematics of the tommotiid *Eccentrotheca helenia* sp. nov. from the early Cambrian of South Australia. *Paleontology* 54, 253–286.
- Smith, A.B., 2012. Cambrian problematica and the diversification of deuterostomes. *BMC Biology* 10, 81.
- Sperling, E.A., Vinther, J., 2010. A placozoan affinity for *Dickinsonia* and the evolution of late Proterozoic metazoan feeding modes. *Evolution & Development* 12, 201–209.
- Steiner, M., Li, G.X., Qian, Y., Zhu, M.Y., Erdtmann, B.-D., 2007. Neoproterozoic to early Cambrian small shelly fossil assemblages and a revised biostratigraphic correlation of the Yangtze Platform (China). *Palaeogeography, Palaeoclimatology, Palaeoecology* 254, 67–99.
- Steiner, M., Hu, S.X., Liu, J., Keupp, H., 2012. A new species of *Hallucigenia* from the Cambrian Stage 4 Wulongqing Formation of Yunnan (South China) and the structure of sclerites in lobopodians. *Bulletin of Geosciences* 87, 107–124.
- Szaniawski, H., 2002. New evidence for the protoconodont origin of chaetognaths. *Acta Palaeontologica Polonica* 47, 405–419.
- Tahata, M., Ueno, Y., Ishikawa, T., Sawaki, Y., Murakami, K., Han, J., Shu, D.G., Li, Y., Guo, J.F., Yoshida, N., Komiya, T., 2013. Carbon and oxygen isotope chemostratigraphies of the Yangtze platform, South China: decoding temperature and environmental changes through the Ediacaran. *Gondwana Research* 23, 333–353.
- Tang, F., Bengtson, S., Wang, Y., Wang, X.L., Yin, C.Y., 2011. *Eoandromeda* and the origin of Ctenophora. *Evolution & Development* 13, 408–414.
- Todd, J.A., Taylor, P.D., 1992. The first fossil entoproct. *Naturwissenschaften* 79, 311–314.
- Uchio, Y., Isozaki, Y., Buslov, M.M., Maruyama, S., 2008. Occurrence of phosphatic microfossils in an Ediacaran–Cambrian mid-oceanic paleo-atoll limestone of southern Siberia. *Gondwana Research* 14, 183–192.
- Van Roy, P., Orr, P.J., Botting, J.P., Muir, L.A., Vinther, J., Lefebvre, B., Hariri, K., Briggs, D.E.G., 2010. Ordovician faunas of Burgess Shale type. *Nature* 465, 215–218.
- Wang, H.Z., Zhang, Z.F., Holmer, L.E., Hu, S.X., Wang, X.R., Li, G.X., 2012. Peduncular attached secondary tiering acrotretoid brachiopods from the Chengjiang fauna: implications for the ecological expansion of brachiopods during the Cambrian explosion. *Palaeogeography, Palaeoclimatology, Palaeoecology* 323–325, 60–67.
- Whittington, H.B., 1985. *The Burgess Shale*. Yale University Press, New Haven.
- Wood, R., Zhuravlev, A.Y., 2012. Escalation and ecological selectivity of mineralogy in the Cambrian Radiation of skeletons. *Earth-Science Review* 115, 249–261.
- Xiao, S.H., Laflamme, M., 2009. On the eve of animal radiation: phylogeny, ecology and evolution of Ediacara biota. *Trends in Ecology & Evolution* 24, 31–40.
- Xiao, S.H., Zhang, Y., Knoll, A.H., 1998. Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite. *Nature* 391, 553–558.
- Xiao, S.H., Yuan, X., Knoll, A.H., 2000. Eumetazoan fossils in terminal Proterozoic phosphorites? *Proceedings of the National Academy of Sciences, USA* 97, 13684–13689.
- Yao, X.Y., Han, J., Jiao, G.Q., 2011. Early Cambrian epibolic gastrulation: a perspective from the Kuanchuanpu Member, Dengying Formation, Ningqiang, Shaanxi, South China. *Gondwana Research* 20, 844–851.
- Yuan, X.L., Chen, Z., Xiao, S.H., Zhou, C.M., Hua, H., 2011. An early Ediacaran assemblage of macroscopic and morphologically differentiated eukaryotes. *Nature* 470, 390–393.
- Zhang, X.G., Pratt, B.R., 2012. The first stalk-eyed phosphatocopine crustacean from the Lower Cambrian of China. *Current Biology* 22, 2149–2154.
- Zhang, X.L., Reitner, J., 2006. A fresh look at *Dickinsonia*: removing it from Vendobionta. *Acta Geologica Sinica* 80, 636–642.
- Zhang, X.G., Siveter, D.J., Waloszek, D., Maas, A., 2007. An epidomite-bearing crown-group crustacean from the Lower Cambrian. *Nature* 449, 595–598.
- Zhang, X.G., Maas, A., Haug, J.T., Siveter, D.J., Waloszek, D., 2010. A eucrustacean metanauplius from the Lower Cambrian. *Current Biology* 20, 1075–1079.
- Zhang, Z.F., Holmer, L.E., Ou, Q., Han, J., Shu, D.G., 2011a. The exceptionally preserved Early Cambrian stem rhynchonelliform brachiopod *Longtancunella* and its implications. *Lethaia* 44, 490–495.
- Zhang, Z.F., Holmer, L.E., Popov, L.E., Shu, D.G., 2011b. An obolellate brachiopod with soft-part preservation from the early Cambrian Chengjiang fauna of China. *Journal of Paleontology* 85, 462–465.

- Zhang, Z.F., Holmer, L.E., Robson, S.P., Hu, S.X., Wang, X.R., 2011c. First record of repaired durophagous shell damages in Early Cambrian lingulate brachiopods with preserved pedicles. *Palaeogeography, Palaeoclimatology, Palaeoecology* 302, 206–212.
- Zhang, Z.F., Holmer, L.E., Skovsted, C.B., Brock, G.A., Budd, G.E., Fu, D.J., Zhang, X.L., Shu, D.G., Han, J., Liu, J.N., Wang, H.Z., Butler, A., Li, G.X., 2013. A sclerite-bearing stem group entoproct from the early Cambrian and its implications. *Scientific Reports* 3, 1–10.
- Zhang, Z.F., Holmer, L.E., Skovsted, C.B., Brock, G.A., Budd, G.E., Fu, D.J., Zhang, X.L., Shu, D.G., Han, J., Liu, J.N., Wang, H.Z., Butler, A., Li, G.X., 2013. A sclerite-bearing stem group entoproct from the early Cambrian and its implications. *Scientific Reports* (in press).
- Zhang, X.L., Shu, D.G., Han, J., Zhang, Z.F., Liu, J.N., Fu, D.J., 2014. Triggers of the Cambrian explosion: hypotheses and problems. *Gondwana Research* 25, 896–909.
- Zhu, M.Y., Zhang, J.M., Yang, A.H., 2007. Integrated Ediacaran (Sinian) chronostratigraphy of South China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 254, 7–61.
- Zhu, M.Y., Gehling, J.G., Xiao, S.H., Zhao, Y.L., Droser, M.L., 2008. Eight-armed Ediacara fossil preserved in contrasting taphonomic windows from China and Australia. *Geology* 36, 867–870.
- Zhu, M.Y., Lu, M., Zhang, J.M., Zhao, F.C., Li, G.X., Yang, A.H., Zhao, X., Zhao, M.J., 2013. Carbon isotope chemostratigraphy and sedimentary facies evolution of the Ediacaran Doushantuo Formation in western Hubei, South China. *Precambrian Research* 176. <http://dx.doi.org/10.1016/j.precamres.2011.07.019> (in press, online:).
- Zhuravlev, A.Y., Riding, R., 2001. Introduction. In: Zhuravlev, A.Y., Riding, R. (Eds.), *The Ecology of the Cambrian Radiation*. Columbia University Press, New York, pp. 1–7.



Xingliang Zhang is a professor at the Department of Geology, Northwest University (NWU), and serves as Vice-Chairman of the International Subcommission of Cambrian Stratigraphy, ICS. He received his Ph.D. in Paleontology and Stratigraphy from NWU. He also worked as a Humboldt Research Fellow at University of Göttingen, Germany, and a postdoctoral research fellow at National Museum of Natural History, Smithsonian Institution, USA. He is a section editor for *Encyclopedia of Geobiology*, and author of the textbook, *Lecture Notes of Geobiology*. His current research interests include the evolution of animals during the Cambrian explosion, and microbial contributions to rocks and minerals.



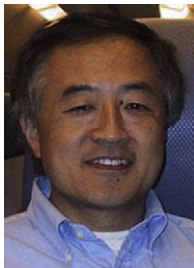
Jian Han is an associate professor at the Department of Geology, Northwest University. Here, he obtained his Ph.D. He also worked as a visiting scholar at Göttingen University, Germany. He has 17 years experience in the study of the Cambrian Chengjiang fauna in Yunnan Province, China. His main research interests include priapulid worms and deuterostomes from the Chengjiang fauna. His recent work centered on the fossil cnidarian embryos from the early Cambrian Kuanchuanpu Formation, Shaanxi Province, China.



Degan Shu is a Distinguished Professor of Evolutionary Paleobiology at Northwest University, PR China. He received his undergraduate training in Paleontology at Peking (Beijing) University, and Ph.D. from China University of Geosciences (Beijing). His research mainly focuses on evolution of early deuterostomes. He discovered the first fish in life history and erected the Phylum Vetulicolia, first proposed the concept or hypothesis “Cambrian Explosion as the unique three-episode event to create the Tree of Animals” in 2008. As a member of Chinese Academy of Sciences and recipient of National First Grade Award of Natural Science, he has authored a dozen of publications in *Nature* and *Science*.



Shigenori Maruyama is a Professor at Earth-Life Science Institute, Tokyo Institute of Technology, graduated with a BSc (1972) from Tokushima University, Japan, and a PhD (1981) from Nagoya Univ., Japan. He became an assistant professor at Toyama University in 1978, a post-doc at Stanford University, USA, moved to the University of Tokyo in 1991 as an associate professor, and in 1994 he became a professor at the Tokyo Institute of Technology. He undertook extensive fieldwork in Japan 1971–1989, in California and the western coast of Canada 1981–1989, and over the world since 1990, after he initiated the decoding Earth History program in over 25 countries. Since 1994 he has organized the multi-disciplinary program, “Superplume Project” supported by STA, Japan, combining geophysics, isotope geochemistry, UHP experiments, and world geology. Major results from this work were published in the edited book, “Superplumes; Beyond Plate Tectonics”, Springer, 569 p. (2007). Current interest is origin and evolution of life in the framework of Galaxy-Genome.



Yukio Isozaki is a professor at the Department of Earth Science & Astronomy, The University of Tokyo. After the Ph.D. education in Geology at Osaka City University, he served as an assistant professor at Yamaguchi University, then associate professor at Tokyo Institute of Technology, before moving to Univ. of Tokyo. His research mainly focuses on subduction-related tectonics/orogeny and history of life, with main contributions in the proposal/definition of ocean plate stratigraphy (OPS) for ancient accretionary complexes, in summarizing the tectonic evolution of the Japanese Islands, and in the discovery of the “superanoxia” and “Kamura cooling event” relevant to the end-Permian mass extinction.