Current understanding on the Cambrian Explosion: questions and answers

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Received: 25 January 2021 / Accepted: 22 May 2021 / Published online: 14 July 2021
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Abstract

The Cambrian Explosion by nature is a three-phased explosion of animal body plans alongside episodic biomineralization, pulsed change of generic diversity, body size variation, and progressive increase of ecosystem complexity. The Cambrian was a time of crown groups nested by numbers of stem groups with a high-rank taxonomy of Linnaean system (classes and above). Some stem groups temporarily succeeded while others were ephemeral and underrepresented by few taxa. The high number of stem groups in the early history of animals is a major reason for morphological gaps across phyla that we see today. Most phylum-level clades achieved their maximal disparity (or morphological breadth) during the time interval close to their first appearance in the fossil record during the early Cambrian, whereas others, principally arthropods and chordates, exhibit a progressive exploration of morphospace in subsequent Phanerozoic. The overall envelope of metazoan morphospace occupation was already broad in the early Cambrian though it did not reach maximal disparity nor has diminished significantly as a consequence of extinction since the Cambrian. Intrinsic and extrinsic causes were extensively discussed but they are merely prerequisites for the Cambrian Explosion. Without the molecular evolution, there could be no Cambrian Explosion. However, the developmental system is alone insufficient to explain Cambrian Explosion. Time-equivalent environmental changes were often considered as extrinsic causes, but the time coincidence is also insufficient to establish causality. Like any other evolutionary event, it is the ecology that make the Cambrian Explosion possible though ecological processes failed to cause a burst of new body plans in the subsequent evolutionary radiations. The Cambrian Explosion is a polythetic event in natural history and manifested in many aspects. No simple, single cause can explain the entire phenomenon.

Keywords Cambrian explosion · Metazoa · Bilateria · Evolution · Darwin's dilemma

Introduction

The Cambrian Explosion is by far the most dramatic chapter in the annals of animal evolutionary history, which laid foundations for animal evolution since the Phanerozoic. The topic has been frequently reviewed by multiple authors and in multiple languages (e.g., Seilacher 1956, 1997; Brasier 1979; Erwin 1991, 2020; Fortey et al. 1996; Conway Morris

2000, 2006; Elicki 2003; Marshall 2006; Shu 2008; Erwin and Valentine 2013; Zhang and Shu 2014; Shu et al. 2014; Zhang et al. 2014; Briggs 2015; Sperling and Stockey 2018), including two German publications in this journal (Sdzuy 1960; Geyer 1998). Interestingly, the review by Sdzuy (1960) was centered on the question about the poverty of animal fossils in the Precambrian and provided an explanation. The paper was organized more or less in a question-and-answer format. Over the last six decades or more, our knowledge on the nature of the Cambrian Explosion has been growing in many folds through multidisciplinary investigations, and a three-phased pattern and sequence was proposed (Cloud 1948; Shu 2008). However, its cause is still poorly understood and thus was listed as one of the Science's mysteries in many places. On the basis of currently update knowledge, here we address a current understanding on this unprecedented evolutionary event in the form of questions and answers in order to benefit a broader readership.

Handling Editor: Joachim Reitner.

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What is the Cambrian Explosion?

The Cambrian Explosion initially stemmed from a palaeontological phenomenon, i.e., the relatively sudden appearance of skeletal remains of diverse animals in the lowest known fossiliferous rocks of the Cambrian, which was noted by William Buckland (1786–1856) in 1930s. The notion could be found in his contribution to the famous Bridgewater treatises, the two volumes entitled “*Geology and mineralogy considered with reference to natural theology* (Pickering, London, 1836)”, which was mentioned in books by Conway Morris (1998) and Levinton (2001). Charles Darwin (1809–1882) thought it a grave difficulty to his theory of evolution and demanded a particular explanation that was hypothetically attributed to imperfection of geological record (Darwin 1859). For quite a long time, the “missing Precambrian history of animal life” stood out as one of the greatest unsolved mysteries in natural science (Schopf 2000). It was Preston Cloud (1912–1991) who alternatively proposed a hypothesis that the diversification of the early Cambrian faunas might be in large part a matter of eruptive evolution in a three-step pattern and sequence: “(1) *relatively sudden appearance of marked variability*; (2) *probable availability and proximity*

of a variety of ecologic niches; and, finally, (3) *increased selective pressure, resulting in the weeding out of inadap-tive or poorly adaptive radicles and leading to a more regularly channeled evolutionary phase for the particular stock involved*” (Cloud 1948), which is conformed to the mode of quantum evolution with an explosive phase (Simpson 1944: fig. 35) (Fig. 1). Such a rapid manner of animal diversification during the Precambrian–Cambrian transition was subsequently called Cambrian explosive evolution (e.g., Seilacher 1956), Cambrian Explosion or radiation (Brasier 1979), and Evolution’s big bang (Levinton 1992; Nash 1995). The term “explosion” is favored here for the marked differences from adaptive radiations in the subsequent geological periods (Erwin and Valentine 2013; Zhan 2018).

Extensive and intensive investigations have shown that the Cambrian Explosion is neither a single event nor purely a biological process, but a stepwise evolutionary event of great magnitude that was manifested in many aspects, e.g., burst of animal body plans, increase of body size, acquisition of biomineralized skeletons, substrate revolution, increase of ecosystem complexity, environmental perturbations and so on. All these will be discussed in following sections.

Fig. 1 Diagram reminiscent of eruptive evolution of Cambrian faunas proposed in Cloud (1948). Redrawn after Simpson (1944: fig. 35)

Was the Darwin's dilemma resolved?

The contrast between Precambrian rocks almost barren of animal fossils and Cambrian rocks in which they may abound had puzzled scientists for over 100 years and was referred to Darwin's dilemma (e.g., Schopf 2000; Conway Morris 2006). However, Darwin himself inferred "... *if the theory be true, it is indisputable that before the lowest Silurian (revised to Cambrian in later editions) stratum was deposited long periods elapsed, as long as, or probably far longer than, the whole interval from the Silurian (Cambrian) age to the present day; and that during these vast periods the world swarmed with living creatures* (Darwin 1859: 287)." The discovery of *Eozoon canadense*, once identified as fossilized shells of giant foraminiferans and later reinterpreted as a pseudofossil (see discussion in Schopf 2000), in the Precambrian Laurentian Formation of Canada was cited by Darwin to support his inference about the existence of living beings long before the Cambrian Period (Darwin 1872). On the one hand, Darwin thought the Cambrian Explosion was inexplicable using his theory and on the other hand he seemed to firmly believe his explanations. This paradoxical combination may lead him draw a conclusion in the end of the Chapter 9 of *On the imperfection of geological record*, which stated "*On this view the difficulties (to his theory of evolution) above discussed are greatly diminished or even disappear* (Darwin 1859: 311)". Taking this case into consideration, it was difficult to know if Darwin really had a dilemma on the Cambrian Explosion.

The hunt for Precambrian fossils has never been ceasing since 1850s. Specimens of *Eozoon* were first discovered in 1858, a year before publication of Darwin's theory of evolution, although their biological interpretation finally collapsed. Since then, of course, much has been learnt. It is, however, a very difficult journey! The existence of life before the Cambrian became widely accepted until 1950s (Schopf 2000). Multidisciplinary investigations did extend the life history deep into Archean (e.g., Shen et al. 2001; Duda et al. 2016; Tashiro et al. 2017; Lepot 2020; Mißbach et al. 2021) but only heightened the sharpness of the beginnings of animal fossils across the Ediacaran–Cambrian transition. All fossil records still point to an explosion of animal life near the beginning of the Cambrian (Levinton 1992), please see discussions below.

What does the fossil record tell us?

Precambrian palaeontologists are at loss to search for animal remains in ancient rocks, but results are somewhat awkward. The findings do not extend the dawn of animal

life much further back. Body, trace, and chemical remains of animals are not as ancient as Darwin predicted but have been found in the time slice just before the Cambrian, i.e., late Ediacaran (~580.0–538.8 Ma). Moreover, most Ediacaran candidates of animals are a bit weird and thus difficult to be placed in any known animal group. More familiar animals arrived in the early Cambrian.

Body fossils

The Ediacaran was far from lifeless, but it was a difficult world! The most impressive fossil record is the three Ediacara-type macrofossil assemblages, termed the Avalon, White Sea, and Nama, occurring in loosely ascending stratigraphic order (Waggoner 2003; Xiao and Laflamme 2009; Boag et al. 2016). Early workers interpreted these soft-bodied organisms as ancestors of later animal phyla based on their symmetry and general appearance (e.g., Glaessner 1984), which appeared to undermine the importance of the Cambrian Explosion. On the contrary, Pflug (1972, 1974) interpreted some forms from the Nama assemblages as colonial organisms (*Petalonamae*) unrelated to modern animals. Seilacher (1989, 1992) went even further to propose that the bulk of the Ediacara-type fossils were representing an extinct kingdom, the Vendobionta, on the basis of their shared characters: foliate bodies, quilted construction, lack of organs, and occurring as impressions. His assignments were later modified by himself (Seilacher 2007). The core members of vendobionts were placed into an extinct group allied to rhizpodean protists such as the *Xenophyophoria* as originally suggested by Zhuravlev (1993). The vendobiont hypothesis implied that the Cambrian Explosion was accompanied with a major extinction event, which re-established the importance of the Cambrian Explosion (Seilacher 1997). Now most Ediacaran workers tend to consider Ediacarans as a grab bag of disparate life forms (Watson 2020) rather than treat them as a homogeneous group. A couple of vendobionts and some newly discovered forms were interpreted as different lineages within the Metazoa (Watson 2020), e.g., *Dickinsonia* as a ctenophore (Zhang and Reitner 2006) or placozoan (Sperling and Vinther 2010), *Haoootia* as a cnidarian (Liu et al. 2014a, b), *Kimberella* as a mollusk (Fedonkin and Waggoner 1997), and *Yilingia* as an annelid or arthropod (Chen et al. 2019). Accordingly, the prominent status of the Cambrian Explosion in life history was questioned again by some researchers (see Watson 2020). However, such placements were mostly based on general resemblance rather than shared diagnostic features. These forms are difficult to relate to living phyla and it is hard to find decedents for them in Cambrian faunas. They were Ediacarans and died off at the end of the Ediacaran. The majority of Cambrian faunas are newcomers.

Of course, there are other taphonomic windows that contain different body designs. Notably, microfossil assemblages from the Ediacaran phosphatic deposits (Xiao and Knoll 2000; Zhang and Zhang 2017) yield abundant spherical fossils that demonstrate patterns of cell adhesion similar to animals (Yin et al. 2019) but they are not necessarily metazoan embryos (Zhang and Zhang 2017; Erwin 2020). Additionally, Ediacaran fossils contain abundant and diverse organisms with a tubular morphology (Fig. 2), including forms either fully soft-bodied or lightly mineralized (Cai et al. 2013; Schiffbauer 2016; Schiffbauer et al. 2016). The tubes are not confined to any particular facies but can be present in both siliciclastic and carbonate rocks. Ediacaran tubes were frequently compared to metazoans with a tubular construction. However, such a simple constructional morphology is utilized today by a variety of multicellular organisms from disparate kingdoms and hence these tubes may very well be a polyphyletic group (Droser et al. 2017). Most Ediacaran tubes went extinct near the Ediacaran–Cambrian boundary though a couple of taxa have a stratigraphical distribution overlapping the lower range of the earliest small shelly fossils of the Cambrian (Yang et al. 2016; Zhu et al. 2017; Cai et al. 2019).

The Cambrian was a refreshed world! Everything looked new to Ediacarans and was much easier to understand. Most living animal phyla made their first appearance in the fossil record during the first 20 million years of the Cambrian Period (Erwin et al. 2011; Zhang and Shu 2014; Shu et al. 2014). Most fossils can be comfortably placed into a stem or crown group of a living phylum. Apart from small shelly fossils that are skeletal remains of many animal lineages, soft-bodied worm-like animal reaching 14 mm wide and 25 cm long was discovered from a sandstone surface of the

Fig. 2 A specimen from the late Ediacaran Gaojiashan Member of the Dengying Formation, Ningqiang, Shaanxi, South China, showing an enigmatic tubular fossil *Gaojiashania* (arrows) along with burrows (image courtesy of Hong Hua)

lowest Cambrian (Zhang et al. 2017a). The preservation is similar to Ediacara-type biotas, which implies that this type of taphonomic window persists into the earliest Cambrian. Many more soft-bodied forms were found in Burgess Shale-type biotas, such as Chengjiang and Qingjiang (Hou et al. 2017; Fu et al. 2019). The Fortunian (ca 533.8–529.0 Ma) phosphorous deposits of the Kuanchuanpu Formation yield diverse of small shelly fossils along with soft-bodied meiofaunas (Bengtson and Yue 1997; Liu et al. 2014a, b). In contrast, there is no unambiguous evidence for metazoans among Ediacaran phosphorous deposits, e.g., the Weng'an biota (Xiao and Knoll 2000) and the Zhenba microfossil assemblage (Zhang and Zhang 2017), though fossils are super abundant. Remarkably similar taphonomic windows yield quite different biotas, which again manifests the power of the Cambrian Explosion (Bottjer et al. 2020).

Trace fossils

The trace-fossil record is continuous through the Ediacaran–Cambrian transition and supports an explosive evolution (Seilacher 1956, 1999; Jensen 2003; Jensen et al. 2005; Mángano and Buatois 2014, 2016). A four-phase evolutionary model was recently proposed (Mángano and Buatois 2020). Late Ediacaran phase 1 is represented by very simple, unbranched trails and shallow burrows (Fig. 2), which demonstrates the presence of motile benthic bilaterians in the Ediacaran; phase 2 (broadly correlated to the Nama Assemblage of the latest Ediacaran) demonstrates a moderate intensity of bioturbation as evidenced by the appearance of more complex and penetrative burrows, bulldozing traces, and drilling predation; phase 3 (the Fortunian, ~538.8–529.0 Ma) is characterized by an unparalleled increase in the number of trace-fossil morphologies, essentially providing overwhelming evidence of a rapid diversification of body plans; phase 4 (~529–509 Ma) reveals an increase in depth and extent of bioturbation and a renewed diversification at ichnogenus level. Although simple traces of bilateral animals were present by 560 Ma (Jensen et al. 2005) or early (Pecoits et al. 2012) and a possible trackway of a bilaterian with paired appendages was found in the latest Ediacaran (Chen et al. 2018), the full suite of metazoan trace fossils that reflect a rapid diversification of body plans does not appear across a broad range of marine environments until close to the earliest Cambrian (Mángano and Buatois 2020).

Chemofossils

Chemofossils, also known as molecular fossils or biological marker compounds (biomarkers for short), are chemical remains of ancient organisms that are either directly extracted from fossil remains or isolated within sedimentary rocks. They are a powerful complement to fossil remains in

revealing the history of life (Briggs and Summons 2014). However, their utility in tracing the history of early metazoans is greatly diminished because most biologically informative molecules are not able to survive geological alterations for millions of years (Briggs and Summons 2014: table 1) and geologically durable biomarkers that are diagnostic for metazoan clades are rarely known to science. Two proposed demosponge biomarkers, 24-isopropylchoestane and 26-methylstigmastane, co-occur continuously through the ~660–540 Ma old marine sequences of the South Oman Salt Basin but are rare or absent in samples younger than the Cambrian (Love et al. 2009; Zumberge et al. 2018). If they were validated the molecular record of sponges would be more than 100 Ma prior to the earliest record of siliceous spicules (Antcliffe et al. 2014). However, sponge origin of the supposed biomarkers has been challenged by a number of studies (e.g., Antcliffe 2013; Botting and Muir 2018; Botting and Nettersheim 2018; Nettersheim et al. 2019; Bobrovskiy et al. 2020; van Maldegem et al. 2020; Love and Zumberge 2021). In addition, coprostanol was proposed as a metazoan biomarker and detected in the iconic Ediacaran fossil *Dickinsonia* (Bobrovskiy et al. 2018). Coprostanol has been known to be produced via the bacterial reduction of steroid coprostanol in the gut of higher mammals, unstable on geological time scales, and absent in much younger, exceptionally preserved animal fossils (Summons and Erwin 2018). Its presence in *Dickinsonia* was unusual and hence led to a hypothesis of distinct metabolic physiology (Summons and Erwin 2018) and a suggestion for additional work to exclude the possibility of exogenous origin (Love and Zumberge 2021). The steroids from *Dickinsonia* specimens were almost exclusively composed of compounds with 27 carbon atoms (cholesteroids), which were thought to be a signature of all animal phyla other than sponges and a few mollusk taxa (Bobrovskiy et al. 2018; Summons and Erwin 2018). In fact, cholesterol can be a sterol of some protists (Boëchat et al. 2007; Kodner et al. 2008) and many algae (Govindan et al. 1993).

Summary

Chemofossil record provides suggestive but not conclusive evidence for the presence of demosponges in pre-Ediacaran rocks. The trace-fossil record indicates trace makers of bilateral animals were in place by 560 Ma, generally coinciding with the divergence of ecdysozoans and lophotrochozoans estimated based on molecular studies (Fig. 3). This in turn suggests that non-bilateral clades (sponges, placozoans, cnidarians and ctenophores) branched earlier than this date in the animal tree (Fig. 3). However, it is curious that unequivocal sponge fossils are generally absent in the Ediacaran (Sperling et al. 2010; Antcliffe et al. 2014). Ediacaran body fossils may contain early representatives of metazoans.

However, they generally lack diagnostic features of metazoans and thus are difficult to link to Cambrian faunas or living phyla. It is likely that during the Ediacaran Period the ancestors of modern marine animals lived alongside Ediacarans (e.g., vendobionts) until the latter went extinct (Gould 1989; Briggs 2015). Both body and trace fossils support an explosive evolution. Most bilateral clades appeared during the first 20 million years of the Cambrian Period. Exceptionally preserved Burgess Shale-type fossil Lagerstätten, e.g., Chengjiang and Qingjiang biotas, indicate that almost all major metazoan clades, including vertebrates, appeared by 518 Ma.

When did animals originate?

It is certain that animal phyla did not originate precisely when we first find them. In other words, the earliest fossil animals yet discovered may not be the very first animals ever to have existed. We cannot be sure how early each clade arose prior to its earliest fossil evidence. Fossil first appearances of animal phyla provide a conservative minimum time estimate for the origins of animal clades (Zhang and Shu 2014). However, fossils are critical to calibrating the age of branching events in a phylogeny and, by extrapolation, to computing a molecular clock. Origins of metazoan clades estimated by molecular clock studies were summarized in Erwin (2020) as the following: the divergence of Metazoa from choanoflagellates is earlier than 900 Ma; the last common ancestor of living animals lies at about 750 Ma; the origin of the Eumetazoa was about 640 Ma; the Bilateria split into the Protostomia and the Deuterostomia at ~630 Ma; deuterostomes diversified at ~580 Ma; lophotrochozoans diverged from ecdysozoans about 600 Ma and both supergroups further diversified at ~560 Ma (Fig. 3).

Molecular timescales for the origin of phyla are relatively poor in precision and usually have startlingly large error ranges (dos Reis et al. 2015: fig. 2). For instance, the Metazoa was estimated to originate between 833 and 650 Ma, with the younger limit close to the earliest record of sponge biomarker. Pisani and Liu (2015) argued that the poor precision may only be overcome by improving our knowledge of the fossil record and fossil-free molecular divergence times were meaningless in deep time. Interestingly, molecular clock estimates for the divergences of crown groups with skeletonized body parts, such as Euarthropoda and Brachiopoda, consistent with their earliest fossil appearances (Erwin et al. 2011; Erwin 2020). Therefore, the earliest record of animal skeletons (Fig. 4) did likely capture their originations and thus provided robust calibrations for refining the molecular timescale.

Fig. 3 Timeline and evolutionary dynamics of Gene Regulatory Networks (GRNs) against holozoan phylogeny based on studies cited in the text. Dashed lines represent lineages with unstable phylogenetic

positions. Later acquisition of lineage-specific genes and/or extensive co-option of existing regulatory components many have contributed to the rapid diversification of animals during the Cambrian explosion

In addition, molecular estimates that might overstate clade ages (Budd and Mann 2020) point to the origin of metazoans and bilaterians tens to hundreds of millions of years earlier than their first appearances in the fossil record (Wray 2015), which led to a suggestion that the Cambrian Explosion is a phenomenon of fossilization, while biological diversity was established in the Neoproterozoic (dos Reis et al. 2015). Therefore, molecular estimates revived the longstanding conundrum of the Cambrian—whether the first animal fossils faithfully reflect an explosion in animal biodiversity or merely an explosion of fossils (Runnegar 1982; Conway Morris 2006). Please see the question below.

Is the Cambrian Explosion a genuine evolutionary event or an artifact?

It is an incontestable fact that fossils of most animal lineages made their first appearance asynchronously in a geologically short period of time during the Ediacaran–Cambrian transition (Erwin et al. 2011; Zhang and Shu 2014; Zhang and Cui 2016), which was frequently interpreted as a taphonomic artifact since Darwin time (e.g., Darwin 1859; Runnegar 1982; Fortey et al. 1996; dos Reis et al. 2015). Fortunately, much has been learned in the last 160 years, not least multiple discoveries of Cambrian and Precambrian soft-bodied fossil Lagerstätten. Multiple sources of evidence are strongly

suggestive of a real evolutionary event being recorded rather than an artifact of an imperfect fossil record (Conway Morris 1998, 2000, 2006; Mángano and Buatois 2014, 2016, 2020; Briggs 2015), e.g., rapid diversification of animals coincided with the evolution of biomineralized shells (Briggs 2015), continuous record of trace fossils (Mángano and Buatois 2020), and the apparent orderly appearance of taxa in the Ediacaran to Cambrian (Zhang and Shu 2014; Zhang and Cui 2016; Budd and Mann 2020). The combination of the body and trace-fossil record demonstrates a progressive diversification through the end of the Neoproterozoic well into the Cambrian (Budd and Jensen 2000). The nature of the Cambrian Explosion is manifested in multiple aspects, which will be discussed below.

The earliest uncontroversial records of bilaterian activity reflected by trace fossils are approximately 560–555 Ma (Jensen 2003; Jensen et al. 2005; Mángano and Buatois 2020), which provide a critical constraint on the timing of appearance of large worm-like animals capable of creeping and/or shallowly burrowing. Phylogenetic affinity of the trace makers is difficult to be determined because a range of bilaterian lineages exploit a worm-like body plan. Since worm-like bilaterians were in place by 560 Ma, it is self-evident that pre-bilateral lineages (Porifera, Placozoa, Cnidaria and Ctenophora) must diverge successively from the main branch of the animal tree before this age. The absence of convinced metazoan fossils earlier than 560 Ma, together with sponge biomarker and molecular estimates (see above), strongly implies a cryptic evolution of early metazoans, which was supposed to be temporally distant to the abrupt increase in diversity and disparity during the Ediacaran–Cambrian transition—the Cambrian Explosion in the strict sense (Smith and Harper 2013). It appears reasonable to assume that these early animals were small and incapable of leaving preservable marks (Valentine and Erwin 1987; Erwin 2020; but see Budd and Mann 2020). However, Daley et al. (2018) argued that taphonomic conditions of the Ediacaran were no inferior to the Cambrian and soft-bodied organisms, either small or large, were found in a range of taphonomic windows of the Ediacaran Period. Yet, undoubted metazoan fossils have not been recovered from rocks earlier than 560 Ma old trace fossils, which raise a possibility that they might be extremely rare or ecologically negligible. Alternatively, it was assumed that original members of the clade may have had different characteristics from those defining the crown group (Erwin 2020). The earlier origin of the Metazoa and the divergence of basal clades were considered as a distinct event (Smith and Harper 2013), which are effectively decoupled from the later increases in body size, acquisition of characteristic body plans and (in some clades) skeletonization as seen across many lineages during the Cambrian Explosion (Erwin et al. 2011; Erwin and Valentine 2013; Sperling and Stockey 2018).

What is the nature of the Cambrian Explosion?

Explosion of fossils resulted from explosion of animals! Fossil record does capture the explosive evolution of animal body plans along with biomineralization, body size variation and increase of ecosystem complexity. Let us come back to the fossil record again and look at the nature of the Cambrian Explosion.

Three-phased explosion of body plans

As discussed above, the earliest trace fossils strongly suggest the presence of vermiform bilaterians in the late Ediacaran. However, a major burst of bilateral body plans took place in the first 20 Ma of the Cambrian (Erwin and Valentine 2013; Zhang and Shu 2014; Mángano and Buatois 2020). Taking the Euarthropoda, the most diversified phylum, for example, molecular clock studies constrained the origin between 561 and 530 Ma (Rota-Stabelli et al. 2013; dos Reis et al. 2015; Lozano-Fernandez et al. 2016), spanning into the Cambrian. The earliest arthropod trace dates to the Fortunian (~538.8–529.0 Ma) (Mángano and Buatois 2020). In addition, divergence time analyses using morphological data also recover a Cambrian origin for the Euarthropoda (Wolfe 2017). The estimated timing of origin is remarkably congruent with the fossil record (Daley et al. 2018).

Within the Bilateria, both ecdysozoan and lophotrochozoan lineages of the Protostomia were well represented in the Terreneuvian Epoch (~538.8–521.0 Ma), while deuterostome lineages did not appear in the fossil record until the Cambrian Stage 3 (~521.0–514.5 Ma). The basal metazoan clades blow the node of the Bilateria ought to be in place in the Ediacaran Period though unequivocal fossils remain to be found. In contrast, basal metazoan clades were well represented in the early Cambrian. Their diversification was in parallel to that of bilaterians.

In this regard, a three-phased model of the Cambrian Explosion was suggested to successively give rise to the three subkingdoms of the Metazoa, i.e., Diploblasta (basal metazoans), Protostomia and Deuterostomia, respectively (Shu 2008; Shu et al. 2014), which ultimately led to the formation of a complete animal tree and hence concluded the Cambrian explosion (Shu et al. 2014; Shu and Han 2020). The three-phased manner appear to coincide with episodic patterns of trace and skeletal fossil records (Mángano and Buatois 2014; Fig. 4). The model was largely based on first fossil appearances of metazoan lineages and thus may vary with emerging discoveries (Zhang and Shu 2014). More recently, a possible trackway of a bilaterian with paired appendages was reported from the late Ediacaran Shibantan biota (Chen et al. 2018) and a number of putative

Fig. 4 Fossil record of mineralized skeletons showing a three-phased biomineralization of metazoan clades. Vertical bars representing mineralogy and stratigraphical ranges of animals with mineralized skeletons. Time scales are based on Peng et al. (2020). Geological record and mineralogy of mineralized taxa are based on the following references: *Clodina* from Yang et al. (2016, 2020), Zhu et al. (2017), Cai et al. (2019); *Namacalathus* from Wood et al. (2002), Wood and Zhuravlev (2012), Wood and Penny (2018); *Namacalathus* from Grotzinger et al. (2000) and Wood (2011); *Sinotubulites* from Chen et al. (2007), Wood and Zhuravlev (2012); Anabarites from Kouchinsky and Bengtson (2002), Yang et al. (2016); Protoconulariids from Kouchinsky et al. (2012); Chancelloriida from Kouchinsky and Karlova (2005), Yun et al. (2021); Hexactinellida from Rigby (1986), Wood and Zhuravlev (2012), and Murdock (2020); Demospongiae from Bengtson et al. (1990), Müller et al. (2008), Wood and Zhuravlev (2012), and Murdock (2020); Calcarea from Kruse et al. (1995, 1996), Wood and Zhuravlev (2012), Murdock (2020); Archaeocyatha from Rozanov and Zhuravlev (1992), Wood and Zhuravlev (2012); Anthozoa from Tynan (1983), Sorauf and Savarese (1995); Protoconodonta from Kouchinsky and Karlova (2005), Mellroy and Szaniawski (2010); Halaxiida from Conway Morris and Peel (1990), Vinther and Nielsen (2005); Hyolitha from Vinn (2006), Kouchinsky (2001), Skovsted and Peel (2011); Cambroclavida from Conway Morris et al. (1997), Steiner et al. (2007); Paracarnachitida from Conway Morris and Chen (1991), Wood and Zhuravlev (2012); Tianzhushanellidae from Kouchinsky et al. (2012); Heliconelloida from Kouchinsky and Karlova (2005), and Zhuravlev (2012); Polyplacophora from Carter and Hall (1990), Treves et al. (2003), Hoare and Pojeta (2006); Scaphopoda from Peel (2006), Murdock (2020); Stenothecida from Rozanov and Zhuravlev (1992), Ushatinskaya and Zhuravlev (1994), Wood and Zhuravlev (2012); Rostroconchia from Kouchinsky (2000), Kouchinsky and Karlova (2005), Murdock (2020); Bivalvia from Runnegar and Bentley (1983), Runnegar (1985); Gastropoda from Parkhaev (2017), Murdock (2020); Cephalopoda from Chen and Teichert (1983), Landing and Kröger (2009); Tommotiida from Kouchinsky and Karlova (2005), Skovsted et al. (2003), Skovsted (2003), Topper and Skovsted (2017); Linguliforma from Skovsted and Holmer (2003), Kouchinsky and Karlova (2005), Murdock (2020); Rhynchonelliformea from Ushatinskaya and Zhuravlev (1994), Ushatinskaya and Malakhovskaya (2006); Bryozoa from Taylor and Weedon (2000), Landing et al. (2010), Taylor et al. (2013); Serpulidae from Kupriyanova et al. (2010); Palaeoscolecida from Han et al. (2007), and Kouchinsky et al. (2012); Lobopodia from Kouchinsky et al. (2012); Braconidiida from Liu et al. (2008), Kouchinsky et al. (2012); Phosphatocopida from Müller (1979), Kouchinsky et al. (2012); Agnostida from Briggs and Fortey (1982); *Pythophilaspis* from Lin et al. (2010); Trilobita from Teigler and Towe (1975), Zhang et al. (2017b); Cirripedia from Lowenstam and Weiner (1992); Decapoda from Bentov et al. (2016a,b); Isopoda from Bentov et al. (2016); Stomatopoda from Bentov et al. (2012); Currey et al. (1982); Ostracoda from Bate and East (1972); Echinodermata from Rozanov and Zhuravlev (1992), Guensburg and Sprinkle (2001); Calcichordata from Dominguez et al. (2002), Lefebvre (2007); Conodontia from Bengtson (1983), Miller (1984); Ascidacea from Lowenstam and Abbott (1975), Chen et al. (2003); Vertebrata from Rücklin et al. (2012)

deuterostomes were recovered from the Fortunian Stage, e.g., meiofaunal deuterostomes (Han et al. 2017; reconsidered as a primitive scalidophoran or the nearest common ancestor of the Bilateria in Shu and Han 2020), a stem group echinoderm (Topper et al. 2019, 2020; but see Zamora et al. 2020), and enteropneust hemichordates (Maletz 2019). These discoveries are critical to constrain the duration of the Cambrian Explosion and hence remain to be tested and verified.

Crown groups along with numbers of stem groups

The Cambrian Explosion produced a rich fauna with or without sclerotized body parts. Both skeletonized and soft-bodied faunas contained numbers of weird forms whose morphologies do not fit easily within living phyla or classes (Valentine 2004) and hence they were traditionally placed in separate phyla or classed. The application of stem- and crown-group concepts assigned most of these weird forms to stem groups of a high-rank crown clade, e.g., a class, a phylum or a subkingdom (Budd and Jensen 2000). Most phylum-level clades of the Metazoa must have been present, at least as stem groups, by the time of the Chengjiang biota (~518 Ma), though a number of living phyla are absent in the fossil record. There are a number of cases that crown groups had appeared at the class level, e.g., Lingulida among Brachiopoda, Bivalvia among Mollusca, and Pancrustacea among Euarthropoda (Erwin and Valentine 2013). However, there might have many more stem groups with a high-rank phylogenetic position. For example, the superphylum Panarthropoda comprises three living phylum-level clades, Tardigrada, Onychophora and Euarthropoda. Many of Cambrian forms (e.g., *Anomalocaris*, *Opabinia* and others) were comfortably placed between the three living phyla (Daley et al. 2018). Each of these weird forms is phylogenetically equivalent to or above the living crown groups and was previously thought to represent a phylum-level body plan (e.g., Whittington 1979; Gould 1989). Some may have a temporary success of diversity and longer evolutionary history, e.g., radiodonts, known from Cambrian to Devonian, represented by 17 genera and 28 species (Wu et al. 2021a,b), and others are probably ephemeral orphans, e.g., *Opabinia* (known only in Burgess Shale). Therefore, it is a prominent feature that the Cambrian was a time of crown groups nested by many stem groups with a high-rank taxonomy of Linnaean system (classes and above).

Broad disparity

Disparity is the diversity of animal forms or body plans, which can be measured by use of Linnaean ranks and a

variety of quantitative approaches (Erwin 2007). Each body plan or a high-rank clade, e.g., a phylum, has a set of distinctive features. It has long been recognized that in no case is a morphological continuum found across a broad range of body plan morphologies nor do phyla resemble each other more closely during their early fossil histories (Valentine 2004). Simply there are morphological gaps between phyla. By analyzing the timing of appearance of Linnaean rank taxa in the fossil record, paleontologists realized that the limits on animal disparity were early in animal evolutionary history (e.g., Erwin et al. 1987). By the reinterpretation of the Burgess Shale fauna, Gould (1989: fig. 3.72) suggested a pattern of rapid, maximal disparity in the early history followed by later removal of most groups (stem groups) by extinction that leaves large morphological gaps among high-rank clades. This pattern is applicable to high-rank clades and metazoans as a whole. Particularly, he argued that that the morphological disparity of arthropods at a single locality (Burgess Shale) surpassed all extant arthropods, which inspired considerable efforts to understand disparity. Subsequent quantitative studies have shown that most clades achieved their maximal disparity (or morphological breadth) during a short time interval close to their first appearance in the fossil record in the early Cambrian (see a review in Erwin 2007; Hughes et al. 2013). A more recent study by mapping of fossil and living metazoan morphospace demonstrated that the majority of phylum-level clades achieved maximal initial disparity in the Cambrian and that the overall disparity was already very broad in the early history of animal evolution, although the envelope of disparity explored by the Metazoa has increased through geological time (Deline et al. 2018). It is worth mentioning that new discoveries of weird forms in Cambrian deposits would increase the morphological breadth of Cambrian animals (e.g., Zeng et al. 2020).

What are causes of disparity? Morphological discreteness among animal clades can be depicted as clumpy occupation of morphospace. A number of views have been offered to explain the clumpiness of metazoan morphospace occupation, i.e., (1) morphological continuum broken up by subsequent extinction, (2) incomplete exploration of morphospace, (3) contingent occupation and elimination, (4) fitness landscapes, and (5) developmental constraints (see a summary in Erwin 2007). These explanations are partially overlapping and may not be mutually exclusive. Recent analyses including fossils and phylogenetic ancestors indicated that the majority of the empirical morphospace has not been explored in metazoan evolutionary history and the morphological discreteness of modern clades is largely a consequence of the extinction of phylogenetic intermediates (stem groups) (Deline et al. 2018).

Increase of generic diversity

Fossil first 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 a moderate increase in the Cambrian Stage 2 (Maloof et al. 2010; fig. 2). Global data in the later stages of the Cambrian are currently not yet available. The pattern of South China shows a different pace, a jump from 11 genera of Small Shelly Fossils (SSFs) in Fortunian to 169 in Stage 2. Stage 3 has the highest diversity (431 genera or more) largely for the contribution of the Chengjiang biota (Li et al. 2007 recompiled by Erwin and Valentine 2013). Up till now, more than 280 species have been described from the Chengjiang biota (Zhu et al. 2019).

Similarly, the increase of ichnodiversity took place in pulses rather than at a steady pace. About ten ichnogenera have been known in Ediacaran. A big jump of 433% increase during the Terreneuvian was followed by a moderate increase of ~40% ichnogenera, which is obviously attributed to the Cambrian Explosion and unparalleled in the rest of the Phanerozoic, emphasizing the uniqueness of this event (Buatois and Mángano 2018; Mángano and Buatois 2020). The pattern of ichnodisparity is well coordinated with that of ichnodiversity (Mángano and Buatois 2020; fig. 5). The two pulses of diversity increase separate the Ediacaran–Cambrian transition into three phases, late Ediacaran, Terreneuvian, and Cambrian Stage 3, respectively (Mángano and Buatois 2014).

Acquisition of mineralized skeletons

Fossil first appearances of metazoan lineages with mineralized skeletons have interesting points. Two-phased metazoan biomineralization was previously proposed, i.e., a fast evolutionary radiation of the Lophotrochozoa during the Terreneuvian followed by radiation of the sclerotized ecdysozoans during Stage 3 (e.g., Kouchinsky et al. 2012). However, there are a number of facts worth a discussion. First, appearances of mineralized lophotrochozoans in the Terreneuvian were preceded by a number of tubular fossils with uncertain affinities (e.g., *Cloudina*, *Sinotubulites*, *Namacalathus*, and *Arnabarites*) and a modular form *Namapoikia* spanning from ~550–539 Ma (Fig. 4). The tubular forms have long been recognized as mineralized metazoans though their phylogenetic affinities remain ambiguous, while *Namapoikia* was interpreted as an encrusting poriferan (Wood and Penny 2018). Second, the Terreneuvian is still a long period, lasting ~18 million years and recorded asynchronous appearances of mineralized lophotrochozoans along with numbers of other clades (Kouchinsky et al. 2012). Third, the Terreneuvian biomineralization can be further subdivided into two pulses: a group of lophotrochozoans (e.g., Halwaxiids,

hyoliths, and molluscs) alongside siliceous sponges, cancelloriids, and protoconulariids became mineralized during the Fortunian (~538.8–529.0 Ma), while another group of lophotrochozoans (brachiopods, tommotiids, and stenotherozooids) accompanied by calcarean sponges, archaeocyaths and corallomorphs was calcified during the Cambrian Stage 2 (~529–521 Ma) (Fig. 4). The Cambrian Stage 3 is featured by an abrupt widespread mineralization of ecdysozoans accompanied by echinoderms (Fig. 4).

Overall, the biomineralization through the Ediacaran–Cambrian transition is a three-phase process (Fig. 4). Each phase crosses a range of lineages. Phase 1 (~550.0–538.8 Ma) is characterized by calcareous tubes and modular structures. Phase 2 (~538.8–521.0 Ma) is the most extensive mineralization event, represented by a wide-range of lophotrochozoan and non-bilaterian metazoan clades, which appeared in two pulses. Phase 3 (~521.0–514.5 Ma) is featured by a widespread mineralization of ecdysozoans along with echinoderms.

Fluctuations of seawater chemistry, e.g., Magnesium/Calcium ratio, were frequently invoked to explain the changing skeletal mineralogy from aragonite to calcite (e.g., Porter 2007; Zhuravlev and Wood 2008). The turning point is the prominent negative excursion of carbon isotopic record in the middle of Stage 2, involving the first appearances of high-magnesium skeletons and a decrease of the Ma/Ca ratio. However, biomineralization is an enzymically controlled process that is different from the abiotic one in multiple aspects (Degens 1976; Degens et al. 1986; Weiner and Dove 2003; Jackson et al. 2007), and the mineralogical evolution of skeletal lineages did not follow the pace of the seawater Magnesium/Calcium ratio through time (Fig. 4). In addition, biocalcification was proposed as a detoxification mechanism because the calcium ion is pharmacologically one of the most disruptive substances for normal cell functions (Simkiss 1977). Accordingly, the widespread biomineralization across metazoan lineages was considered as a response to the increase of toxic Ca^{2+} level in the ocean during the Precambrian–Cambrian transition (Kazmierczak et al. 1985; Degens et al. 1985, 1986). It should be noted that the fossil record indicates that numbers of entirely soft-bodied animals lived alongside those with mineralized skeletons though Ca^{2+} concentration of the seawater was increasing during the Cambrian Explosion (Arp et al. 2001; Lowenstein et al. 2001, 2003), which suggests a detoxification of Ca^{2+} threat other than biocalcification. Furthermore, it is difficult for seawater chemistry hypotheses to explain the timing of mineralization in a specific lineage and successive appearances of phosphatic skeletons from distantly related lineages. Notably, why did the sudden mineralization of ecdysozoans preceded by a widespread biomineralization of lophotrochozoans? The seawater chemistry provides cations and anions that are prerequisites for animal making

skeletons, but it alone is insufficient to drive biomineralization during the Ediacaran–Cambrian transition. Alternatively, biomineralization among animal lineages has long been considered as an escalating defensive response driven by increasing predation pressure (e.g., Vermeij 1990), while the advent of microphagous predators postdates the initial episode of biomineralization and requires a trigger as well (Zhang and Shu 2014; Zhang et al. 2014). Finally, or intrinsically, metazoan lineages separately acquired the ability to form biomineralized skeletons through lateral gene transfer of mineral-forming gene toolkits during the Cambrian Explosion (Jackson et al. 2011) or biomineralization is genetically a deep homology that was independently co-opted in different lineages in different time (Erwin 2020; Murdock 2020).

Increase of body size

The maximum body volume of organisms preserved in the fossil record has increased by ~16 orders of magnitude over the last 3.5 billion years, demonstrating two pronounced ~6-ordered jumps of approximately equal magnitude in the mid-Paleoproterozoic (~1.9 Ga) and during the Ediacaran through Ordovician (~635.0–443.8 Ma), respectively. Each size step required a major innovation in organismal complexity—first, the eukaryotic cell and later, eukaryotic multicellularity, and corresponded to an oxygenation period (Payne et al. 2009).

The second size increase was manifested by appearances of large complex multicellular organisms (e.g., algae, vendobionts, tubular forms, and metazoans) and the duration embraces the Cambrian Explosion. The earliest Cambrian was characterized by Small Shelly Fossils but there were examples of Fortunian fossils (Zhang et al. 2017a; Marusin and Grazhdankin 2018) comparable to the body size of Ediacara-type fossils. The large size was reached before the Cambrian Explosion. A quantitative study of skeletal species from Siberia demonstrated marked changes in maximum linear body size dimensions but no unidirectional trend throughout the early Cambrian (Zhuravlev and Wood 2020). However, the variation of the linear body size was in interesting paces: the size of archaeocyath, hyolith, and helcionelloid mollusc species varied in a synchronous rhythm over million-year timescales, with peaks positively correlated with origination rate and total species diversity, which appear to be a consequence of external drivers. The response of brachiopods is quite different, calcitic shells showing a general increase in body size while phosphatic shells decreasing in size through time (Zhuravlev and Wood 2020).

Increase of ecosystem complexity

Microbially dominated ecosystems appeared billions of years before the Cambrian Explosion and persisted into the earliest Cambrian (e.g., Buatois et al. 2014; Duda et al. 2016). The modern-style, metazoan-dominated ecosystems are essentially the outcome of the Cambrian Explosion (Erwin and Tweedt 2012; Zhang and Shu 2014). Ecological networks expanded considerably in both size and complexity between the Ediacaran and the early Cambrian as measured by the number of life modes (Bambach et al. 2007; Bush et al. 2011; Hua et al. 2020), complexity of food web (Dunne et al. 2008), and ecosystem engineering (Erwin and Tweedt 2012; Mángano and Buatois 2014). A total of 12 different life modes were recognized in Ediacaran macrofossil assemblages (Avalon, White Sea, and Nama) and 30 in Chengjiang and Burgess Shale biotas (Bambach et al. 2007), with a gain of 24 and a loss of 6 life modes through the Ediacaran–Cambrian transition. Relatively, a minor positive ecological feedback during the Ediacaran was followed by a substantial increase during the early Cambrian, principally through bioturbation and the appearance of a number of structural engineers (Erwin and Tweedt 2012); a major shift in benthic ecological structure (agronomic revolution) resulted in the establishment of the Phanerozoic-style ecology during the Cambrian Stage 2 (~529–521 Ma), which in turn drove a further diversification of deposit-feeding strategies by Cambrian Stage 3 (~521.0–514.5 Ma), favoring an ecological spillover scenario (Mángano and Buatois 2014). The fundamental structure of metazoan marine food webs appears to have been established by the Cambrian Stage 3 as seen in the Chengjiang biota (~518 Ma).

How long did the Cambrian Explosion last?

To answer this question, we have first to define the opening and closure of this unprecedented evolutionary event. It is generally accepted that the arrival of most metazoan body plans must mark the end of the Cambrian Explosion, which was followed by broad-scale evolutionary stasis throughout the remainder of the Phanerozoic (Gould 1989; Paterson et al. 2019; Erwin 2020; Shu and Han 2020). If so, the first appearance of trilobite (~521 Ma) is a good marker. By the arrival of trilobites, or about 18 million years into the Cambrian Period, the great burst of evolutionary novelty and innovation transitioned to more traditional dynamics of speciation and extinction with fewer morphological novelties (e.g., Paterson et al. 2019). The opening of the event may not exactly coincide with the Ediacaran–Cambrian

boundary (~538.8 Ma). Metazoans may have appeared more than ~750–660 million years ago as suggested by molecular and biomarker studies, well before the Cambrian. The earliest physical remains of definitely metazoan origin are traces of bilateral animals about 560 million years ago, which can be used as a minimal calibrating time for the origin of bilaterians. Non-bilaterian clades must have successively diverged from the main branch of animal phylogeny before this age. However, they were ecologically negligible, or their diversification might be later in the Ediacaran–Cambrian transition for the paucity of physical remains in much earlier strata. Ecologically it took metazoans more than 100 million years to take over the ocean, from their emergence in the Cryogenian (~720–635) or earlier, through a long silent period, becoming ecologically non-negligible by 560 Ma, further through an ecological revolution during the first 18 Ma of the Cambrian, and finally forming the metazoan-dominated ecosystem by 521 Ma. Fossil record also indicates that most metazoan body plans appeared after 560 Ma. Therefore, the maximal duration of the Cambrian Explosion is about 40 Ma. The episodic biomineralization across a range of animal lineages was embraced in this time window (Fig. 4).

Forty million years is rapid in the larger scheme of Earth's history, just about 1% of life's history. The Cambrian Explosion is a multifold event, involving morphological innovations, skeletonization, and ecological revolution. Most body plans emerged within this time window. The birth of each body plan might be even in a much shorter time interval. It, therefore, raises a question, "Does the Cambrian Explosion pose a challenge to evolution?" The answer is straightforward. Millions or tens of millions of years is geologically short, but it is plenty of time for evolutionary change as fossil record tells us. Early animals had plenty of time to invade new niches, invent new organs, make shells, and change body design.

What is the genetic basis of the Cambrian Explosion?

Whole-genomic sequences of a broad array of metazoans have demonstrated that only a small fraction of genomes constitute developmental Gene Regulatory Networks (GRNs) that control the construction of body plans and hence is usually considered as an intrinsic prerequisite for the early diversification of metazoans. The key question is, when did GRNs that are complex enough for constructing metazoan body plans as complex as Cambrian animals evolved? Although the genetic makeup of Cambrian animals was unavailable, it can be inferred by comparative molecular developmental studies. Thus, tracing the evolution of GRNs across a robust phylogeny of the Metazoa is crucially

important for understanding the diversification of metazoan body plans during the Cambrian Explosion.

The basic framework of metazoan phylogeny has been stabilized for more than 20 years (Fig. 3). Choanoflagellates have long been recognized as the closest living relatives of animals and they together constitute the Choanozoa, which, together with Filasterea and Ichthyosporea, form the Holozoa. The monophyly of the Metazoa is currently well recognized, consisting of a number of paraphyletic non-bilateral clades and the monophyletic Bilateria. The Bilateria is composed of three superphylum-level clades (deuterostomes, ecdysozoans and lophotrochozoans) and the Xenoacoelomorpha (a small group of bilaterians lacking a coelom). But some relationships within animals remain controversial. Among non-bilateral clades, ctenophores were controversially placed to be basal to the Porifera, sister to the Eumetazoan (Laumer et al. 2019), or together with the Cnidaria, revive the Coelenterata (Pett et al. 2019); the Placozoa was placed as a sister clade to the Eumetazoa (which together comprise the Epitheliozoa) or to the Cnidaria (Laumer et al. 2019). Within the Bilateria, the Xenoacoelomorpha was either basal to the Nephrozoa (protostomes and deuterostomes) or at a basal position within deuterostomes (Laumer et al. 2019; Philippe et al. 2019); there are other uncertainties within the three major bilateral clades that are beyond the scope of this discussion.

The genome evolution across the tree of metazoans shows interesting points: (1) Many of the core elements of the metazoan regulatory genome have an ancient origin among the Holozoa (Erwin 2020). (2) The developmental system of metazoans appears to be precociously configured, e.g., genes used in cell-type differentiation and patterning in metazoans are already present in choanoflagellates; sponges possess large numbers of genes otherwise found only in eumetazoans; placozoans have many genes that are important in eumetazoan development and numbers of gene families associated in a broad sampling of bilaterians with the specification of neurons and myocytes, with antero-posterior patterning, and with organogenesis, although they lack nerve or muscle cells and show no indication of bilateral features; cnidarians have many genes that mediate the development of tissues and organs in triploblastic forms (Erwin and Valentine 2013). (3) There are distinctive differences between the developmental architectures of non-bilaterians and bilaterians, relatively flat regulatory hierarchies against a more hierarchical, and more interconnected GRNs (Erwin 2020). (4) Gene gains, losses and duplications dynamically evolved and have unbalanced distributions across the tree; gene duplication ratio was high at deep nodes leading to metazoans and the birth rate decreased progressively as animals diversified into clades; around one-third of genes gained at deep nodes below the Nephrozoa and another one-third comprising lineage-specific genes (no homologues in other taxa) acquired very late; it is not only

key innovations but also the evolutionary dynamics of gene gain and loss that shape the vast morphological disparity of animals, notably deuterostomes, ecdysozoans, and Xenacoelomorpha were characterized by no gene gain but rampant differential gene loss (Fernández and Gabaldón 2020).

The trace-fossil record indicates bilaterians were in place by 560 Ma. The Cambrian Explosion was from above this node and non-bilateral clades must originate earlier though they were underrepresented in Precambrian deposits. The rapid diversification of pre-bilateral phyla along with bilateral clades as seen in the fossil record may have resulted from a later acquisition of lineage-specific genes during the time window of ~560–520 Ma. Another crucial point is the complexity of the last common ancestor of protostomes and deuterostomes (PDA). Early comparative studies between vertebrates and arthropods suggested a morphologically and genetically complex PDA, with a central nervous system, gut, eyes, segmentation, and other features (e.g., Carroll et al. 2001). If so, the bilateral clades diverged without requiring the invention of novel genes. Therefore, the Cambrian Explosion was regarded as an ecological phenomenon (Carroll 2005). However, Erwin (2020) argued that deep homologies of developmental tools had limited morphological expression and thus suggested a less complex PDA either developmentally or morphologically, with a variety of cell types and patterning systems (anterior–posterior, dorsal–ventral). He also proposed that the developmental machinery for appendages, eyes, gut formation, segmentation and other features arose independently in the major bilaterian clades after the PDA, largely through extensive co-option of existing regulatory components (Erwin 2020).

Did environmental changes drive the Cambrian Explosion?

The final assemblage of the super continent Gondwana and the opening of the Iapetus Ocean were characteristic tectonic events during Ediacaran–Cambrian transition and hence were frequently discussed as a tectonic backdrop for the Cambrian Explosion (e.g., Zhang et al. 2014). Continental-scale transgressive sequences dis- or un-conformably overlie the Precambrian rocks of varying age (Peters and Gaines 2012) and are usually rich in phosphorus. Climate might be warm or hot (Boucot et al. 2009; Hearing et al. 2018; Scotese et al. 2021). Atmosphere was well oxygenated, and the free oxygen content was constrained between 10%PAL and 40%PAL (Sperling et al. 2015; Zhang and Cui 2016). The ocean was rich in nutrient (Sperling and Stockey 2018) but not much saltier than today (Knauth 1998; Hay et al. 2006). Fluctuations of seawater chemistry, e.g., the increase of Ca^{2+}

concentration (Arp et al. 2001; Lowenstein et al. 2003) did not obstruct the pace of evolution. Marine redox was heterogeneous in space and volatile in tempo, with anoxic or euxinic water bodies present from time to time and places to places (Wood and Erwin 2017; He et al. 2019; Wei et al. 2021). Oxygenated seafloor was expanding through time (Li et al. 2017).

Indeed, the Earth became well habitable for metazoans! On the basis of the time-equivalence, these environmental changes were often considered as extrinsic triggers of the Cambrian Explosion (see a review in Zhang et al. 2014). In particular, marine redox fluctuations were frequently proposed to be a likely trigger for the early animal innovation (e.g., Wei et al. 2021). However, these environmental changes were not unique in the time window of the Cambrian Explosion, but have all occurred during the Phanerozoic. Organisms are well known to passively response to environmental changes, but they may actively shape their environments through ecological feedbacks. Such ecological interactions are ongoing all the time, yet no explosion of body plans has been seen in the subsequent Phanerozoic. Therefore, searching for an environmental cause might be unavailing as James W. Valentine stated “*Paleoenvironmental signals that can be related to the origins of body plans seem extremely different to discover. The signals from the late Neoproterozoic and Cambrian rocks are difficult to interpret, and none of them as yet confirm that any extraordinary environmental events were causally associated with the Cambrian Explosion* (Valentine 2004: 519)”. Moreover, habitable conditions, notably availability of oxygen (Nursall 1959), are merely a prerequisite for diversification of body plans but they are insufficient to explain the extent of morphological innovations of the Cambrian Explosion (Erwin 2015).

Is the Cambrian Explosion an ecological phenomenon?

Both environmental habitability and developmental system were necessary parts of any explanation, but neither is a sufficient prerequisite for the Cambrian Explosion. Thus, it is becoming increasingly appreciated that the Cambrian Explosion was an ecological phenomenon (Carroll 2005; Conway Morris 2006; Budd 2008; Erwin et al. 2011; Erwin and Tweedt 2012), consisting largely of a cascade of knock-on events that emerged from multicellularity and mobility (e.g., Budd 2008). Any evolutionary event must run through ecology and the Cambrian Explosion is no exception. Metazoans have become ecologically non-negligible since the late Ediacaran. The complex ecologies were subject to both continuing expansion and feedback, thereby resulting in the evolution of metazoan-dominated ecosystem since the early

Cambrian (Conway Morris 2006). Many ecological hypotheses have been proposed as drivers (see a review in Zhang et al. 2014), but none can satisfy geological, paleontological, and molecular records (Marshall 2006). The crux of these ecological drivers is new opportunities (available in new adaptive zones or released by mass extinct) and arm race. Again, ecological drivers are not unique during the Cambrian Explosion and thus fail to explain why the “explosion” happened when it did (Marshall 2006). However, the Cambrian Explosion did take place under these circumstances. Ecology must contribute the ecological expanding of metazoans and the increase of ecosystem complexity, in particular through positive feedback that is distinctive from negative feedback seen in subsequent radiation events (Erwin and Valentine 2013). However, this argument might immediately collapse when asking the following question.

Why did no new phyla arise in subsequent evolutionary radiations?

It is hard to believe that external ecology will explain the entire phenomenon of the Cambrian Explosion (Gould 1989). The main defense for this argument relies on the fact that few phyla has arisen since the closure of the Cambrian Explosion though ecological opportunities were released by “big five” mass extinctions and available during the terrestrialization in later geological periods. It sounds like a strong defense. The uniqueness of the Cambrian Explosion lies in that it was the first time for animals to explore a barrel world. Animals had attempted morphological and ecological possibilities in a short time window and generated numbers of body plans including many forms that are difficulty to be placed in high-rank taxa (phyla and classes) of the Linnaean classification system but in most cases can be assigned to stem or crown clades of current phylogenetic framework. However, not all is possible, successful options are limited, and convergence may lead to the same evolutionary solution (Conway Morris 2003). Non-functional attempts might be eliminated immediately, short-lived or temporarily successful attempts (stem groups) went extinct for restricted supply of resources or catastrophes, and only limited number of attempts survive to today with their extant descendants being classified into phyla and classes based on their distinctiveness. Most options, if not all, had already been attempted in the early history. Subsequent extinctions did not eliminate all high-rank clades. Many clades with survivors radiated after extinction but extinct forms (e.g., trilobite and chancellorids) never occurred again! Animals did explore additional options in later radiation events (Deline et al. 2018) but new forms (e.g., terrestrial counterparts of arthropods and vertebrates) were still in the broad frame of early attempts.

How did the Cambrian Explosion happen?

The Cambrian Explosion is not purely a biotic process but a polythetic event of natural history that requires many sets of necessary conditions from molecules to forms, from isotopes to habitability, and so on. In other words, whichever was unavailable it could not happen and, reversely, when everything was ready it did not necessarily happen though it may take place at any time. The Cambrian Explosion is far more complicated than any historical event, which is extremely difficult to explain because complex patterns of causality, importance of contingency, and interactions of many different processes are all interwoven together. Complex histories do not have single, easily testable causes (Erwin and Valentine 2013). While the Cambrian Explosion did take place under circumstances when the world oceans became habitable for various forms of animals, the developmental GRNs were sufficiently complex for constructing complex forms, and resource supply was less restricted. It seems that opportunities were in every corner! Metazoans emerged earlier, and became ecologically non-negligible in the late Ediacaran, and finally dominated marine ecosystems by the closure of the Cambrian Explosion. Early metazoans shared seafloors with Ediacarans (vendobionts and tubular forms of uncertain affinity) for the last 20 million years of the Ediacaran, although their ecological relationships are less known. Metazoans might be ecologically humble during the Ediacaran Period, but they followed the path of evolving organs and systems, developing orderly repetition of body parts (e.g., segmentation), and attempting other possibilities, which enable the evolution of morphological, physiological, ecological variations and complexity. While Ediacarans kept their less differentiated body designs, tissue-grade organization, and probably osmotic physiology. Consequently, Ediacarans died off at the end of their era for unknown reasons (Darroch 2021). Thereafter metazoans rapidly diversified and generated number of phylum-rank stem or crown lineages with different fates in the first 20 million years of the Cambrian Period. Some immediately diverged in ecology and morphology and persisted to today (e.g., arthropods and mollusks), some may temporarily succeed in diversity but became extinct sooner or later, and some have remained lonely though they have survived into today.

Acknowledgements We are grateful to Linhao Cui, Cong Liu, and Yuhua Qiao for technical assistance and Hong Hua for providing a photograph of Figure 3. Thanks also go to Joachim Reitner (Göttingen) and Mike Reich (Munich) for constructive comments. This research was supported by Natural Science Foundation of China (41890845, 41621003, 41930139, 41772011), 111 Project (D17013), and Key Scientific and Technological Innovation Team Project in Shaanxi Province.

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