Integrated record of environmental change and evolution challenges the Cambrian Explosion

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Abstract

The ‘Cambrian Explosion’ describes the rapid increase in animal diversity and abundance, as manifest in the fossil record, between ~ 540 and 520 million years ago (Ma). This event, however, is nested within a far more ancient record of macrofossils extending at least into the late Ediacaran, ~571 Ma. The evolutionary events documented during the Ediacaran–

Cambrian interval coincide with geochemical evidence for the modernisation of Earth's biogeochemical cycles. Holistic integration of fossil and geochemical records leads us to challenge the notion that the Ediacaran and Cambrian worlds were markedly distinct, and places biotic and environmental change within a longer-term narrative. We propose that the evolution of metazoans may have been facilitated by a series of dynamic and global changes in redox conditions and nutrient supply, which, together with potential biotic feedbacks, enabled turnover events that sustained phases of radiation.

In this synthesis, we argue that early metazoan diversification should be recast as a series of successive, transitional radiations that extended from the late Ediacaran and continued through the early Palaeozoic. We conclude that while the Cambrian Explosion represents a radiation of crown-group bilaterians, it was simply one phase amongst several older, and younger, metazoan radiations.

1. Introduction

The 'Cambrian Explosion', starting at ~540 Ma, is considered to mark the abrupt appearance in the fossil record of abundant and diverse metazoans. This was accompanied by an increase in complexity of morphologies and behaviours, individual size and disparity, the first representatives of most extant phyla, and the rise of metazoan-dominated marine ecosystems (1). Although most workers acknowledge that metazoans originated considerably before the Cambrian (e.g. 2,3, though see 4), the 'roots' of the 'Cambrian Explosion' are much debated. The initiation of this event is debated; around the Ediacaran–Cambrian boundary (5), in the terminal Ediacaran (6), or even deeper still, at either the appearance of the Nama Assemblage (~550–541 Ma; 7), or at the Avalon–White Sea assemblages boundary at ~561 Ma (2,7,8), or, based on molecular phylogenies, in the Tonian or Cryogenian ~720 Ma (1). Furthermore, independent faunal turnover events and metazoan radiations are recognised in the subsequent early Palaeozoic, and so the relationship of these to evolutionary and ecological innovations across the Ediacaran–Cambrian boundary must be understood (9-11).

Whilst knowledge of individual aspects of these evolutionary developments is advancing, our broader understanding of early animal evolution is often hampered by highly compartmentalised, rather than holistic, study. Insights from diverse palaeobiological records have only recently been integrated with high-resolution geochemical studies and models, revealing much about the operation of the Earth System during this interval, such as the interaction between ecosystem engineers and oceanic biogeochemistry (e.g. 12-16). Global correlation between key sections, aided by accurate and precise radiometric dating, is a continuous work in progress. Yet, holistic integration of datasets across the broader Ediacaran–Cambrian interval may enable us to address profound uncertainties, such as how seemingly different biotas might be related (8,17); whether one or more mass extinctions occurred during this interval (7); the evolutionary response, if any, to changes in oceanic redox conditions and nutrient availability (15,16, 18-20) and, the resolution of conflicting evidence for the origin of major metazoan clades from molecular clock, biomarker, and palaeontological data (e.g. 2,4). Without comprehensive geobiological and temporal integration we risk missing the bigger, and more significant, evolutionary picture.

We focus here on integrating the tractable fossil and environmental proxy records of the Ediacaran to Cambrian interval to document the diversification of animals and their behaviour. This integration reveals a record of interactions between environmental change and biological evolution, culminating in the establishment of crown group metazoan phyla. Our compilation enables a re-evaluation of the record, and explores the potential drivers of early metazoan evolution.

2. Environmental change versus evolutionary innovation

The late Cryogenian to Cambrian interval shows evidence for dramatic changes in the carbon cycle (Figure 1b) and ocean redox conditions (Figure 1c) (Box 1). These geochemical changes, potentially driven by tectonic readjustment (21), coincide with a series of major biotic innovations (Figure 1a), including the appearance of metazoan motility by ~565 Ma, biomineralisation by ~550 Ma, and bilaterian crown groups and predators by ~535 Ma (Box 2). A causal relationship between these records has long been proposed (e.g. 22). In particular, there is a broad consensus that dissolved oxygen provision reached a threshold, or series of thresholds, during the Neoproterozoic, allowing the diversification of metazoans and their increasing metabolic demands (23-25). However, there remains considerable debate as to whether oxygenation was the main driver of early metazoan evolution after this initial physiological requirement was met (e.g. 18,23,26). Indeed, the relationship between oxygen availability and biotic response was likely to have been complicated by the operation of ecological and genetic factors, as well as poorly understood feedbacks between life and the broader Earth System.

Different geochemical proxies yield information with varying levels of spatial and temporal resolution. Local marine palaeoredox reconstruction via iron speciation and Rare Earth Element (REE) profiles in several key sequences indicates that Cryogenian to early Cambrian open marine conditions were typified by redox-stratification (e.g. 14, 23). Most, but not all, sampled basins record a shallow and highly dynamic chemocline above deeper ferruginous waters. However, redox proxy data are unavailable for many important successions, most notably Morocco, Spain, Australia, India and the Ukraine. In addition, the targeting of fine-grained facies has led to considerable bias in existing data (27), and the paucity of deep water successions for key intervals during the Ediacaran has prevented

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BOX 1: Oxygen and biogeochemical cycles during the Ediacaran–Cambrian

The non-uniformitarian nature of the oceans across the Ediacaran–Cambrian interval, continuing into the Ordovician, is evidenced by considerable instability in the carbon isotope record in inorganic carbonates. The magnitude of the largest known negative carbonate carbon isotope ($\delta^{13}C_{carb}$) excursion in the geological record, the Ediacaran Shuram/Wonoka anomaly, has a nadir of -12‰ (22). Following recovery to positive values prior to 551–548 Ma, $\delta^{13}C_{carb}$ remained relatively unperturbed for the final ~10 Myr of the Ediacaran (the Ediacaran positive isotopic plateau: EPIP), before falling again to values indicative of the basal Cambrian negative carbon isotope excursion (BACE) (e.g. 28-30). The BACE pre-dates the first appearance of *Treptichnus pedum* (31,32), while in South China it correlates with the *Asteridium–Heliosphaeridium–Comasphaeridium* (AHC) acritarch assemblage and the *Anabarites trisulcatus–Protohertzina anabarica* (small shelly fossils) Assemblage Zone (33-34). A number of further short-lived $\delta^{13}C_{carb}$ excursions continue to punctuate the Cambrian (29,35) and Ordovician chemostratigraphic records (36), exhibiting a progressive decline in overall excursion magnitude into the Phanerozoic (e.g. 37).

Proposed explanations for $\delta^{13}C_{carb}$ anomalies throughout this interval are variable and remain contentious (e.g. 22, 38), but they may, at least in part, be related to dynamic change in redox and nutrient cycling. While selenium isotopes suggest a generally progressive oxygenation through the Neoproterozoic (39), compiled data show that oceanic redox conditions oscillated dramatically over million year timescales, before a permanent and stable oxygenated state was achieved (40). The exact timing of these events, confirmation of their global extent, as well as the drivers for such rapid and global changes, however, remains unclear. Mo and U isotopes show that an increase in oxygenation was punctuated by intervals of expanded anoxic seafloor (41-43); low Th/U ratios show a positive correlation with $\delta^{13}C$ values at multiple sites across the Ediacaran–Cambrian boundary, suggesting that the BACE is a response to the widespread development of shallow marine anoxia (44-45). A shift in the marine sulphur cycle, as recorded by $\delta^{34}S$, is possibly consistent with increasingly widespread sulphate reduction under anoxic conditions around ~550 Ma (22,46).

Others have argued for intervening late Ediacaran ‘oceanic oxygenation events’ (OOEs) (Figure 1c) at around 575 Ma (OOE2), ~560 Ma (OOE3) - possibly coincident with the start of the Shuram - and at ~540 Ma (OOE4) (40,47), although differing redox proxies are not always consistent with the timing of these intervals. For example, on the basis of N isotopes, oxic intervals have been proposed ~551–543 Ma, ~544–529 Ma, and ~521–517 Ma (see 48). Diverse proxies suggest that the global ocean became progressively more oxygenated through the early Cambrian until ~520 Ma, after which time there was a return to more widespread anoxia (49,50). The Sinsk Event, accompanied by a negative CIE, is a further short-lived anoxic interval at ~513 Ma (11). Independent proxies suggest that full oxygenation of the deep oceans was not reached until the Devonian (27,51).

BOX 2: The metazoan fossil record between ~571–520 Ma

The oldest macrofossils of the so-called ‘Ediacaran macrobiota’ are known from the Drook Formation, Newfoundland (52), and are dated at ~571 Ma (53). Although their precise phylogenetic position remains unclear, at least some taxa are reasonably interpreted to have been total group metazoans (54). The wider macrobiota includes a range of complex organisms with tubular, frondose, modular, and sheet-like morphologies that likely include multiple clades (e.g. 55). These have been grouped within three proposed biotic ‘assemblages’ (recurrent community compositions) that appear to be predominately controlled by facies rather than age (56): the Avalon (~571–555 Ma), White Sea (~560–551 Ma), and Nama (~555–541 Ma) assemblages (57,58). Frondose taxa (e.g. *Charnia*, *Arborea*) dominate the Avalon Assemblage, and are accompanied by rare candidate cnidarians (59), but both the diversity and taxonomic disparity of macroscopic soft-bodied organisms increase significantly after ~560 Ma (3,60). The first identifiable motile, heterotrophic organisms are *Kimberella quadrata*, *Yorgia* and *Dickinsonia* from Russia, at ~558–555 Ma, the latter being highly likely to have been a metazoan on the basis of ichnological, developmental and biomarker evidence (see 54,61). A widespread record of surface locomotory trace fossils exists from at least 560 Ma (62; see also 63), and these diversify in form and complexity through the late Ediacaran (64-67). Latest Ediacaran assemblages show a marked reduction in soft-bodied macrofossil diversity, but witness the appearance of organic-walled (e.g. *Corumbella*) and skeletal tubular fossils, and a diversification of bilaterian trace fossils (9, 62). The oldest skeletal macrofossil, *Cloudina*, which also shows the first possible evidence for predatory borings (68), is known globally from ~550 Ma (69). *Cloudina* could form reefs (70, but see 71) and together with the late Ediacaran (~543 Ma) *Paraconularia*, is plausibly interpreted as a total-group cnidarian (and, therefore, a crown-eumetazoan).

The Ediacaran–Cambrian boundary is defined by the first appearance of the complex trace fossil *Treptichnus pedum* (72), presently dated to 541 Ma based on the inferred correlation of successions from Newfoundland, Namibia and Oman. The earliest Cambrian (Fortunian) fossil record shows a marked increase in ichnofossil abundance, size and complexity in shallow marine environments (9). The first probable crown-group molluscs and brachiopods appear in the late Fortunian or early Stage 2 (73). There is also a notable rise of bilaterian predators (74). The Early to Middle Cambrian then hosts a variety of lagerstätten that document crown group representatives of disparate skeletal and non-biomineralising animal phyla (e.g. 33), as well as increases in body size across many animal clades, skeletonization, and the expansion of ecological networks (1).

These patterns in the fossil record are yet to be converted into a coherent understanding of the dynamics of how metazoan phyla appeared and evolved (5), but quantitative analysis of lophotrochozoan skeletal species from the terminal Ediacaran to Cambrian Stage 5 (~545–505 Ma) on the Siberian Platform show a disjunct temporal distribution that suggests that the radiation of bilaterian metazoans occurred in two phases, separated by an extinction event. The first was dominated by lophophorate, brachiopod, and mollusc stem groups from ~542–513 Ma, and the second was marked by radiating brachiopod and mollusc crown group species from ~513 Ma, extending to the Great Ordovician Radiation Event (GOBE) (73).

unequivocal distinction between global layer-cake redox stratification of the oceans and highly dynamic Oxygen Minimum Zones (OMZs) overlying potentially oxic basinal waters. There is growing evidence for the existence of OMZs in early Cambrian basins (75-77).

Many global proxies allow only for estimates of expanded seafloor anoxia, and do not differentiate between deep and shallow marine settings. Consequently, it is not clear if such expansions restricted the habitable area of the shallow shelf, where most biodiversity resides. At least some biotas throughout this interval were subject to upwelling incursions of oxygen deficient water, controlled by local changes in relative sea level and productivity (77). Therefore, the entire Ediacaran–Cambrian radiation, and indeed beyond, may have occurred under relatively low oxygen levels, but with highly dynamic, fluctuating redox conditions prevalent on local (ecological), as well as global and evolutionary, temporal and spatial scales (19).

Biotic response to changing redox: a role for instability?

While all extant metazoans need oxygen, their demands are not equal. Modern low-oxygen regions are heterogeneous and dynamic habitats that support low diversity communities of opportunistic and non-skeletal metazoans, many of which are meiofaunal: large, skeletal, and motile metazoans, which form complex, biodiverse ecosystems, typically require higher oxygen levels (23). Experimental work has demonstrated that certain early-diverging clades (poriferans and ctenophores) may have very low oxygen demands, since they lack hypoxia-inducible factor (HIF) pathways to maintain cellular oxygen homeostasis (78,79). This suggests that stem-group metazoans, and the metazoan Last Common Ancestor, may also have lacked the HIF pathway, and so could have metabolized aerobically under very low environmental oxygen concentrations (79). Animals most likely originated in a non-uniformitarian world of low atmospheric oxygen, and almost certainly before the permanent oxygenation of the deep ocean. However, it remains unclear as to whether animal diversification and increased ecosystem complexity was driven extrinsically by the expansion of permissive oxic niches, or by genetic or developmental innovations that enabled animals to expand into the oxic realm.

Where palaeoredox proxy data are integrated with biotic distribution, metazoans are usually restricted to localised oxygenated habitats, either above a shallow chemocline, or potentially below an OMZ (e.g. 76, 80). The instability of the chemocline would therefore have provided strong anactualistic controls on the distribution of metazoans, and potentially on the taphonomic windows for their preservation. Ediacaran and Cambrian sediments deposited below the chemocline (or within an OMZ) may therefore be expected to lack metazoan life assemblages.

At least regionally stable ocean oxygenation following the Gaskiers glaciation broadly coincides with the appearance of soft-bodied Ediacaran macroscopic biota in Newfoundland (181). Extensive ocean oxygenation is argued to have occurred coincident with the end of the Shuram event, ca. 560–551 Ma (see review of 75). This event is broadly coincident with the first evidence for probable motile, heterotrophic, and muscular bilaterians, although dating and global correlation are not well constrained, and integrated, local, datasets are not available to establish cause and effect (104). It is also not clear whether the rise of mobile bilaterians and predators required additional ecological triggers (23). Records from the open oceanic Laurentian margin (632–540 Ma), the Nama Group (~550–538 Ma), and the variably restricted Yangtze Block (635–520 Ma), all show continued redox instability after the first fossil evidence for (probable) metazoans (see review of 75). The first skeletal metazoans appear at ~550 Ma, under local conditions of continued redox stratification (80), and before an interval of expanded anoxia (43). However, in the Nama Basin, integrated Fe speciation and Ce anomaly data show that in-situ Ediacaran skeletal metazoans did not occupy low oxygen waters (14).

These dynamic carbon and redox records are also closely tied to probable changes in nutrient cycling, but mechanistic details are far from clear (15,20,48,49). For example, step changes in the burial of phosphorus and organic carbon, driven by evolutionary innovations, have been argued to have progressively lowered marine phosphate concentrations (15). Each step change would result in a pulse of marine oxygenation, but over long timescales the decrease in C_{org}/P burial ratios would drive atmospheric oxygen levels down, and slowly deoxygenate the oceans (15).

Others have noted that the low total organic carbon content in Neoproterozoic shales suggests that the ocean at this time may have had a lower flux of primary productivity to the seafloor than in the Phanerozoic (20). An expected consequence of this nutrient-limitation is that biotas would have small body sizes, and sparse and heterogeneous global distributions (20). Analysis of N isotopes over the late Ediacaran to early Cambrian interval supports the hypothesis that pulses of oxygenation, punctuated by regional anoxic events of shoaling chemoclines, were closely associated with an increase in nutrients that boosted primary productivity of large-celled, eukaryotic phytoplankton, perhaps in turn stimulating metazoan evolution (49).

Individual marine basins continued to record unstable redox conditions over short timescales well into the Cambrian, with dominantly ferruginous and even euxinic conditions particularly in shelf and slope environments (e.g. 40,75,76,80). Adjacent basins can show different redox histories, and the oxic chemocline often shoaled during sea-level transgressions (75,80). While some studies propose regional deepening of the oxycline during Cambrian Stage 2, with an accompanying increase in biological diversity (82,83), others have shown that anoxic or low-oxygen concentrations may have prevailed for extended intervals that contain notably biodiverse faunas, such as those recorded by the Chengjiang biota (76). However, just as we know little about the spatial scales of Ediacaran-Cambrian redox heterogeneity, we also know little quantitatively about the lateral distribution, and patchiness, of benthic biotas.

In a world with lower atmospheric oxygen than today, the habitability of benthic marine environments may have been governed by oxygen demand, dependent on rates of primary production, rates of oxygen replenishment via atmospheric mixing and diffusion, and the sinking rates of dominant primary producers (76). The distribution of shallow marine habitable zones would therefore have evolved dynamically as a result of changes in nutrient availability forced by changes in circulation, upwelling and sea level.

The processes driving biotic response to rising atmospheric oxygen levels, which may have manifest as a deepening of the chemocline, an increase in local redox stability, or a reduction of global redox heterogeneity, are not clear. Increasing oxygen levels have been proposed to result in an increase in overall biodiversity, the rise of new, more metabolically-demanding traits such as motility and skeletonisation, or the formation of more complex food webs and ecosystems (23). Increasing areal occupation of seafloor, or changes in biogeography as habitable settings expanded and connected, may also be expected. Globally expansive anoxia is expressed locally as heterogeneous, poorly ventilated basins, but whether habitable shallow shelf space was reduced or fragmented during past anoxic intervals is unknown. This emphasises the need to integrate global and local redox proxies. Notably, integrated geochemical and biotic data show that diverse Cambrian communities were established under dynamic redox conditions in oxic refugia (76), essentially under similar conditions to far lower diversity, terminal Ediacaran ecosystems. Hence, the relationship between the evolution of metazoan ecosystems and increasing atmospheric oxygen and redox stability appears far more complex than direct, linear, cause and effect.

It is possible that fluctuations in redox may, in fact, reinforce rather than hinder evolutionary transitions, with variability in near-surface oceanic oxygenation promoting morphological evolution and novelty (19). Several major radiations, including across the Ediacaran–Cambrian boundary, the GOBE, and the mid-late Triassic, follow intervals of protracted or dynamic shallow marine anoxia. These dynamic conditions may have created opportunities for the generation of evolutionary novelty in soft-bodied benthos, which then provided ancestral stock for subsequent skeletonized lineages once oxic conditions became widespread, connected, and stable (19).

The period of globally expanded anoxia at ~ 551 Ma has been proposed to coincide with a reduction in diversity of the Ediacaran macrobiota as manifest in the depauperate Nama Assemblage (41). But data from the Nama Group, Namibia, show that the transition towards globally widespread anoxic conditions post-dates the first appearance of both the skeletal and soft-bodied fauna of the Nama Assemblage, demonstrating that this expansion did not coincide with the decline of the Ediacaran biota (43). This expansion may rather reflect a geochemical response to an ecological innovation or change (15,43). We note that the diversification of ichnofossils in Namibia, and the appearance of organic-walled tubular taxa, broadly coincides with the subsequent reduction of global anoxic seafloor conditions.

New lineages of crown-group bilaterians appear after Ediacaran–Cambrian boundary anoxia at ~540 Ma, and again after an interval of anoxia at ~520 Ma (50). After this, we see two phases of radiation separated by the Sinsk Event extinction (73). The first is dominated by non-bilaterian and bilaterian stem groups from ~542–513 Ma, and the second is marked by radiating non-bilaterian and bilaterian crown group species from ~513 through to the Ordovician radiation. This second radiation may have been interrupted by the late Cambrian SPICE anoxic event (35), coincident with a negative carbon isotope excursion, which marked a further minor extinction, but also ushered in the GOBE (Figure 1). We thus postulate that waves of metazoan innovation immediately followed intervals of dynamic redox conditions (following the model of 19), throughout the Ediacaran to Ordovician periods.

Understanding ecology and redox at the local scale: evidence for biotic replacement?

The apparent drop in biodiversity between the comparatively diverse White Sea Assemblage and the Nama Assemblage, and the disappearance of Ediacaran soft-bodied macrobiota at the end of the Ediacaran has been suggested to have been mediated by increasing competition and predation following the rise of bilaterian or crown-group animals.

The rise of bioturbation, predation, biomineralisation and grazing by bilaterians may also have perturbed sediment stability and reduced the availability of Dissolved Organic Carbon (DOC): the so-called ‘biotic replacement’ model, involving ecosystem engineering (84-86).

Multiple bedding surfaces in late Ediacaran successions from Australia, China and Russia (Figures 2a, b) demonstrate co-occurrence of prominent horizontal burrows, such as *Lamonte* and *Helminthoidichnites,* with mobile soft-bodied taxa, such as *Yorgia* and *Dickinsonia*, and tubular and frondose macro-organisms (65,66,87). Many such occurrences can be reasonably assumed to record contemporary communities. Such co-existence continues into the earliest Cambrian, where relatively large trace fossils, such as *Treptichnus*, are found alongside putative *Swartpuntia*-like impressions in the earliest Cambrian Stage 3 (Figure 2c). We see no evidence of direct competitive replacement, but rather of probable sustained co-existence, in both shallow marine carbonate and siliciclastic settings.

For biotic replacement to occur, taxa must be both spatially co-located and have similar resource requirements, yet spatial analyses of contemporary communities find only very limited instances of resource competition. Integrated sedimentological and redox models for key fossiliferous Ediacaran successions in Avalonia (Newfoundland), south Australia, western Russia, the Yangtze Block (South China) and Namibia reveal the diversity of settings occupied by early metazoans (Figure 3).

The Drook to Renews Head formations of western Avalonia, eastern Newfoundland (~571–566 Ma), represent the Avalon Assemblage (Figure 3a) and were deposited in deep marine environments (e.g. 88). Benthic colonisation, mainly by sessile, frondose rangeomorphs, occurs after the appearance of stable oxic conditions (53,81). The biota from the Ediacara Member, South Australia (~560–550 Ma), represents the shallow marine White Sea Assemblage (Figure 3b; based on data in 89), which hosts rangeomorphs, soft-bodied motile taxa such as *Kimberella* (89) and *Dickinsonia* and trace fossils (62). The broadly coeval White Sea region of western Russia (Figure 3c) shows distinct facies-based soft-bodied assemblages, with *Charnia* communities in deeper settings and shallower, pro-deltaic White Sea and Nama-like Assemblages (56). Both assemblages suggest occupation of at least intermittently oxic settings permissible for life habits, potentially with relatively high metabolic oxygen demands (90). The Dengying Formation, China (~551-541 Ma), shows persistent and long-lasting redox stratification, with deep ferruginous waters commonly encroaching onto the shallow platform (e.g.12). The highly fossiliferous shallow marine bituminous Shibantan Member (Figure 3d) bears soft-bodied frond-like taxa, tubular forms, vendotaenids and trace fossils, as well as biota characteristic of the Avalon and Nama Assemblages (65,66,91), and shows intermittent ventilation during storm events (92,93). By contrast, the time-equivalent mixed carbonate and siliciclastic deposits of the Gaojiashan Member of the Dengying Formation record a very different assemblage, dominated by tubular skeletonising forms including *Cloudina* and *Sinotubulites*, and non-biomineralised tubular *Gaojiashania*, *Conotubus* and *Shaanxilithes* (94-97). These communities likewise grew under intermittently well-ventilated conditions, but with incursions of anoxia (98). Finally, the mixed siliciclastic and carbonate deposits of the uppermost Nama Group, southern Namibia (Figure 3e), were deposited in a predominantly offshore, storm-dominated shelf environment from ~542–540 Ma (99). These contain the complex trace fossils *Streptichnus narbonnei*, in addition to soft-bodied macrofossils (86,100). Thinly bedded limestone units recording deposition during highstands host skeletal *Namacalathus* and *Cloudina*. Palaeoredox conditions are interpreted as dominantly stable and oxic (80,86).

These analyses show an increase in morphological and ecological complexity through time, critically with an increase in the co-existence of taxa, particularly trace-makers. Organic tubular and trace fossil taxa co-occur locally, and indeed over millions of years (supporting 4 and 8, but *contra* 17). However, where soft-bodied and skeletal biotas co-existed, they predominantly occupied different parts of basins. For example, taxa such as *Cloudina* and *Namacalathus* occupied carbonate sedimentary settings, with pre-existing clades (such as rangeomorphs) generally found in siliciclastic settings. This is noteworthy, since in mixed sedimentary successions clastics dominate transgressive systems tracts, but carbonates dominate highstand systems tracts.

Changes in seawater chemistry and the rise of biomineralisation

The global onset of widespread calcareous biomineralisation at ~550 Ma, probably in low latitudes with supersaturated waters with respect to calcium carbonate (101), may suggest the operation of an extrinsic trigger. Terminal Ediacaran to Cambrian putative metazoan skeletal taxa are morphologically and mineralogically diverse, showing independent acquisition of skeletons in diverse taxonomic groups (102). Many share the inferred presence of a precursor organic skeleton, and possess apparently simple microstructures (101), including the first putative poriferans (103). Some skeletal taxa known from carbonate successions appear to have non-skeletal, organic-walled counterparts in siliciclastic facies e.g. *Cloudina-Conotubus*; *Sinotubulites-Corumbella*; and *Protolagena-Sicylagena* (104). Early metazoan skeletal clades commonly co-opted carbonate minerals in concert with ambient ocean chemistry, potentially driven by inferred changing seawater Mg/Ca ratios (105). Fluid inclusion data, models, and early marine cements all suggest that seawater Mg/Ca progressively lowered during the Ediacaran to early Cambrian (106,107). The first skeletal macrofossils coincide with the appearance of widespread high-Mg calcite and/or aragonite early marine cements, implying that calcareous biomineralisation may have been facilitated by increased relative calcium concentrations (e.g. 106).

3. Were the Ediacaran and Cambrian biotas distinct?

Arguments for mass extinction and ecological replacement across the Ediacaran to Cambrian transition have emphasised taxonomic and ecological differences between the Ediacaran and Cambrian biotas (85). For example, typical Ediacaran and Cambrian trace fossils are claimed to be distinct in size and complexity. While most soft-bodied Ediacaran taxa and some skeletal taxa are lost, the gaps and biases in the record, and the absence of sufficient chronostratigraphic control, preclude definitive statements as to gradual or rapid rates of decline, but do nonetheless support phases of faunal turnover (Figure 4).

Potential evidence for a mass extinction at the Ediacaran–Cambrian boundary requires establishing the presence of a severe and global environmental perturbation that is synchronous with a rapid reduction in biodiversity (8). The BACE has been suggested to mark a major perturbation coincident with the mass extinction of soft-bodied macrobiota, but an absence of dateable beds has hampered the construction of sufficiently high resolution correlation schemes to establish global synchronicity of this event (see reviews of 8,9,85). Likewise, frequent unconformities across the Ediacaran–Cambrian boundary at many important fossiliferous sections make this hypothesis difficult to test (see Supplementary Fig. 1). A literal reading of the record shows the main decrease in soft-bodied benthic biodiversity to have occurred ~5–10 Myr prior to the Ediacaran–Cambrian boundary (3,85). Indeed, despite the abundance of lagerstätten, the current inventory does not provide a continuous record through the interval, and there is also a notable dearth of precisely dated assemblages at and around the Ediacaran–Cambrian boundary. Widespread development of shallow marine anoxia coincident with the BACE would suggest a potential agent for mass extinction, but the mechanisms driving the BACE are poorly known (8). We suggest that such an anoxic episode would appear to be just one of several similar, both preceding and succeeding, redox perturbations.

A case for successive, transitional assemblages

At a local scale, Ediacaran biotas can be highly variable and can differ dramatically within successive beds (e.g. 108,109). This community heterogeneity suggests high beta (between community) diversity, suggesting that the representativeness of palaeobiological information may be restricted. In contrast, global, long-term biotic patterns in diversity across this interval have been considered to be tractable, and have statistical support (8,58).

Age ranges of key fossil genera, and the minimum ages implied by higher phylogenetic relationships, indicate temporal overlap between taxa typically perceived as 'Ediacaran' or 'Cambrian' (Figure 4). First, examples of organisms at least superficially similar to the Ediacaran macro-organism *Swartpuntia* are known in the Cambrian (110,111), and putative links have been made between frondose Cambrian forms and Ediacaran rangeomorphs (112-114). In addition, there are documented late Ediacaran occurrences of complex treptichnid trace fossils, some of which have been convincingly attributed to bilaterian priapulid worms (e.g. 110).

Secondly, high-resolution carbon isotope chemostratigraphy and biostratigraphy for a terminal Ediacaran to Cambrian succession on the eastern Siberian Platform show the presence of a succession of diverse fossil assemblages before the start of the BACE (6). Here, a mixed Ediacaran and Cambrian skeletal biota (*Cloudina, Anabarites, Cambrotubulus)* appears in limestones within the EPIP (Figures 2d,e). The co-occurrence of cloudinids with various other skeletal species, representing a number of diverse clades of early Cambrian aspect, has also been documented elsewhere in Siberia, South China, and Kazakhstan (6,115,116). The agglutinated fossils *Platysolenites* and *Spirosolenites*, which occur globally in the Cambrian (117), also co-occur with 'Ediacaran' *Cloudina, Vendotaenia*, and

Namacalathus on the Western Siberian Platform (118). There is, therefore, evidence for considerable diversification of characteristic Cambrian-type skeletal taxa prior to the BACE.

Thirdly, trace fossils made by mobile burrowing bilaterians first appear in the latest Ediacaran and continue as identical traces into the Cambrian (e.g. *Helminthoidichnites*, *Archaeonassa*). Although their trace makers are unknown and may have changed over time, the continuity of these traces suggests that at least some behaviours of soft-bodied denizens of the latest Ediacaran, and therefore potentially some of the higher-level taxonomic groups to which they belong, continued across the boundary (4,119) (Figure 4).

These integrated data show that taxa attributed to so-called Ediacaran and earliest Cambrian skeletal biotas overlap in some localities, without notable biotic turnover. In addition, there may be a close relationship between organic-walled and skeletal tubular taxa (104), further supporting a transitional assemblage acquiring skeletonisation in permissive settings. Extrapolation of radiometric dating from South China (120), the northern Siberian Platform (121), and Oman (122), constrains this transitional skeletal biota to ~545–540 Ma.

Rather than distinct Ediacaran and Cambrian biotas, we here make a case for a succession of taxonomically distinct biotas or assemblages (Figure 4b–d), each of which is marked by the appearance of new biological traits and ecological strategies, and which were to a greater or lesser extent governed by facies. First, the Avalon (~571–557 Ma), White Sea (~560–551 Ma), and Nama (~555–541 Ma) assemblages (57,58), with frond-dominated Avalonian assemblages later embellished by a ‘second wave’ (3) of Ediacaran diversification in the White Sea Assemblage. The White Sea Assemblage documents increased diversity and taxonomic disparity of macroscopic soft-bodied organisms, including the first motile bilaterians and trace fossil makers (although we note the global dearth of shallow marine facies coeval with the Avalon Assemblage). By contrast, latest Ediacaran successions from Namibia, Paraguay, Brazil, USA, Siberia and China document lower diversity assemblages of soft-bodied taxa, but two distinct new body plans also appear: organic-walled tubular taxa in shallow marine clastic settings, and biomineralising tubular taxa in previously largely unoccupied shallow marine carbonate environments (17,32,35). After the Ediacaran–Cambrian boundary we see a radiation of probable stem group members of bilaterian phyla and non-bilaterians, and then a second radiation of inferred crown group members of bilaterian phyla, which continue to diversify in the GOBE (73).

As noted in the distribution of Phanerozoic Evolutionary Faunas (EF; Figure 4), the boundaries between these assemblages are not defined by complete replacement of one EF by the next, but rather by the rise to ecological dominance of groups whose origins predate that rise (8).

4. Conclusions

The Ediacaran–Cambrian palaeontological and geochemical records reveal a progressive addition of biological novelty of form and process, and complexity within the Metazoa. Highly heterogeneous and fluctuating redox conditions throughout the late Ediacaran to early Palaeozoic interval, with successive but temporary expansions of oxic seafloor and possibly changing availability of phosphorous and nitrogen, facilitated the transition from low oxygen Proterozoic oceans to more extensively oxygenated Phanerozoic oceans, and the rise of modern biogeochemical cycles. This geochemical instability may have driven pulses of evolutionary innovation, but biotic feedbacks are poorly understood. Ecological and evolutionary responses to this instability could have wide reaching implications for discussions of gradualistic versus punctuated evolution.

We argue that the record can be considered as a succession of assemblages, with the establishment of Cambrian crown-group animal ecosystems built on several successive Ediacaran advances as well as environmental and biotic feedbacks. The oldest record of

Ediacara-type macrofossils appears to be dominated by probable non-bilaterian metazoans, with bilaterian metazoans appearing by ~560 Ma. A reduction in diversity occurs at ~551 Ma and this is closely followed by the appearance of the first biomineralised taxa, but a well-documented expansion of seafloor anoxia postdates these events. Bilaterians, including predators, diversify after an episode of widespread anoxia at the Ediacaran–Cambrian boundary, immediately succeeded by an inferred 'oceanic oxygenation event' at ~540 Ma. Inferred stem group poriferans, molluscs, and brachiopods were seemingly devastated by the early Cambrian Sinsk anoxic event (~513 Ma), in contrast to inferred crown group bilaterian phyla whose diversification continues through to the GOBE.

There is currently no compelling evidence for either significant competitive replacement, or biotic replacement, from the latest Ediacaran to Cambrian. Indeed, we conclude that a discrete "Cambrian Explosion" event is difficult to isolate temporarily or indeed define. The rise of early metazoans can be more simply and holistically recast as a series of successive, transitional radiation events, perhaps mediated via complex environmental change, which extended from the Ediacaran and continued to the early Palaeozoic.

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Figure legends

Figure 1. Integrated geochemical and biotic record between 670 and 480 million years ago. **A)** First appearance of major evolutionary milestones: 713–635 Ma, range of demosponge biomarker (24-isopropylcholestane) (123); Minimum age for marine planktonic algae (Archaeplastida) 659–645 Ma (124); 635–590 Ma, possible stem-group cnidarian *Lantianella laevis* (125), phosphatised proposed animal embryos (126); >570.95 Ma, juvenile *Charnia masoni* (127); ~565 Ma, candidate for the earliest surface locomotion trace fossil (63); ~550 Ma, earliest skeletal animals, *Cloudina* (69) and earliest possible evidence for predation (borings in *Cloudina* (68)); First appearance datum of the trace fossil *Treptichnus pedum* (72); Earliest trilobite *Profallotaspis jakutensis*. **B)** Ediacaran C-isotope compilation modified after (128,129), and references therein. Cambrian C-isotope profile conforms to composite curve of (29) (full details provided in Supplementary Information). **C)** Schematic evolution of redox conditions based on compiled iron speciation data (27,75,130) and proposed widespread anoxic intervals and ‘oceanic oxygenation events’ (40,41,43,47,50). Diagonal stripes indicate regional differences in redox state. Paucity of truly basinal shale deposits prevents determination of the redox state of the global oceanic deep basin (indicated by white question marks).

Figure 2. Key transitional Ediacaran and Cambrian taxa. **A)** Representative taxa of the Avalon biota of Newfoundland, ~566 Ma, almost uniquely comprised of soft-bodied, frondose members of the Ediacaran biota. **B)** Ediacaran *Arborea* with associated trace fossil, Flinders Ranges, South Australia. SAM P49393. **C)** *Corumbella,* organic-walled tubular fossil, latest Ediacaran Corumbá Group, SE Brazil. **D)** *Anabarites trisulcatus*, Ust'-Yudoma Formation, Kyra-Ytyga River, SE Siberia. Photo credit A. Fedorov. **E)** *Cloudina*, S. China, photo credit S. Xiao. **F)** Transitional small shelly fossil biota, SE Siberia (from (6)). **G)** Bilobed trace fossils from the Ediacaran Dengying Fm., Wuhe, South China, occurring on beds adjacent to surfaces bearing non-mineralized tubular organisms (e.g. *Wutubus*) and soft-bodied Ediacaran macrobiota (e.g. *Pteridinium* and *Charniodiscus*). **H)** Cambrian *Swartpuntia*-like moulds alongside trace-fossils including *Treptichnus*, Uratanna Fm., Flinders Ranges, South Australia. SAM P36399/36403. Scale bars: B) = 10 mm, G) = 20 mm, C) = 5 mm, D) = 300µm, E) = 1 mm, H) = 10 mm.

Figure 3. Ediacaran ecosystem dioramas for single, conformable sequences from **A)** Avalonia, **B)** Australia, **C)** Western Russia (White Sea Region), **D)** the Yangtze Block, China, and **E)** Namibia. Each shows the distribution of contemporary biota within the local sedimentological and redox setting, and the relative water depth. See SI for key to stylised biota.

Figure 4. A) Temporal occurrence ranges for key soft-bodied, organic-walled, biomineralised, and trace fossil Ediacaran and transitional Cambrian taxa (references in SI). Minimum and maximum duration of hiatus associated with the Ediacaran/Cambrian is shown. **B)** Key evolutionary innovations. **C)** Distribution and succession of transitional assemblages. **D)** Evolutionary dynamics showing the temporal distribution of stem and crown

groups in non-bilaterians and bilaterians (73), and major anoxic events and ‘oceanic oxygenation events’ (OOEs) (51,52,54,59,62). E/C = Ediacaran/Cambrian. Full details in SI.