

1 **Integrated record of environmental change and evolution challenges the Cambrian**
2 **Explosion**

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4 Rachel Wood^{1*}, Alexander G. Liu², Frederick Bowyer¹, Philip R. Wilby³, Frances S. Dunn^{3,4},
5 Charlotte G. Kenchington^{2,5}, Jennifer F. Hoyal Cuthill^{2,6}, Emily G. Mitchell², and Amelia
6 Penny⁷.

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8 ¹ School of GeoSciences, University of Edinburgh, James Hutton Road, Edinburgh EH9 3FE,
9 UK. *email: Rachel.Wood@ed.ac.uk

10 ² Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2
11 3EQ, UK.

12 ³ British Geological Survey, Nicker Hill, Keyworth, Nottinghamshire NG12 5GG, UK.

13 ⁴ School of Earth Sciences, Life Sciences Building, 24 Tyndall Avenue, Bristol BS8 1TQ,
14 UK.

15 ⁵ Department of Earth Sciences, Memorial University of Newfoundland, 300 Prince Philip
16 Drive, St. John's, Newfoundland A1B 3X5, Canada.

17 ⁶ Earth-Life Science Institute, Tokyo Institute of Technology, Tokyo, 152-8550, Japan.

18 ⁷ Finnish Museum of Natural History, University of Helsinki, Jyrängöntie 2, 00560 Helsinki,
19 Finland.

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 macrofossils 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

100

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‰ (22). Following recovery to positive values prior to 551–548
108 Ma, $\delta^{13}\text{C}_{\text{carb}}$ remained relatively unperturbed for the final ~ 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 ~ 550 Ma (22,46).

130 Others have argued for intervening late Ediacaran ‘oceanic oxygenation events’ (OOEs)
131 (Figure 1c) at around 575 Ma (OOE2), ~ 560 Ma (OOE3) - possibly coincident with the start
132 of the Shuram - and at ~ 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).

141

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).

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 Renew's 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-biom mineralised
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 *Streptichnus 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

513 **Materials & Correspondence.** Please address all correspondence and material requests to
514 Rachel.Wood@ed.ac.uk.

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864
865

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.