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## Integrated records of environmental change and evolution challenge the Cambrian Explosion

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1 **Integrated records of environmental change and evolution challenge the Cambrian**  
2 **Explosion**

3

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20

21 **Abstract**

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

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

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

38

## 39 **1. Introduction**

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

51 recognised in the subsequent early Palaeozoic, and so the relationship of these to evolutionary  
52 and ecological innovations across the Ediacaran–Cambrian boundary must be understood (9-  
53 11).

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

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

75

## 76 **2. Environmental change versus evolutionary innovation**

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

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

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

103 The non-uniformitarian nature of the oceans across the Ediacaran–Cambrian interval,  
104 continuing into the Ordovician, is evidenced by considerable instability in the carbon isotope  
105 record in inorganic carbonates. The magnitude of the largest known negative carbonate  
106 carbon isotope ( $\delta^{13}\text{C}_{\text{carb}}$ ) excursion in the geological record, the Ediacaran Shuram/Wonoka  
107 anomaly, has a nadir of  $-12\text{‰}$  (22). Following recovery to positive values prior to 551–548  
108 Ma,  $\delta^{13}\text{C}_{\text{carb}}$  remained relatively unperturbed for the final  $\sim 10$  Myr of the Ediacaran (the  
109 Ediacaran positive isotopic plateau: EPIP), before falling again to values indicative of the  
110 basal Cambrian negative carbon isotope excursion (BACE) (e.g. 28-30). The BACE pre-dates  
111 the first appearance of *Treptichnus pedum* (31,32), while in South China it correlates with the  
112 *Asteridium–Heliosphaeridium–Comasphaeridium* (AHC) acritarch assemblage and the  
113 *Anabarites trisulcatus–Protohertzina anabarica* (small shelly fossils) Assemblage Zone (33-  
114 34). A number of further short-lived  $\delta^{13}\text{C}_{\text{carb}}$  excursions continue to punctuate the Cambrian  
115 (29,35) and Ordovician chemostratigraphic records (36), exhibiting a progressive decline in  
116 overall excursion magnitude into the Phanerozoic (e.g. 37).

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

130 Others have argued for intervening late Ediacaran ‘oceanic oxygenation events’ (OOEs)  
131 (Figure 1c) at around 575 Ma (OOE2),  $\sim 560$  Ma (OOE3) - possibly coincident with the start  
132 of the Shuram - and at  $\sim 540$  Ma (OOE4) (40,47), although differing redox proxies are not  
133 always consistent with the timing of these intervals. For example, on the basis of N isotopes,

134 oxic intervals have been proposed ~551–543 Ma, ~544–529 Ma, and ~521–517 Ma (see 48).  
135 Diverse proxies suggest that the global ocean became progressively more oxygenated through  
136 the early Cambrian until ~520 Ma, after which time there was a return to more widespread  
137 anoxia (49,50). The Sinsk Event, accompanied by a negative CIE, is a further short-lived  
138 anoxic interval at ~513 Ma (11). Independent proxies suggest that full oxygenation of the  
139 deep oceans was not reached until the Devonian (27,51).

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

143 The oldest macrofossils of the so-called ‘Ediacaran macrobiota’ are known from the  
144 Drook Formation, Newfoundland (52), and are dated at ~571 Ma (53). Although their precise  
145 phylogenetic position remains unclear, at least some taxa are reasonably interpreted to have  
146 been total group metazoans (54). The wider macrobiota includes a range of complex  
147 organisms with tubular, frondose, modular, and sheet-like morphologies that likely include  
148 multiple clades (e.g. 55). These have been grouped within three proposed biotic  
149 ‘assemblages’ (recurrent community compositions) that appear to be predominately  
150 controlled by facies rather than age (56): the Avalon (~571–555 Ma), White Sea (~560–551  
151 Ma), and Nama (~555–541 Ma) assemblages (57,58). Frondose taxa (e.g. *Charnia*, *Arborea*)  
152 dominate the Avalon Assemblage, and are accompanied by rare candidate cnidarians (59),  
153 but both the diversity and taxonomic disparity of macroscopic soft-bodied organisms increase  
154 significantly after ~560 Ma (3,60). The first identifiable motile, heterotrophic organisms are  
155 *Kimberella quadrata*, *Yorgia* and *Dickinsonia* from Russia, at ~558–555 Ma, the latter being  
156 highly likely to have been a metazoan on the basis of ichnological, developmental and  
157 biomarker evidence (see 54,61). A widespread record of surface locomotory trace fossils  
158 exists from at least 560 Ma (62; see also 63), and these diversify in form and complexity  
159 through the late Ediacaran (64–67). Latest Ediacaran assemblages show a marked reduction in  
160 soft-bodied macrofossil diversity, but witness the appearance of organic-walled (e.g.  
161 *Corumbella*) and skeletal tubular fossils, and a diversification of bilaterian trace fossils (9,  
162 62). The oldest skeletal macrofossil, *Cloudina*, which also shows the first possible evidence  
163 for predatory borings (68), is known globally from ~550 Ma (69). *Cloudina* could form reefs  
164 (70, but see 71) and together with the late Ediacaran (~543 Ma) *Paraconularia*, is plausibly  
165 interpreted as a total-group cnidarian (and, therefore, a crown-eumetazoan).

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

176 These patterns in the fossil record are yet to be converted into a coherent understanding of  
177 the dynamics of how metazoan phyla appeared and evolved (5), but quantitative analysis of  
178 lophotrochozoan skeletal species from the terminal Ediacaran to Cambrian Stage 5 (~545–  
179 505 Ma) on the Siberian Platform show a disjunct temporal distribution that suggests that the  
180 radiation of bilaterian metazoans occurred in two phases, separated by an extinction event.  
181 The first was dominated by lophophorate, brachiopod, and mollusc stem groups from ~542–  
182 513 Ma, and the second was marked by radiating brachiopod and mollusc crown group  
183 species from ~513 Ma, extending to the Great Ordovician Radiation Event (GOBE) (73).

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184  
185 unequivocal distinction between global layer-cake redox stratification of the oceans and  
186 highly dynamic Oxygen Minimum Zones (OMZs) overlying potentially oxic basinal waters.  
187 There is growing evidence for the existence of OMZs in early Cambrian basins (75-77).

188 Many global proxies allow only for estimates of expanded seafloor anoxia, and do not  
189 differentiate between deep and shallow marine settings. Consequently, it is not clear if such  
190 expansions restricted the habitable area of the shallow shelf, where most biodiversity resides.  
191 At least some biotas throughout this interval were subject to upwelling incursions of oxygen  
192 deficient water, controlled by local changes in relative sea level and productivity (77).

193 Therefore, the entire Ediacaran–Cambrian radiation, and indeed beyond, may have occurred  
194 under relatively low oxygen levels, but with highly dynamic, fluctuating redox conditions



195 prevalent on local (ecological), as well as global and evolutionary, temporal and spatial scales  
196 (19).

197

198 ***Biotic response to changing redox: a role for instability?***

199 While all extant metazoans need oxygen, their demands are not equal. Modern low-  
200 oxygen regions are heterogeneous and dynamic habitats that support low diversity  
201 communities of opportunistic and non-skeletal metazoans, many of which are meiofaunal:  
202 large, skeletal, and motile metazoans, which form complex, biodiverse ecosystems, typically  
203 require higher oxygen levels (23). Experimental work has demonstrated that certain early-  
204 diverging clades (poriferans and ctenophores) may have very low oxygen demands, since  
205 they lack hypoxia-inducible factor (HIF) pathways to maintain cellular oxygen homeostasis  
206 (78,79). This suggests that stem-group metazoans, and the metazoan Last Common Ancestor,  
207 may also have lacked the HIF pathway, and so could have metabolized aerobically under  
208 very low environmental oxygen concentrations (79). Animals most likely originated in a  
209 non-uniformitarian world of low atmospheric oxygen, and almost certainly before the  
210 permanent oxygenation of the deep ocean. However, it remains unclear as to whether animal  
211 diversification and increased ecosystem complexity was driven extrinsically by the expansion  
212 of permissive oxic niches, or by genetic or developmental innovations that enabled animals to  
213 expand into the oxic realm.

214 Where palaeoredox proxy data are integrated with biotic distribution, metazoans are  
215 usually restricted to localised oxygenated habitats, either above a shallow chemocline, or  
216 potentially below an OMZ (e.g. 76, 80). The instability of the chemocline would therefore  
217 have provided strong anactualistic controls on the distribution of metazoans, and potentially  
218 on the taphonomic windows for their preservation. Ediacaran and Cambrian sediments

219 deposited below the chemocline (or within an OMZ) may therefore be expected to lack  
220 metazoan life assemblages.

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

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

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

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

263 In a world with lower atmospheric oxygen than today, the habitability of benthic marine  
264 environments may have been governed by oxygen demand, dependent on rates of primary  
265 production, rates of oxygen replenishment via atmospheric mixing and diffusion, and the  
266 sinking rates of dominant primary producers (76). The distribution of shallow marine

267 habitable zones would therefore have evolved dynamically as a result of changes in nutrient  
268 availability forced by changes in circulation, upwelling and sea level.

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

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

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

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

311

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

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

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

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

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

335 The Drook to Renewes Head formations of western Avalonia, eastern Newfoundland  
336 (~571–566 Ma), represent the Avalon Assemblage (Figure 3a) and were deposited in deep  
337 marine environments (e.g. 88). Benthic colonisation, mainly by sessile, frondose  
338 rangeomorphs, occurs after the appearance of stable oxic conditions (53,81). The biota from  
339 the Ediacara Member, South Australia (~560–550 Ma), represents the shallow marine White  
340 Sea Assemblage (Figure 3b; based on data in 89), which hosts rangeomorphs, soft-bodied  
341 motile taxa such as *Kimberella* (89) and *Dickinsonia* and trace fossils (62). The broadly

342 coeval White Sea region of western Russia (Figure 3c) shows distinct facies-based soft-  
343 bodied assemblages, with *Charnia* communities in deeper settings and shallower, pro-deltaic  
344 White Sea and Nama-like Assemblages (56). Both assemblages suggest occupation of at least  
345 intermittently oxic settings permissible for life habits, potentially with relatively high  
346 metabolic oxygen demands (90). The Dengying Formation, China (~551-541 Ma), shows  
347 persistent and long-lasting redox stratification, with deep ferruginous waters commonly  
348 encroaching onto the shallow platform (e.g. 12). The highly fossiliferous shallow marine  
349 bituminous Shibantan Member (Figure 3d) bears soft-bodied frond-like taxa, tubular forms,  
350 vendotaenids and trace fossils, as well as biota characteristic of the Avalon and Nama  
351 Assemblages (65,66,91), and shows intermittent ventilation during storm events (92,93). By  
352 contrast, the time-equivalent mixed carbonate and siliciclastic deposits of the Gaojiashan  
353 Member of the Dengying Formation record a very different assemblage, dominated by  
354 tubular skeletonising forms including *Cloudina* and *Sinotubulites*, and non-biomineralised  
355 tubular *Gaojiashania*, *Conotubus* and *Shaanxilithes* (94-97). These communities likewise  
356 grew under intermittently well-ventilated conditions, but with incursions of anoxia (98).  
357 Finally, the mixed siliciclastic and carbonate deposits of the uppermost Nama Group,  
358 southern Namibia (Figure 3e), were deposited in a predominantly offshore, storm-dominated  
359 shelf environment from ~542–540 Ma (99). These contain the complex trace fossils  
360 *Streptichmus narbonnei*, in addition to soft-bodied macrofossils (86,100). Thinly bedded  
361 limestone units recording deposition during highstands host skeletal *Namacalathus* and  
362 *Cloudina*. Palaeoredox conditions are interpreted as dominantly stable and oxic (80,86).

363 These analyses show an increase in morphological and ecological complexity through  
364 time, critically with an increase in the co-existence of taxa, particularly trace-makers. Organic  
365 tubular and trace fossil taxa co-occur locally, and indeed over millions of years (supporting 4  
366 and 8, but *contra* 17). However, where soft-bodied and skeletal biotas co-existed, they

367 predominantly occupied different parts of basins. For example, taxa such as *Cloudina* and  
368 *Namacalathus* occupied carbonate sedimentary settings, with pre-existing clades (such as  
369 rangeomorphs) generally found in siliciclastic settings. This is noteworthy, since in mixed  
370 sedimentary successions clastics dominate transgressive systems tracts, but carbonates  
371 dominate highstand systems tracts.

372

### 373 ***Changes in seawater chemistry and the rise of biomineralisation***

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

390

391



392 **3. Were the Ediacaran and Cambrian biotas distinct?**

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

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

417

418 *A case for successive, transitional assemblages*

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

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

432 Secondly, high-resolution carbon isotope chemostratigraphy and biostratigraphy for a  
433 terminal Ediacaran to Cambrian succession on the eastern Siberian Platform show the  
434 presence of a succession of diverse fossil assemblages before the start of the BACE (6). Here,  
435 a mixed Ediacaran and Cambrian skeletal biota (*Cloudina*, *Anabarites*, *Cambrotubulus*)  
436 appears in limestones within the EPIP (Figures 2d,e). The co-occurrence of cloudinids with  
437 various other skeletal species, representing a number of diverse clades of early Cambrian  
438 aspect, has also been documented elsewhere in Siberia, South China, and Kazakhstan  
439 (6,115,116). The agglutinated fossils *Platysolenites* and *Spirosolenites*, which occur globally  
440 in the Cambrian (117), also co-occur with ‘Ediacaran’ *Cloudina*, *Vendotaenia*, and

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

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

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

455 Rather than distinct Ediacaran and Cambrian biotas, we here make a case for a succession  
456 of taxonomically distinct biotas or assemblages (Figure 4b–d), each of which is marked by  
457 the appearance of new biological traits and ecological strategies, and which were to a greater  
458 or lesser extent governed by facies. First, the Avalon (~571–557 Ma), White Sea (~560–551  
459 Ma), and Nama (~555–541 Ma) assemblages (57,58), with frond-dominated Avalonian  
460 assemblages later embellished by a ‘second wave’ (3) of Ediacaran diversification in the  
461 White Sea Assemblage. The White Sea Assemblage documents increased diversity and  
462 taxonomic disparity of macroscopic soft-bodied organisms, including the first motile  
463 bilaterians and trace fossil makers (although we note the global dearth of shallow marine  
464 facies coeval with the Avalon Assemblage). By contrast, latest Ediacaran successions from  
465 Namibia, Paraguay, Brazil, USA, Siberia and China document lower diversity assemblages of

466 soft-bodied taxa, but two distinct new body plans also appear: organic-walled tubular taxa in  
467 shallow marine clastic settings, and biomineralising tubular taxa in previously largely  
468 unoccupied shallow marine carbonate environments (17,32,35). After the Ediacaran–  
469 Cambrian boundary we see a radiation of probable stem group members of bilaterian phyla  
470 and non-bilaterians, and then a second radiation of inferred crown group members of  
471 bilaterian phyla, which continue to diversify in the GOBE (73).

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

476

#### 477 **4. Conclusions**

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

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

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

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

506

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510

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512

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524

525

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## 866 **Figure legends**

867

868 **Figure 1.** Integrated geochemical and biotic record between 670 and 480 million years ago.

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

884

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

898  
899 **Figure 3.** Ediacaran ecosystem dioramas for single, conformable sequences from **A)**  
900 Avalonia, **B)** Australia, **C)** Western Russia (White Sea Region), **D)** the Yangtze Block,  
901 China, and **E)** Namibia. Each shows the distribution of contemporary biota within the local  
902 sedimentological and redox setting, and the relative water depth. See SI for key to stylised  
903 biota.

904  
905 **Figure 4.** **A)** Temporal occurrence ranges for key soft-bodied, organic-walled,  
906 biomineralised, and trace fossil Ediacaran and transitional Cambrian taxa (references in SI).  
907 Minimum and maximum duration of hiatus associated with the Ediacaran/Cambrian is  
908 shown. **B)** Key evolutionary innovations. **C)** Distribution and succession of transitional  
909 assemblages. **D)** Evolutionary dynamics showing the temporal distribution of stem and crown

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