

Decline and fall of the Ediacarans: late-Neoproterozoic extinctions and the rise of the modern biosphere

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ABSTRACT

The end-Neoproterozoic transition marked a gradual but permanent shift between distinct configurations of Earth's biosphere. This interval witnessed the demise of the enigmatic Ediacaran Biota, ushering in the structured trophic webs and disparate animal body plans of Phanerozoic ecosystems. However, little consensus exists on the reality, drivers, and macroevolutionary implications of end-Neoproterozoic extinctions. Here we evaluate potential drivers of late-Neoproterozoic turnover by addressing recent findings on Ediacaran geochronology, the persistence of classical Ediacaran macrobionts into the Cambrian, and the existence of Ediacaran crown-group eumetazoans. Despite renewed interest in the possibility of Phanerozoic-style 'mass extinctions' in the latest Neoproterozoic, our synthesis of the available evidence does not support extinction models based on episodic geochemical triggers, nor does it validate simple ecological interpretations centred on direct competitive displacement. Instead, we argue that the protracted and indirect effects of early bilaterian innovations, including escalations in sediment engineering, predation, and the largely understudied impacts of reef-building, may best account for the temporal structure and possible selectivity of late-Neoproterozoic extinctions. We integrate these processes into a generalised model of early eumetazoan-dominated ecologies, charting the disruption of spatial and temporal isotropy on the Ediacaran benthos as a consequence of diversifying macrofaunal interactions. Given the nature of resource distribution in Ediacaran ecologies, the continuities among Ediacaran and Cambrian faunas, and the convergent origins of ecologically disruptive innovations among bilaterians we suggest that the rise of Phanerozoic-type biotas may have been unstoppable.

Key words: mass extinction, ecosystem engineering, Ediacaran Biota, Bilateria, Eumetazoa, Neoproterozoic.

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I. INTRODUCTION

The Ediacaran Biota encompasses a heterogeneous suite of macroorganisms appearing in the fossil record around 575 million years ago (Ma), during the Ediacaran period [~635–539 Ma (Darroch *et al.*, 2018; Bowyer *et al.*, 2022)] and generally occurring in benthic settings dominated by bacterial matground ecologies (Gehling, 1999). Classic Ediacaran soft-bodied macrofossils, henceforth informally referred to as ‘Ediacarans’, comprise disparate frondose, modular, and lobate body plans (Fig. 1) conventionally thought to have become extinct, or at least to have faded from ecological dominance, in the terminal Ediacaran (Darroch *et al.*, 2018; Hoyal Cuthill, 2022). Due to a scarcity of obvious homologies with living taxa, their constructional morphology and phylogenetic placement have proved notoriously controversial (e.g. Seilacher, 1989; reviewed in Runnegar, 2022). However, recent analyses based on exceptionally preserved soft tissues (Hoyal Cuthill & Han, 2018) and developmental patterns (Dunn, Liu & Donoghue, 2018;

Dunn *et al.*, 2019b, 2021; Dunn, Liu & Gehling, 2019a) suggest that at least some Ediacarans may lie on the stem of Eumetazoa – the clade of tissue-grade animals comprising the vast majority of present-day metazoan biodiversity (Runnegar, 2022). As the earliest credible palaeontological window on animal evolution, the Ediacaran Biota illuminates its tempo and mode, helping to reconcile fossil evidence with molecular clocks hinting at a cryptic Neoproterozoic (~1000–539 Ma) history (Cunningham *et al.*, 2017; Yang *et al.*, 2007).

This Neoproterozoic rise of animals unfolded amid some of the most pronounced biogeochemical upheavals in Earth history (Butterfield, 2015b). Establishing whether the Ediacarans’ demise marks the first observed eukaryotic mass extinction (Laflamme *et al.*, 2013) is critical to map the impacts of such events on the evolution of the biosphere, and their role in the appearance of modern, animal-dominated ecologies amid the ensuing Cambrian Explosion (Marshall, 2006; Butterfield, 2011). The Cambrian Explosion witnessed some of the most radical remodelling of food webs,

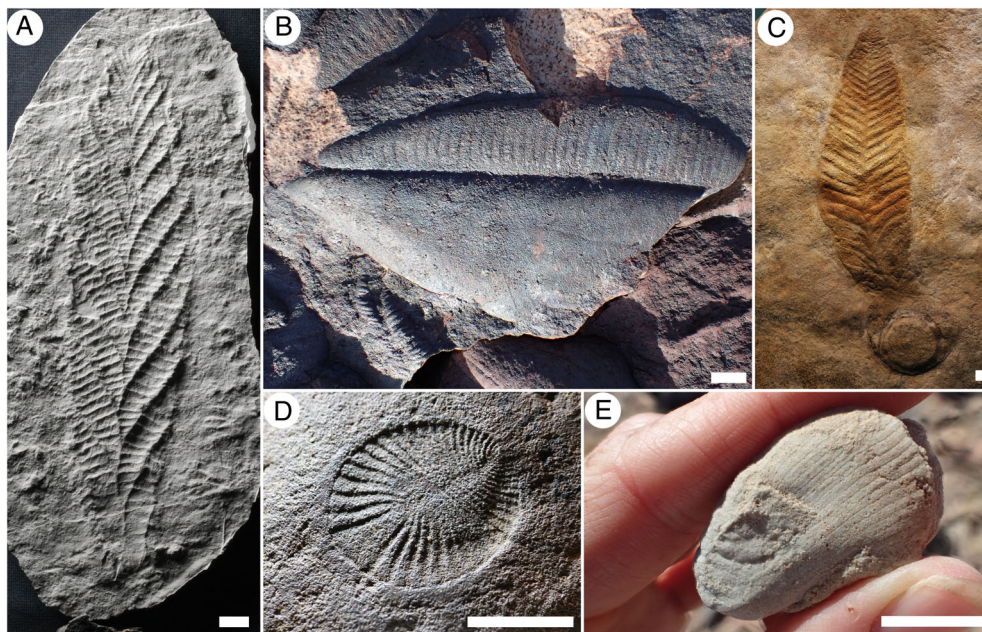


Fig. 1. Representative specimens of Ediacaran soft-bodied organisms. (A) Rangeomorpha: cast of the *Charnia masoni* holotype (LEIUG 232) from the Charnwood Forest, UK (Avalon assemblage) showing nested branching frond elements departing from a semi-rigid central axis. (B) Erniettomorpha: *Pterinidium simplex*, a recumbent three-lobed erniettomorph, from the terminal Ediacaran Nama Group of Namibia (Nama assemblage). (C) Arboreomorpha: *Arborea arborea* (SAM P19690a) from the Ediacara Member of the Rawnsley Quartzite (White Sea assemblage), South Australia, showcasing tubular frond elements and an articulated holdfast for anchorage to the substrate. (D) Dickinsoniomorpha: *Dickinsonia costata* (SAM PG4742) from the White Sea of Australia. This representative dickinsoniomorph had a flattened, quilted-mat-like ‘segmented’ body plan. (E) Erniettomorpha: *Ermiella plateauensis*, from the Nama Group. The upper body of this organism comprises at least one layer of tubes defining a broadened bilobed frill, which surrounded a central opening. Below an equatorial seam, the tubes assemble into a basal sac-like anchor. Scale bars = 10 mm. Institutional abbreviations: LEIUG, Leicester City Museum; SAM, South Australia Museum.

ocean ventilation, life-sediment interactions, and developmental and behavioural modes in Earth history, precipitating changes that laid the evolutionary and ecological groundwork for the modern biosphere (Erwin & Valentine, 2013; Butterfield, 2011). If these changes were set in motion by unpredictable episodes of biotic ‘reset’ like the mass extinctions punctuating the Phanerozoic (Hull, 2015) the emerging evidence for continuity between the Ediacaran and Cambrian worlds (Wood *et al.*, 2019) may be called into question, strengthening the case for the Cambrian Explosion as an evolutionary ‘singularity’ (Butterfield, 2015a) precipitated by unique geological contingencies. Therefore, the disappearance of the Ediacaran Biota offers a virtually unique opportunity to tackle evolutionary questions at a planetary scale. We do so by evaluating the tempo and mode of the transition between Ediacaran and Phanerozoic biotas based on recent multidisciplinary findings.

First (Section II) we assess the degree to which traditional Ediacaran macrofossil ‘assemblages’ record biotic turnover around the close of the Neoproterozoic. We then integrate the geochemical proxy record of Ediacaran redox and carbon cycle perturbations (Section III) with recent geochronological data to assess whether these Earth systems ‘anomalies’ emerge as strong candidate extinction drivers. Then, we discuss how the traditional alternative to abiotic explanations for Ediacaran extinctions, the ‘biotic replacement’ model (Laflamme *et al.*, 2013; Darroch *et al.*, 2018), may be refined in light of emerging evidence from the fossil record (Section IV) and highlight persisting uncertainties and promising research avenues under this hypothesis (Section V). In particular, we single out bilaterian diversification as a persistent and highly consequential trend in Ediacaran macroevolution, grounded in fundamental features of resource distribution in late-Neoproterozoic ecosystems and their information landscape (Section V). By mapping these evolutionary changes in their geobiological context, we set out to offer an updated view on the timing, drivers, and implications of the Ediacaran–Cambrian transition, a global and permanent ‘stable state shift’ (Butterfield, 2011) at the roots of the modern biosphere.

II. THE NATURE AND REALITY OF EDIACARAN ‘ASSEMBLAGES’

To address questions concerning the tempo, mode, and drivers of the late-Neoproterozoic turnover, resolving temporal succession within the Ediacaran biota is key. Traditionally, the Ediacaran Biota has been partitioned into three taxonomically distinct ‘assemblages’ (Fig. 2; Waggoner, 2003). The ‘Avalon’ assemblage mostly comprises frondose rangeomorphs and arboreomorphs (Darroch *et al.*, 2018) together with probable early poriferans (Suarez & Leys, 2022) and cnidarians (Dunn *et al.*, 2022). The ‘White-Sea’ assemblage is significantly more taxonomically and ecologically diverse, encompassing disparate soft-bodied taxa such as

erniettomorphs, the motile dickinsoniomorphs and bilateralomorphs (Darroch *et al.*, 2018), and diverse radial multilobed forms (Cracknell *et al.*, 2021; Rahman *et al.*, 2015) together with the earliest documented bilaterian animals (Fedonkin & Waggoner, 1997; Jensen, Droser & Gehling, 2006; Evans *et al.*, 2020). This picture contrasts with a significant reduction in the diversity and disparity of Ediacarans in the ‘Nama’ assemblage, which terminates at the Cambrian boundary. In this assemblage erniettomorphs, rangeomorphs, and arboreomorphs co-occur with an expanded range of tubicolous metazoan biomineralisers and bilaterian ichnofossils (Boag, Darroch & Laflamme, 2016; Darroch *et al.*, 2018). Finally, although most of the Nama Ediacarans disappear near the Cambrian boundary some frondose and modular body plans have been suggested to persist until at least 518 Ma (Zhao *et al.*, 2022; Hoyal Cuthill, 2022), attesting to late-surviving Ediacaran-grade animals in the midst of the Cambrian Explosion (Fig. 2).

While variously interpreted as a product of palaeobiogeographical (Meert & Lieberman, 2008) ecological (Grazhdankin, 2004), or taphonomic (Narbonne, 2005) overprints, the discrepancies between at least some Ediacaran assemblages most likely yield a genuine evolutionary signal (Carbone *et al.*, 2015). The taxonomic differences between Avalonian and White Sea biotas may mostly reflect bathymetric rather than temporal variation: the two assemblages overlap chronostratigraphically and occur in distinct depositional contexts, with the Avalon typically restricted to deep-water settings (Boag *et al.*, 2016; Bowyer *et al.*, 2022). However, the distinctiveness of White Sea and Nama assemblages cannot be fully attributed to palaeoenvironmental variation. Facies potentially denoting estuarine and shoreface settings suggest that White Sea communities (McMahon *et al.*, 2020) thrived in disturbed nearshore environments reminiscent of classic Nama localities (Darroch *et al.*, 2016; but see Gehling & Droser, 2013) and bathymetric overlap has been confirmed by comprehensive multivariate analyses (Boag *et al.*, 2016). Further, both lithology and location of provenance are generally poor predictors of association between Ediacaran taxa (Boag *et al.*, 2016; Muscente *et al.*, 2019), ruling out first-order taphonomic and palaeogeographical controls.

Overall, although a second-order ecological overprint cannot be excluded, the taxonomic discrepancies between White Sea, Nama, and Cambrian communities probably disclose a temporal succession reflecting three chapters in the decline of Ediacarans (Muscente *et al.*, 2019; Bowyer *et al.*, 2022) and the diversification of the animal phyla. The first, at ~550 Ma, is the transition from diverse White Sea ecologies to the ‘depauperate’ Nama assemblage. The second records the decline of Nama Ediacarans around the Ediacaran–Cambrian boundary, ~539 Ma. Finally, the last Ediacarans may have become extinct no earlier than the Cambrian Series 2, Stage 3, and possibly persisted up until 508 Ma (Conway Morris, 1993; Jensen, Gehling & Droser, 1998; Hagadorn & Waggoner, 2000; Hagadorn, Fedo & Waggoner, 2000; Shu *et al.*, 2006;

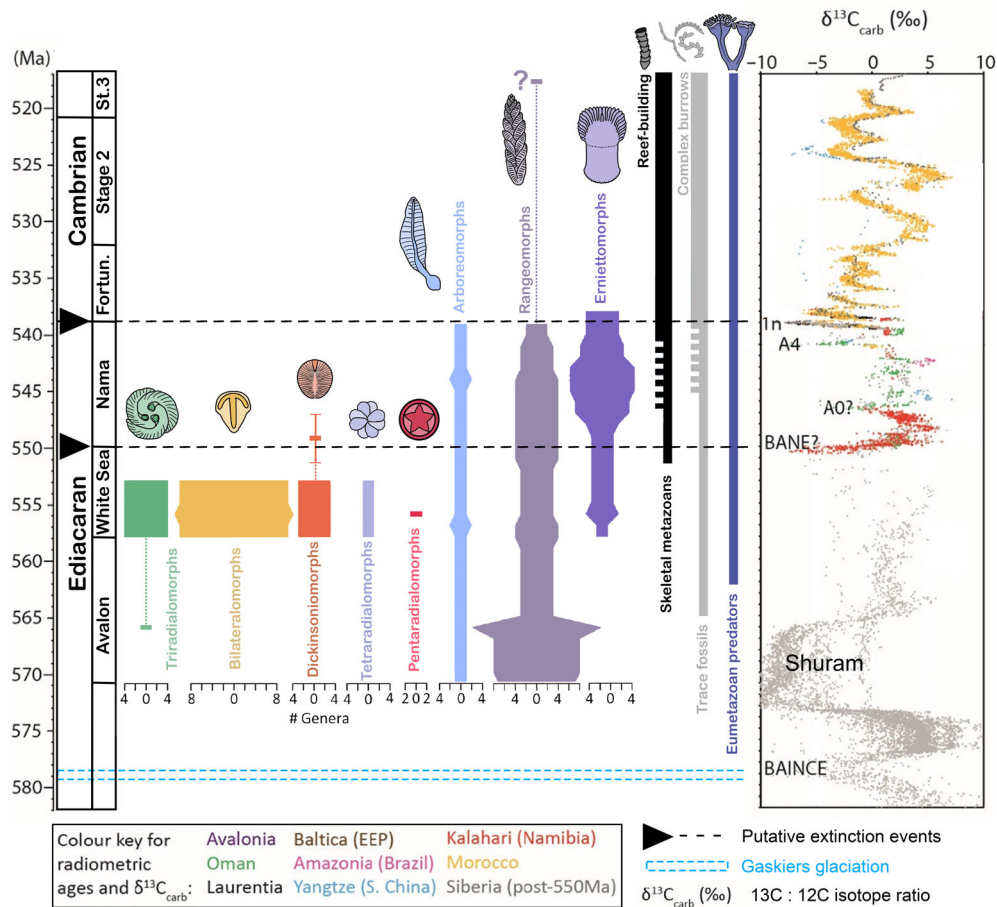


Fig. 2. Ediacaran geochemistry and biotic change, after Darroch *et al.* (2018) and including faunal data from Penny *et al.* (2014), Wang *et al.* (2021), Hoyal Cuthill (2022), and Dunn *et al.* (2022). *Stromatoveris* is included as tentatively related to rangeomorphs based on Hoyal Cuthill & Han (2018). Uncertainty in the temporal range of *Dickinsonia* in the Shibantan Lagerstätte is indicated by the corresponding error bar (Xiao *et al.*, 2021). Stratigraphic and carbon isotope ($\delta^{13}\text{C}_{\text{carb}}$) data from model B in Bowyer *et al.* (2022). Names of negative carbon isotope excursions follow the nomenclature established therein: BANE? marks the basal Nama negative $\delta^{13}\text{C}_{\text{carb}}$ excursion, A0 and A4 mark negative $\delta^{13}\text{C}_{\text{carb}}$ excursions with radiometric ages inferred from the Ara Group, Oman. In is equivalent to the basal Cambrian carbon isotope excursion (BACE) (Bowyer *et al.*, 2022). The pre-Shuram BAINCE is the Baiguoyuan negative carbon isotope excursion (Zhu *et al.*, 2013). Ma, million years ago.

Hoyal Cuthill & Han, 2018; Zhao *et al.*, 2022; Hoyal Cuthill, 2022). This downfall in three acts – which cannot be explained as the result of taphonomy or limited sampling – requires a historical and evolutionary explanation.

III. QUESTIONING ABIOTIC ‘CATASTROPHES’

The mass extinction events recorded in the Phanerozoic – up to six in total (Dal Corso *et al.*, 2020) – were initiated by overwhelmingly abiotic triggers (Bond & Grasby, 2017), raising the possibility that Ediacaran extinctions can be explained by similarly episodic environmental ‘catastrophes’. This hypothesis is currently undergoing a renaissance, fuelled in large part by the study of late Ediacaran proxies for massive geochemical alterations and their putative coincidence with

biotic turnover (e.g. Yang *et al.*, 2021; Evans *et al.*, 2022). However, the geochemical record indicates that a consensus on environmental ‘catastrophes’ as the drivers of Ediacaran extinctions is premature. Instead, their tempo and mode, as reflected by isotopic proxies, suggest that extrinsic abiotic triggers imparted at most second-order control on the late-Ediacaran turnover.

The timing of Ediacaran extinctions and geochemical anomalies (Fig. 2) offers equivocal support for causal links. Some episodes of Ediacaran turnover did overlap with massive carbon cycle perturbations, reflected in negative carbon-isotope excursions (NCIEs). A globally correlative ‘basal Nama’ negative excursion (BANE) around 550 Ma broadly coincides with the appearance of skeletal metazoans and bilaterian burrows in Namibia, South China, and Brazil (Yang *et al.*, 2021). The ‘basal Cambrian carbon isotope excursion’ (BACE), which occurs near the close of the Neoproterozoic

at ~539 Ma (Bowyer *et al.*, 2022), similarly accompanies the transition between Nama and Cambrian-type faunas. However, the largest Ediacaran NCIE, the Shuram anomaly, has been bracketed by radioisotopic dating between ~574.0 and ~567.3 Ma – well before both Ediacaran extinction pulses, and overlapping in time with the Avalon biota (Rooney *et al.*, 2020). The correlation between Ediacaran extinctions and carbon cycle anomalies is further weakened by putative ~546.5 Ma and ~541 Ma NCIEs (Fig. 2), neither of which heralds significant turnover pulses (Bowyer *et al.*, 2022).

Possible associations between Ediacaran NCIEs and classic mass extinction ‘horsemen of the apocalypse’, such as volcanism and anoxia (Bond & Grasby, 2017), are also equivocal. $\delta^{238}\text{U}$ proxies suggest that the Basal Nama NCIE coincided with a shift towards widespread anoxia, which persisted throughout the terminal Ediacaran (Zhang *et al.*, 2019). However, the same $\delta^{238}\text{U}$ proxies suggest that the Shuram anomaly may have been coupled to an episode of widespread ocean oxygenation (Zhang *et al.*, 2019; Li *et al.*, 2020b). A smaller, transient rise in oxygen levels is also registered around the base of the Cambrian (Zhang *et al.*, 2019). Therefore, the causal links between NCIEs and Ediacaran redox fluctuations, if any, remain ambiguous. A potential stratigraphic correlation between the BACE and Laurentian volcanic outgassing (Hodgin *et al.*, 2021) is interesting and requires further study, especially given the tight coupling of Phanerozoic volcanism, anoxia, and mass extinctions (Bond & Grasby, 2017) and possible isotopic evidence of widespread marine anoxia in terminal Ediacaran oceans [e.g. Tostevin *et al.*, 2019; Li *et al.*, 2020a; but see Wei *et al.* (2023) for contrasting indicators of widespread oxygenation]. Nonetheless, the proposed causal links between anoxia and Ediacaran extinctions are at odds with persistent, widespread oceanic euxinia throughout the diversification of the Ediacaran Biota (e.g. Sahoo *et al.*, 2016; Cherry *et al.*, 2022) and evidence of rangeomorphs and arboreomorphs thriving in at least transiently anoxic settings (Cherry *et al.*, 2022; Boag *et al.*, 2018). Interpretations of the BACE as the signature of an ‘extinction trigger’ also conflict with its timing. In Siberia (Zhuravlev & Wood, 2018; Bowyer *et al.*, 2022) and South China (Cai *et al.*, 2019) the diversification of Cambrian-type faunas began before the BACE (Zhuravlev & Wood, 2018). Similarly, Namibian strata comprising both macrofossils and uranium isotope-yielding carbonates reveal that depauperate Nama communities dominated by skeletal metazoans appeared before the onset of a possible terminal Ediacaran pulse of anoxia (Tostevin *et al.*, 2019).

What’s more, even if we allow a link between Ediacaran anomalies and extinctions the direction of causality is ambiguous, given the powerful top-down effects of biology on ocean chemistry. This is particularly relevant to cases in which the onset of biotic turnover may have preceded the geochemical anomalies (Tostevin *et al.*, 2019; Zhuravlev & Wood, 2018; Cai *et al.*, 2019; Bowyer *et al.*, 2022) described above. Suspension-feeding animals exert top-down control on ocean ventilation by enhancing advective mixing and

dissolved organic carbon (DOC) removal (Butterfield, 2009). Externally opening compartments with putative ciliary pumping in rangeomorphs (Butterfield, 2020) and the fluid-dynamics of radialomorphs (Rahman *et al.*, 2015; Cracknell *et al.*, 2021) and erniettomorphs (Gibson *et al.*, 2019; Darroch *et al.*, 2022) suggest suspension feeding (although see Darroch *et al.*, 2023a), with possible commensalistic aggregates (Gibson *et al.*, 2019; Darroch *et al.*, 2022) enhancing vertical mixing while exploiting turbulence for nutrient advection. If ocean oxygenation during the Shuram NCIE (Zhang *et al.*, 2019) stemmed at least in part from the assembly of the poriferan (Suarez & Leys, 2022) and eumetazoan (Butterfield, 2020) DOC-removal pumps, its disruption in ‘depauperate’ late-Ediacaran communities might have promoted a shift from oxygenated, low-suspended-carbon to turbid, stratified anoxic waters.

The late-Ediacaran bioturbation surge (Cribb *et al.*, 2019) may have imparted additional redox forcing. Enhanced bioturbation disrupts organic carbon burial and non-linearly increases sediment retention of phosphorus. Both mechanisms could promote anoxia (Van De Velde *et al.*, 2018; but see Laakso *et al.*, 2020), which may in turn precipitate nitrogen limitation by favouring nitrate-reducing bacteria (Tyrrell, 1999). Nitrogen or, perhaps more plausibly, phosphorus (Xiang *et al.*, 2018) limitation itself may have driven the decline in primary productivity proposed by Brasier (1992) to account for late-Neoproterozoic NCIEs. Alternatively, by contributing to the oxidation of sedimentary pyrite and sulfate production, stepped-up bioturbation around the White Sea–Nama and Ediacaran–Cambrian boundaries may have promoted the anaerobic oxidation of DOC and ensuing precipitation of authigenic carbonate, offering another causal driver of NCIEs (Muscente *et al.*, 2018). These processes suggest that Ediacaran communities actively reshaped ocean geochemistry rather than waxing and waning at its mercy, and may at least partly explain the erratic carbon isotope perturbations characterising the latest Neoproterozoic (Yang *et al.*, 2021). Given the possibility of such reverse causality, putative ‘abiotic’ extinction triggers might at least in part be nothing but geochemical manifestations of a build up of large-scale biotic impacts.

Finally, the signal from the Ediacaran–Cambrian fossil record itself appears increasingly incompatible with abrupt, externally triggered mass extinctions. Whilst the evidence for biotic decline between the White Sea and Nama assemblages remains robust (Bowyer *et al.*, 2022), their taxonomic overlap has considerably increased with enhanced sampling (Boag *et al.*, 2016; Bowyer *et al.*, 2022). Classic White Sea taxa such as dickinsoniomorphs (Xiao *et al.*, 2021; Wang *et al.*, 2021) and *Kimberella* (Vaziri, Majidifard & Laflamme, 2018) are now described from Nama-interval assemblages in multiple continents, confirming a protracted decline. Further, increased within-community structuring and narrower niche breadths in the Nama assemblage suggest a refinement of ecological partitioning relative to the White Sea (Eden, Manica & Mitchell, 2022). This emerging picture strongly contradicts post-catastrophe ‘recolonisation’ scenarios

predicting a prevalence of ‘disaster taxa’ – the generalist, ecologically tolerant ‘weedy’ organisms dominating mass extinction aftermaths (Sahney & Benton, 2008) – in the Nama, highlighting instead a remarkable continuity of niche contraction and specialisation trends across the late Ediacaran and early Phanerozoic (Eden *et al.*, 2022). The increasingly well-documented presence of conulariids (Leme, Van Iten & Simões, 2022), protoconodonts, anabaritids, and other distinctively Cambrian metazoans close to the nadir of the BACE (Bowyer *et al.*, 2022; Topper *et al.*, 2022), and that of both soft-bodied (Hoyal Cuthill, 2022) and biomineralised (Cai *et al.*, 2017; Han *et al.*, 2017; Yang *et al.*, 2016; Park *et al.*, 2021) Ediacaran survivors into the Phanerozoic also clashes with expectations of a radical biotic reset near the Cambrian boundary. Together with a lack of unambiguous mass extinction triggers, the gradual phase-out of Ediacaran ecologies suggests that environmental catastrophes are in themselves insufficient to account for end-Neoproterozoic extinctions and the rise of Phanerozoic biotas.

IV. ENEMIES WITHIN? REFRAMING ‘BIOTIC REPLACEMENT’

The traditional alternative to ‘catastrophe’ hypotheses centred on abiotically driven Ediacaran mass extinctions has been the ‘biotic replacement’ hypothesis (Laflamme *et al.*, 2013), which entails ecological displacement of Ediacarans by crown-group eumetazoans, cast as ecological or morpho-functional innovators which eclipse the Ediacaran biota through predation, competition, or ecosystem engineering (Laflamme *et al.*, 2013; Darroch *et al.*, 2015). While we argue that biotic replacement still represents a credible primary driver of Ediacaran extinctions, recent palaeontological evidence requires refinement of this model. In particular, new data have shown a long coexistence of Ediacarans and crown-group eumetazoans, which coincides with the increasingly apparent continuity in ecological and evolutionary trends spanning Ediacaran assemblages and the Neoproterozoic–Cambrian boundary.

The notion of a ‘Garden of Ediacara’ (McMenamin, 1986) devoid of predation suggests at once a sharp discontinuity between late-Neoproterozoic and Phanerozoic ecologies and an intuitively appealing ‘overkill’ scenario of biotic replacement, in which the rise of carnivorous cnidarians and bilaterians overwhelmed and rapidly extirpated the non-mineralised Ediacaran biota. Similarly, ecospace takeover by Nama eumetazoans may be taken to imply a competitive advantage over the comparatively ‘ineffectual’ and ‘static’ niche occupancy of Ediacarans (Schiffbauer *et al.*, 2016). However, recent fossil discoveries demonstrate the coexistence of Ediacarans and crown-group eumetazoans as early as the Avalon (Dunn *et al.*, 2022) and perhaps as late as the mid-Cambrian (Zhao *et al.*, 2022; Hoyal Cuthill, 2022). Meanwhile, other findings dramatically expand their

known range of interactions in the White Sea assemblage, at the ecological apex of the Ediacaran Biota (Tarhan *et al.*, 2018, 2015; Droser, Tarhan & Gehling, 2017; Bowyer *et al.*, 2022). These discoveries suggest that models of wholesale biotic replacement are no longer tenable, and that a higher-resolution picture of Ediacaran ecological interactions is needed to explain late-Neoproterozoic extinctions.

The rise of crown-group eumetazoans, and particularly the evolution of coelenterate-grade predators, stands among the proposed biotic drivers of late-Ediacaran extinctions. Darroch *et al.* (2016) suggested that Nama-aged plug-shaped burrows (Fig. 3A), interpreted as the product of early anthozoans, reflect the emergence of predatory cnidarians. Harvesting of hypothetical larvae of Ediacarans in suspension was thus proposed as a possible driver of the decline of Ediacarans. However, caution must be exercised when inferring the life habits of Ediacaran cnidarians by direct analogy with living predatory forms: extant carnivorous cnidarians are partly the product of hundreds of millions of years of co-evolution with animal zooplankton (Brasier, 2009), and some living anthozoans feed on phytoplankton (e.g. Fabricius, Genin & Benayahu, 1995). Moreover, this hypothesis must contend with the presence of a large, potentially predatory (Dunn *et al.*, 2022; Schiffbauer, 2022; Laflamme, 2022) cnidarian, *Auroralumina* (Fig. 4E), already in the Avalon-aged Charnwood Forest deposit (Dunn *et al.*, 2022). The phylogenetic placement of *Auroralumina*, a probable stem-group medusozoan (Dunn *et al.*, 2022), suggests that the diversification of crown-group cnidarians was already underway amid the Ediacaran Biota’s earliest burst of diversification (Fig. 2; Shen *et al.*, 2008). This is consistent with the discovery of conulariids, another group of probable medusozoans (Dunn *et al.*, 2022; Leme *et al.*, 2022), in terminal Ediacaran strata (Leme *et al.*, 2022). Moreover, under most possible topologies of the metazoan tree of life (e.g. Dohrmann & Wörheide, 2013; Pisani *et al.*, 2015; Whelan, Kocot & Halanych, 2015; Laumer *et al.*, 2018; Schultz *et al.*, 2023) the medusozoan affinities of *Auroralumina* imply that members of – minimally – the stem-group of Bilateria must also have been coincident with the Avalon assemblage. Despite uncertainty surrounding the inter-relationships of the non-bilaterian animal lineages, there remains only one plausible topology – where placozoans form a sister group to bilaterians – in which Avalonian cnidarians would not also require Avalonian bilaterians. This result is rarely recovered by molecular phylogenetic analyses and enjoys at best weak statistical support (e.g. Collins, 1998; Silva, Muschner & Bonatto, 2007). Therefore, the presence of cnidarians in the Avalon assemblage likely indicates that bilaterians were also present. Coupled with the evidence for ‘Cambrian Ediacarans’ (Hoyal Cuthill, 2022), this suggests a possible ~50 million year (Myr) (or longer) coexistence of Ediacarans and total-group Bilateria.

Predatory activity by emerging bilaterians has also been proposed as a key driver of Ediacaran extinctions (e.g. Gehling & Droser, 2018). However, early bilaterians increasingly appear to have been an integral component of

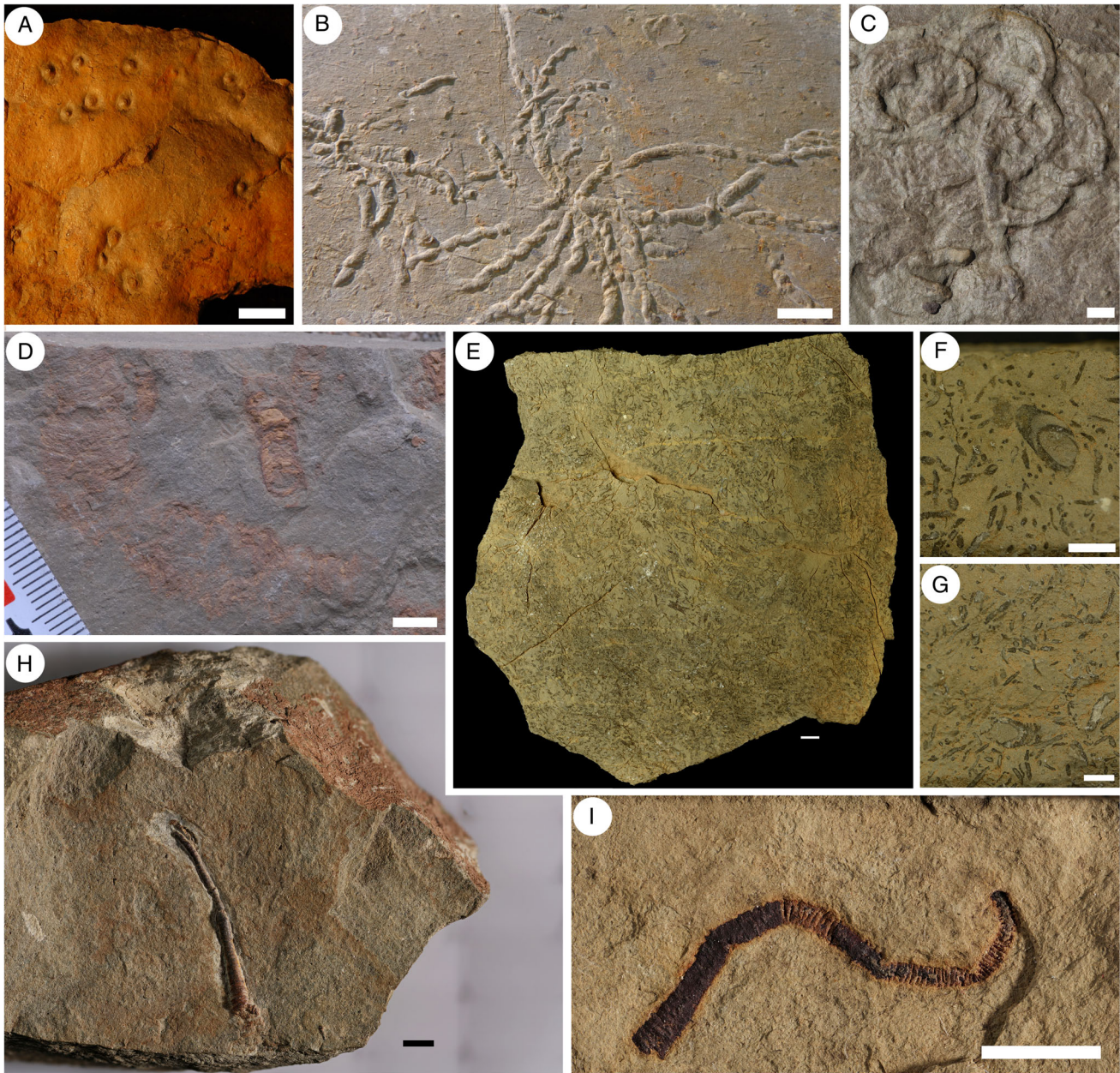


Fig. 3. Terminal Ediacaran ichnofossils, biomineralisers and tube-dwelling epifauna. (A) Plug-shaped *Bergaueria* burrows from the Nama Group (Farm Nudaus, Nudaus Formation), preserved on bed top. (B) The treptichnid *Streptichnus narbonnei* (NESM-F-626) from the upper Spitskop Member (Farm Swartpunt) of the Nama Group preserved on bed underside, showing distinctive rope-like morphology and arrangement of burrows radiating from central points. (C) *Parapsammichmites* (Nama Group, Feldschuhhorn Member) preserved on bed top. (D) DSC0026 *Gaojiashania cyclus*, a soft-bodied epibenthic tubelike organism, from the late-Ediacaran Gaojiashan Lagerstätte (Dengying Formation) of South China. (E) GSNF314A, a bedding plane from Zebra River (Nama assemblage, Zaris Formation, Namibia) showing fragmentary biomineralisers, most likely in the form of bioclasts. (F, G) Enlarged views of GSNF314A showing biomineralised cloudinid tubes in cross section. (H) *Conotubus hemiannulatus*, a weakly mineralised tubular organism, collected in the Gaojiashan Lagerstätte. (I) Specimen of the tube-dwelling metazoan *Saarina* (USNM-WCF_005_01) from the late-Ediacaran Wood Canyon Formation of Nevada. Scale bars = 10 mm. Institutional abbreviations: DSC, Shaanxi Natural History Museum; GSNF, Geological Society of Nevada; NESM, Museum of the Geological Survey of Namibia; USNM, Smithsonian Institution, National Museum of Natural History.

those same White Sea communities in which the Ediacaran biota reached the apex of its diversity. Despite early suggestions of a cnidarian affinity, the slug-like animal *Kimberella*

(Fig. 4D) almost certainly represents a total-group bilaterian (Fedonkin & Waggoner, 1997; Butterfield, 2006). The evidence marshalled in support of spiralian or even molluscan

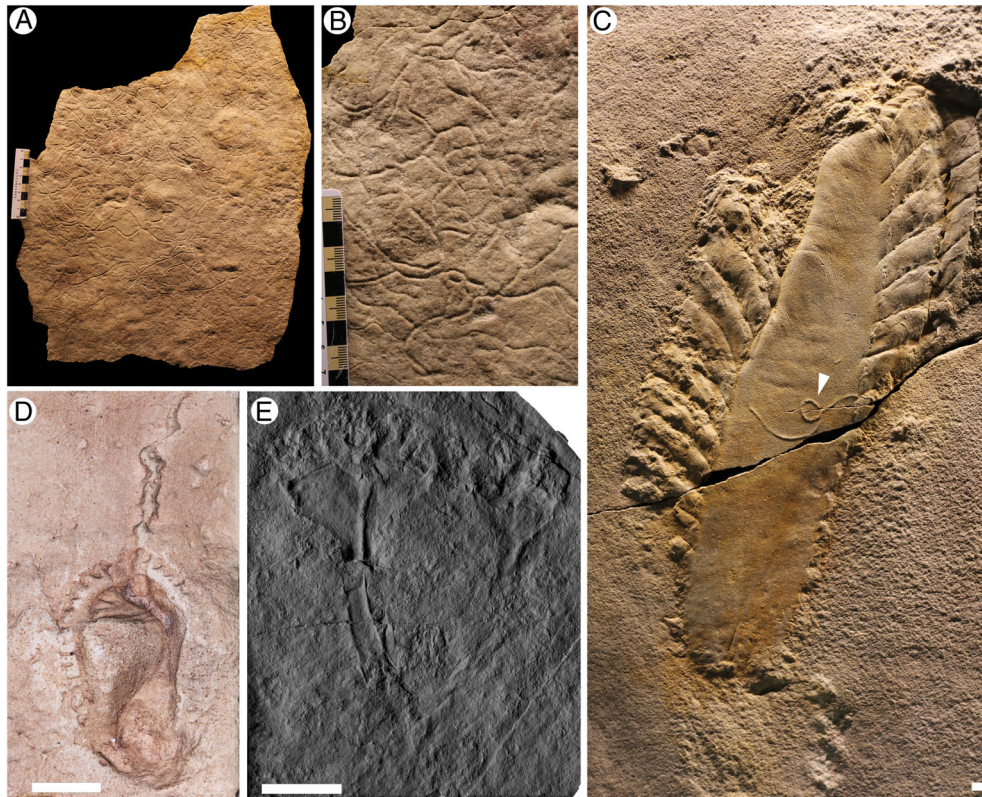


Fig. 4. The rise of eumetazoans in the Avalon and White Sea assemblages. (A) SAM P42142, sandstone slab from the White Sea assemblage of South Australia preserving *Helminthoidichnites* undermat trails in negative epirelief, with centimetric rule for scale. (B) Enlarged view of the area adjacent to the rule in A. (C) ‘*Arborea*’ (?Pambikalbae), an enigmatic multi-lobed frond from the White Sea of Australia, with an associated *Helminthoidichnites*-type ichnofossil (white arrow). (D) *Kimberella quadrata* (OUMNH.PAL-ÁT.00279/p), an enigmatic mollusc-like bilaterian from the White Sea of South Australia and Russia. (E) Plastotype (GSM 106119) of *Auroralumina attenboroughii*, a probable stem-group medusozoan cnidarian from Charnwood Forest, UK (Avalon assemblage). Scale bars = 10 mm (C, D) and 50 mm (E). Institutional abbreviations: GSM, British Geological Survey, Nottingham; OUMNH, Oxford University Museum of Natural History; SAM, South Australia Museum.

affinities for this organism is debated (reviewed in Budd & Jensen, 2017), but raises the possibility that major bilaterian superphyla had already diverged by the time of the White Sea assemblage, in accordance with molecular clock predictions (e.g. dos Reis *et al.*, 2015). If so, their limited body fossil presence would suggest that most representatives of these superphyla were either anatomically and functionally indistinguishable from classic Ediacarans or diminutive and morphologically inconspicuous – as potentially exemplified by *Ikaria* (Evans *et al.*, 2020). Nonetheless, the bilaterian ichnofossil *Helminthoidichnites* is common in White Sea localities (Fig. 4A–C; Jensen *et al.*, 2006). Although their scalloped aspect hints at musculature and a coelom displacing sediment by peristalsis (Evans *et al.*, 2020), these shallow horizontal traces are not compatible with destructive matground-mining (Gehling & Droser, 2018; Droser *et al.*, 2017). Instead, the heterogeneity generated by dynamic macrofaunal interactions – including bilaterian matground engineering – may have fostered the diversity of White Sea Ediacarans (Droser *et al.*, 2017), promoting the spread of evolutionary innovations such as motility to

access and exploit variegated resource patches (Mitchell *et al.*, 2020; Ivantsov & Zakrevskaya, 2023).

More broadly, it is increasingly apparent that ecological relationships between Ediacarans and other metazoans are not readily explained by simple antagonism. The White Sea biota flourished on ‘textured organic surface’ (TOS) matgrounds – organosedimentary consortia of bacteria, protozoa, and agglomerations of tubular metazoan problematica like *Fumisia* (Tarhan *et al.*, 2018). The latter frequently associate with *Aspidella* holdfast clusters, suggesting that frondose Ediacarans preferentially colonised matgrounds stabilised by metazoan aggregates (Tarhan *et al.*, 2015). Hence, the question is not how other emerging animal clades ‘out-competed’ (Grazhdankin, 2014) the Ediacarans with whom they formed complex mixed ecosystems, but whether this dynamic equilibrium collapsed from within.

Shallowly buried Ediacaran macrofossils crosscut by *Helminthoidichnites* scavengers (Gehling & Droser, 2018) offer a window onto how the resource heterogeneity characterising White Sea communities may have ultimately initiated such a ‘collapse’. As per Budd & Jensen’s (2017)

'Savannah Hypothesis', dead Ediacarans embodied concentrated hotspots of organic carbon that could be harvested by displacing overlying sediment and biofilm veneers. Such Ediacaran 'whale-fall' scavenging may have fostered the bilaterian transition from epimat grazing to shallow-sediment penetration (Budd & Jensen, 2017). In turn, by mixing superficial sediments with oxygen and organics, bioturbation may have established bridgeheads for deeper, substrate-destabilising forms of matground mining previously precluded by sharp intra-mat and intra-sediment redox gradients (Budd & Jensen, 2017; Gehling & Droser, 2018), even though extensive sediment column oxygenation by bioirrigators probably did not occur until the mid-late Cambrian (Cribb *et al.*, 2023). Recent findings conform well to the predictions of this model, supporting a protracted escalation in late-Ediacaran bilaterian ecosystem engineering.

In particular, the 551–543 Ma Shibantan Lagerstätte of South China can be convincingly interpreted as 'transitional' between the White Sea and Nama assemblages on both geochronological and biostratigraphic grounds (Xiao *et al.*, 2021; Wang *et al.*, 2021). Shibantan bedding planes are characterised by high horizontal bioturbation intensity together with much sparser vertical burrows. In some cases, both horizontal and vertical components co-occur within the same traces, presumably reflecting epibenthic locomotion interspersed with under-mat feeding (reviewed in Xiao *et al.*, 2021). Isotopic proxies suggest that infault burrowers in the Shibantan may have substantially increased sediment porewater oxygenation (Huang *et al.*, 2022; Xiao *et al.*, 2021), agreeing with ichnofossil evidence. Furthermore, *Yilingia* body fossils (Chen *et al.*, 2019) and trackways showing possible evidence for paired appendages (Chen *et al.*, 2018) confirm the existence of decimetre-scale, apparently metameric late-Ediacaran bioturbators already up to ~10 Myr before the Ediacaran–Cambrian boundary (Xiao *et al.*, 2021; Wang *et al.*, 2021). Meanwhile, North American ichnofossils – including oblique predator or suspension feeder-type burrows co-occurring with dickinsoniomorphs – betray a gradual escalation in bioturbation diversity and intensity starting in White Sea communities (Carbone & Narbonne, 2014; Carbone *et al.*, 2015). In at least some settings, this expansion of bioturbation may even have taken the form of vertical burrowing, as suggested by centimetre-sized, U-shaped Mongolian ichnofossils which might date to the White Sea interval (Oji *et al.*, 2018). Taken together, these findings contradict the claim that significant increases in bilaterian complexity and ecosystem engineering only manifest in already 'depauperate' classic Nama localities, and hence could not contribute to White Sea–Nama turnover (Evans *et al.*, 2022).

Nonetheless, bilaterian traces in classic late-Nama localities record a further escalation of ecosystem engineering, heralding the rise of 'wormworld' (Schiffbauer *et al.*, 2016). *Contra* Tarhan *et al.* (2018), Namibian Nama-group ichnofossils do reflect significantly more intrusive bioturbation modes relative to White Sea communities (Cribb *et al.*, 2019). Diverse Nama ichnotaxa show sediment penetration in addition to

movement along the sediment–water interface, with abundant mat grazers potentially contributing to expose the substrate to burrowers (Turk *et al.*, 2022; Darroch *et al.*, 2021). Horizontal trails increase in complexity and diversity and are joined by abundant plug-like *Conichnus* and *Bergaueria* burrows potentially produced by cnidarians (Fig. 3A; Darroch *et al.*, 2021). Significantly, centimetre-wide, high-relief sub-horizontal *Parapsammichnites* (Fig. 3C) also record sediment 'bulldozing' with active tunnel backfilling (Buatois & Mángano, 2018). In support of models suggesting self-amplifying bioturbation depth *via* sediment mixing or irrigation (Herringshaw, Callow & McLroy, 2017; Budd & Jensen, 2017), Ediacaran burrowing reached its acme in the uppermost Nama group in the form of treptichnids (Fig. 3B; Darroch *et al.*, 2021; Turk *et al.*, 2022). These arcuate burrows radiate vertical probes reminiscent of Cambrian and Recent priapulids (Jensen & Runnegar, 2005; Vannier *et al.*, 2010), embodying a new, matground-destabilising bioturbation mode qualitatively distinct from any associated with White Sea or Shibantan bilaterians. This Namibian bioturbation surge matches the ichnofossil signal from North America (Carbone & Narbonne, 2014; Tarhan *et al.*, 2020), South America (Parry *et al.*, 2017), Europe (Högström *et al.*, 2013), and China (Weber, Steiner & Zhu, 2007), and in light of its global spread and consistency it deserves serious scrutiny as an extinction driver (Darroch *et al.*, 2018, 2021; Turk *et al.*, 2022).

It has been argued that biotic replacement is unlikely to explain Ediacaran turnover, and particularly White Sea–Nama extinctions (Evans *et al.*, 2022), because it would require prolonged co-occurrence of bilaterian ichnofossils with soft-bodied taxa. However, evidence for precisely such a prolonged co-occurrence has also been suggested to make replacement-driven extinctions unlikely (Eden *et al.*, 2022). Both objections cannot be valid at once. The second objection is tangential to the question: escalation and innovation in bilaterian ecosystem engineering, rather than the appearance of the first bilaterian trace fossils *per se*, underpin biotic replacement models (Darroch *et al.*, 2023b). The first objection would be more serious, but is inconsistent with palaeontological support for a protracted co-occurrence (e.g. Carbone & Narbonne, 2014; Xiao *et al.*, 2021; Bowyer *et al.*, 2022) as documented above, and with contemporary evidence for ecosystem engineering driving catastrophic shifts in community composition on monthly to decadal timescales (reviewed in e.g. Crooks, 2002; Karatayev, Burlakova & Padilla, 2002; Matsuzaki *et al.*, 2009). Notably, these rapid impacts encompass the catastrophic declines in temperate forest floras attributed to burrowing by invasive earthworms (Bal, Storer & Jurgensen, 2018; Frelich *et al.*, 2006) and taxonomic turnover and permanent stable-state shifts in aquatic ecosystems due to bilaterian bioturbation (Crooks, 2002; Matsuzaki *et al.*, 2009). While the evolutionary underpinnings of bilaterian ecosystem engineering may have been assembled gradually, modern analogues suggest that once in place their impacts could have been all but geologically instantaneous.

The timing of Ediacaran extinctions is thus compatible with ‘biotic replacement’.

Actualistic analogies suggest that the causal mechanisms by which such a ‘replacement’ may have occurred are varied and non-mutually exclusive (Fig. 5). In Section V, hypothetical drivers of biotic replacement are discussed, taking into account their compatibility with the fossil evidence and the timing of the disappearance of Ediacaran macroorganisms.

V. OPEN QUESTIONS FOR THE ‘BIOTIC REPLACEMENT’ HYPOTHESIS

(1) Ecosystem engineering and the extinction selectivity hypothesis

While direct evidence for antagonistic interactions between Ediacarans and crown-group eumetazoan clades remains elusive, the relative timing of their respective appearance and disappearance from the fossil record could hint at possible extinction mechanisms (e.g. Darroch *et al.*, 2021, 2023b). In particular, the White Sea–Nama transition may not have impacted all guilds equally (Fig. 2; Darroch *et al.*, 2021). Although terminal Ediacaran remnants suggest a protracted decline (Wang *et al.*, 2021), dickinsoniomorphs, radialomorphs, and bilateralomorphs are conspicuously absent from classic Nama communities (Darroch *et al.*, 2015, 2021). Notwithstanding their disparate body plans, these were shallow-water (Eden *et al.*, 2022), prostrate epibenthic organisms, physically and nutritionally tied to the matgrounds at the sediment–water interface. Radialomorphs were likely epibenthic suspension feeders (Rahman *et al.*, 2015; Cracknell *et al.*, 2021) or filter feeders obtaining their food from matgrounds through ciliary transport of suspended organic particles (Ivantsov & Zakrevskaya, 2021b). Putative bilateralomorphs like *Parvancorina* (Paterson *et al.*, 2017) may also have been passive low-tier suspension-feeders, whereas chains of positive imprints trailing behind *Dickinsonia* hint at a motile

grazer (Sperling & Vinther, 2010; Ivantsov & Zakrevskaya, 2022). Of all Ediacarans, members of this matground-dweller guild were arguably those interacting most intimately with bilaterians (e.g. Gehling & Droser, 2018).

Recently, the selectivity of the White Sea–Nama extinction has been questioned based on assemblage comparisons by Evans *et al.* (2022), who argued for an anoxia-driven ‘environmental catastrophe’ impacting all guilds equally. Notably, though, prostrate taxa are not scored as a distinct category by Evans *et al.* (2022). Given the greater proximity of prostrate Ediacarans to oxygen-rich cyanobacterial matgrounds (e.g. Gehling & Droser, 2018), their preferential demise around the White Sea–Nama transition – if confirmed – could be at odds with anoxia-driven extinction models. Significant differences in life habit and ecological tier between White Sea Ediacarans and Nama survivors, current limitations in taxon sampling and palaeoenvironmental resolution, and a non-significant decline of taxa scored as feeding directly on matgrounds in Evans *et al.* (2022) also suggest that extinction selectivity by ecotype may be confirmed by future studies. Should this be the case, extinction selectivity could help to hone in on causal links between ecosystem engineering and Ediacaran turnover (Fig. 5).

In modern ecosystems, sediment-resuspension by bilaterian burrowers can displace low-tier suspension feeders by clogging their feeding apparatus (Rhoads & Young, 1970). High-tier Nama suspension feeders, exploiting nutrients higher up in the water column (Gibson *et al.*, 2019), may have been comparatively safe from fouling. However, bilateralomorphs, dickinsoniomorphs, and radialomorphs feeding at the substrate–water interface would have been more severely impacted by sediment-resuspension. Unlike the surviving ‘prostrate’ Ediacaran *Pteridinium* from the Nama assemblage, bilateralomorphs and radialomorphs were in all likelihood not semi-infaunal (Darroch *et al.*, 2022). In addition, the shallow-water settings in which these taxa lived (Eden *et al.*, 2022) display the highest intensity of bioturbation (Darroch *et al.*, 2021) and abundance of skeletal metazoans

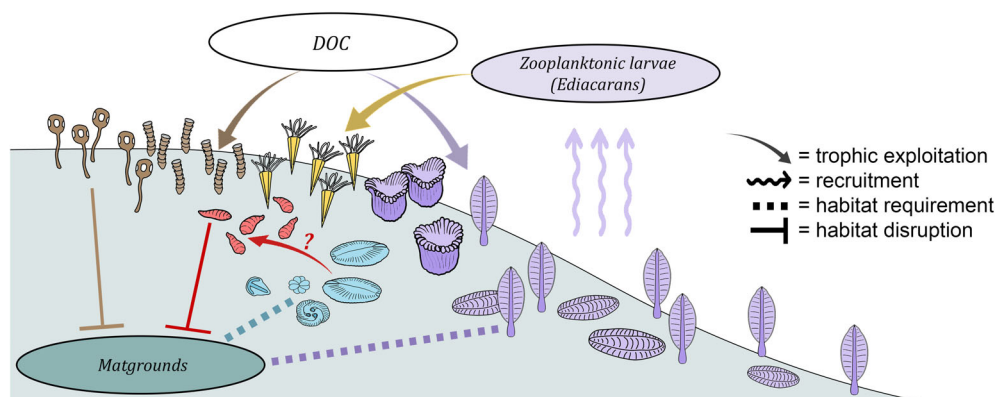


Fig. 5. Schematic illustration of the main hypothesised negative interactions between constituents of the Ediacaran biota and crown-group eumetazoans. Brown denotes reef-builders, yellow is cnidarian-grade metazoans, red is bilaterians, light blue is prostrate and motile benthic Ediacarans (radialomorphs, bilateralomorphs, dickinsoniomorphs), and violet is sessile frondose or modular Ediacarans. Proposed ecological interactions are summarised by symbols in the key on the right. DOC, dissolved organic carbon.

(Eden *et al.*, 2022) in the Nama assemblage. This indicates a general proximal–distal trend in the escalation of bilaterian activity (Fig. 5; Buatois *et al.*, 2020). If confirmed by future analyses, these patterns may suggest that bilateralomorphs, dickinsoniomorphs, and radialomorphs were, on several counts, first in the line of ecological restructuring.

Enhanced bioturbation in the Nama interval also precipitated at least partial matground removal and destabilisation (Buatois & Mángano, 2018). Frond holdfasts and Nama ichnofossils typically segregate on different facies (Darroch *et al.*, 2016, 2022; Xiao *et al.*, 2021), agreeing with the preference for undisturbed facies shown by modern bioturbation-intolerant taxa (Rhoads & Young, 1970). Darroch *et al.* (2021) suggested that motile Ediacarans able to track intact substrates were less affected by matground disruption than anchored fronds. However, White Sea grazers exhibit spatial patterns compatible with temporary feeding aggregations and avoidance of previously exhausted patches (Mitchell *et al.*, 2020). Hence, even partial matground disruption might have severely restricted or fragmented their feeding-ranges, exposing grazers to resource depletion and perhaps impacting them even more severely than anchored Ediacarans. More speculatively, matgrounds fouled by recalcitrant sediment may also have become refractory to surficial digestion and absorption by dickinsoniomorphs (Sperling & Vinther, 2010).

Those Ediacarans most susceptible to sediment engineering, resuspension, and any additional bilaterian impacts might have entirely succumbed to the Wormworld, whereas higher-tier or deeper-water (Eden *et al.*, 2022) Nama suspension-feeders may have endured negative trophic interactions and non-linear escalations of ecosystem engineering up to the ‘ecological tipping point’ (Cairns, 2004) marked by Cambrian-style mat-mining. Intriguingly, a treptichnid surge closely accompanies the disappearance of erniettomorphs and rangeomorphs in radiometrically dated Nama sections (Linnemann *et al.*, 2019). In this light, the extinctions marking the end of the White Sea and Nama assemblages may grade into a more continuous process of taxonomic decline, consistent with the faunal overlap between the two assemblages as well as Cambrian biotas (Eden *et al.*, 2022; Hoyal Cuthill, 2022).

(2) Is bilaterian predation a plausible extinction driver?

As in the case of bioturbation, the temporal overlap of White Sea Ediacarans with crown-group eumetazoans cautions against models of wholesale ecological displacement of the Ediacaran biota through predation (e.g. McMenamin, 1986). However, it also does not exclude an escalation of predation, particularly among diversifying crown-group bilaterians, from the set of possible drivers of Ediacaran extinctions (Fig. 5; Darroch *et al.*, 2023b). Unfortunately, the evidence to test this possibility remains scant.

Diverse Ediacaran macrofossils crosscut by vermiform traces do show that at least occasional faunivory was already

well established in White Sea bilaterians. However, all evidence for bilaterian consumption of Ediacarans is limited to scavenging, as indicated by the shallow burial of target carcasses before tunnelling (Gehling & Droser, 2018). Given the taxonomic range and relative abundance of scavenged Ediacarans, the coincident lack of evidence for predation on them might reflect a genuine biotic signal. However such evidence, including hypothetical indirect signatures of predation in the form of damage repair (Kenchington, Dunn & Wilby, 2018), is absent even in the latest Nama interval, despite the appearance of priapulid-grade burrows suggesting the existence of infaunal predators (Vannier *et al.*, 2010; Darroch *et al.*, 2021; Turk *et al.*, 2022). Phanerozoic priapulids, including Cambrian taxa, are known to feed on detritus or small, epibenthic animals such as molluscs, annelids, brachiopods (Vannier *et al.*, 2010) and possibly cnidarians (Han *et al.*, 2007). By analogy, this suggests that terminal Ediacaran predation by priapulid-grade burrowers may have taken place primarily among small bilaterians and other crown-eumetazoans rather than at the expense of large, soft-bodied Ediacarans. If it occurred, direct predation of Ediacarans by priapulid-grade bilaterians may have been restricted to early developmental stages – a suggestion that, on the basis of the available fossil data, is untestable.

Despite this lack of evidence and even if Nama priapulomorphs did not feed upon Ediacarans directly, the cascading effects of their predatory activities may have contributed to the degradation of White Sea-type biotas. In particular, negative impacts on TOS, which are integral to White Sea ecologies but virtually absent in the Nama (Tarhan *et al.*, 2018; Darroch *et al.*, 2021), may have substantially impoverished late-Ediacaran communities. The inclusion of the putative tubular cnidarian *Archotuba* in the diet of Cambrian priapulids (Han *et al.*, 2007) suggests that the sessile, tubular coelenterate-grade metazoans of White Sea TOS consortia (Tarhan *et al.*, 2018) could also have been targeted by similar predators, at least in early ontogeny. If so, predatory pressure might have contributed to the replacement of non-biomineralised taxa integral to TOS, such as *Funisia* (Tarhan *et al.*, 2018; Gehling & Droser, 2018) by skeletonised reef-builders, breaking the integration of sessile metazoans and matgrounds that had fostered the diversity of White Sea ecologies (Tarhan *et al.*, 2018; Droser *et al.*, 2017). The fact that bilaterian predation could in principle have been a key driver of Ediacaran extinctions, but one that may permanently escape direct detection in the fossil record, highlights the need to tackle this hypothesis through alternative approaches, potentially including theoretical modelling based on extant analogue systems and indirect testing through spatial ecological techniques (Mitchell *et al.*, 2019, 2020).

(3) The rise of biomineralisers: a role in Ediacaran extinctions?

Alongside a bioturbation surge and the appearance of possible priapulomorph burrowers, the Nama interval witnessed a

global spread of biomineralised taxa (Fig. 3D–I; Penny *et al.*, 2014; Warren *et al.*, 2017; Cai *et al.*, 2019; Selly *et al.*, 2020; Turk *et al.*, 2022). Taxonomically overlapping faunas comprising rangeomorphs, erniettomorphs, and skeletal metazoans occur in Namibia (Darroch *et al.*, 2016), Nevada (Selly *et al.*, 2020), South America (Becker-Kerber *et al.*, 2017), Iran (Vaziri *et al.*, 2018), and China (Xiao *et al.*, 2021; Chen *et al.*, 2022). While there is no direct evidence for a predatory overkill of Ediacarans, specimens of the skeletal metazoan *Cloudina* occur in the terminal-Ediacaran of Namibia (Hua, Pratt & Zhang, 2003), Brazil (Becker-Kerber *et al.*, 2017) and China (Bengtson & Zhao, 1992). Insofar as they likely represent protective structures, *Cloudina*'s multi-layered biomineralised skeleton may foreshadow the escalatory predator–prey arms races generally considered a hallmark of Phanerozoic evolution (Hong, Zhe & Xunlai, 2007; Wood & Zhuravlev, 2012). Support for this hypothesis comes from *Cloudina* specimens with shell perforations (Hua *et al.*, 2003; Becker-Kerber *et al.*, 2017; Bengtson & Zhao, 1992) that fit diagnostic criteria for predatory boreholes (Schiffbauer *et al.*, 2016; Becker-Kerber *et al.*, 2017), even though alternative abiotic origins have been proposed (Debrenne & Zhuravlev, 1997).

The mutual cementation of *Cloudina* shells is also interpretable as an anti-predatory adaptation hindering access and manipulation (Penny *et al.*, 2014). Together with those of the skeletal eumetazoan *Namacalathus*, *Cloudina* agglomerations laid the structural groundwork for massive, stratified terminal Ediacaran reefs (Wood & Curtis, 2015). Whereas scattered *Cloudina* thickets may represent detritus, and not pioneer reef-builders (Mehra & Maloof, 2018), microbially encrusted upright agglomerations are best interpreted as genuine bioconstructions (Álvaro *et al.*, 2020). In Namibian Nama localities, thrombolitic clots and stromatolitic laminae contributed to accrete such structures into large biostromes and bioherms, their neptunian dykes colonised by additional biomineralisers like *Namapoikia* (Penny *et al.*, 2014).

Although their role in the extinction of Ediacarans remains under-investigated, these early metazoan-microbialite reefs smothered tracts of coastal benthos with topographically heterogeneous, biomineralised substrates (Wood & Curtis, 2015) recalcitrant to grazing and possibly hostile to soft-bodied Ediacarans. Significant negative associations between Nama biomineralisers and soft-bodied Ediacarans suggest ecological segregation, but the degree to which this reflects ecological displacement rather than environmental preferences or taphonomy remains unclear (Eden *et al.*, 2022; Darroch *et al.*, 2022). DOC-harvesting by reef builders might also have precipitated trophic competition with suspension-feeding Ediacarans (Fig. 5; Darroch *et al.*, 2022; Butterfield, 2020). Unlike the latter, reef-top metazoan suspension feeders were plausibly sheltered from resuspension fouling by their impervious substrate, as suggested by the dearth of bioturbation characterising reef carbonates (Darroch *et al.*, 2022). As in the case of bioturbation – the shallow-water and prostrate dickinsoniomorphs, bilateralomorphs, and radialomorphs

(Eden *et al.*, 2022) may have been most severely affected by this benthic surge of metazoan ecosystem engineering (Darroch *et al.*, 2022).

(4) Navigating the ‘Wormworld’? Hints from Nama Ediacarans and Cambrian survivors

In light of the protracted, taxonomically disparate ecological escalation documented by White Sea and Nama assemblages, the temporal overlap of bilaterian ichnofossils, biomineralisers, and Ediacarans helps to refine, but does not invalidate, the biotic replacement model. Whereas environmental catastrophe explanations are inconsistent with the drawn-out downfall of the Ediacaran biota, a gradual but escalatory upping of ecological pressure is consistent with the timing and pattern of its disappearance from the fossil record. Sparse but intriguing ‘Ediacaran remnants’ from the Cambrian fit the expectations of such a protracted extinction (Hoyal Cuthill, 2022).

Frondose or modular architectures directly comparable to those of *bona fide* Ediacarans occur in *Paramackenzia* from the ~518 Ma Chengjiang Lagerstätte (Zhao *et al.*, 2022) and a suite of fragmentary remains from lower Cambrian strata worldwide (reviewed in Hoyal Cuthill, 2022). Tentatively, phylogenetic analyses (Hoyal-Cuthill & Han, 2018) have also recovered the frondose *Stromatoveris* from Chengjiang (Shu *et al.*, 2006) as a close relative of rangeomorphs. The frondose architecture of the ~508 Ma Burgess Shale *Thaumataptilon* (Conway Morris, 1993) is similarly reminiscent of Ediacaran rangeomorphs and arboreomorphs (Hoyal Cuthill, 2022). Moreover, the early Cambrian ‘psammocoral’ *Spatangopsis* has been suggested to be a modified anchor for a frondose form, although no frond has been found in association with this fossil (Savazzi, 2012). With the study of ‘Cambrian Ediacarans’ still in its infancy after a long history of dismissals (Hoyal Cuthill, 2022), morphofunctional or ecological inferences are necessarily tentative. Nonetheless, a suite of characters occurring in at least some of these taxa stands out as deserving further study.

In addition, described Cambrian Ediacarans typically show a highly modular construction (Zhao *et al.*, 2022) or carry multiple, radially arranged fronds or petaloids (Hoyal Cuthill & Han, 2018; Hoyal Cuthill, 2022). This architecture is shared by many Nama Ediacarans, such as *Swartpuntia*, *Rangea*, and *Pteridinium* (Ivantsov & Zakrevskaya, 2021a). It is possible that instead of representing adaptations to low-oxygen conditions (Evans *et al.*, 2022) the repetitive body plans of these Ediacaran taxa offered redundancy in the face of external insults, including predation or disturbance (Kenchington *et al.*, 2018) but also encrustation by sessile eumetazoans (e.g. Hoyal Cuthill & Han, 2018). While currently speculative, this hypothesis might be tested by searching for further fossil evidence for such interactions, possibly coupled to signs of overcompensatory growth in response to damage (Kenchington *et al.*, 2018). Second, many Cambrian and Nama Ediacarans traded the ‘holdfasts’ of earlier frondose taxa for weighted, sediment-filled anchors. Among these

are erniettomorphs, *Rangea* and, more tentatively, *Spatangopsis* (Ivantsov *et al.*, 2016; Vickers-Rich *et al.*, 2013; Savazzi, 2012). Notably, this has been suggested to reflect a decrease in the availability of biomats for holdfast attachment (Savazzi, 2012) – a proposal yet to be fully tested through spatial ecology and palaeoenvironmental analyses. Third, several Nama and Cambrian Ediacarans are increasingly interpreted as semi-infaunal based on palaeontological and sedimentological evidence. These include *Pteridium* (Darroch *et al.*, 2022), *Ermetta* (Elliott *et al.*, 2016; Ivantsov *et al.*, 2016) and possibly *Spatangopsis*, which may have been capable of limited upwards motility through sediment (Savazzi, 2012). The lifestyle of these Ediacarans may thus suggest considerable tolerance to sediment fouling and even burial. Amid the aftermath of the Nama bioturbation surge, the ‘Cambrian agronomic revolution’ (Mángano & Buatois, 2017), this trait might offer another tantalising clue on key selective pressures acting on the last ‘Ediacarans’ as they negotiated the dynamic, animal-dominated benthos of the new aeon (Butterfield, 2011).

VI. THE RISE AND RISE OF THE PHANEROZOIC WORLD

Taken together, the taxonomic, ecological, and macroevolutionary continuities among Ediacaran assemblages and the Cambrian world appear increasingly robust with enhanced sampling and novel analytical techniques (e.g. Eden *et al.*, 2022; Bowyer *et al.*, 2022; Hoyal Cuthill, 2022; Turk *et al.*, 2022). This does not mean that the possible roles of extrinsic catastrophic events such as flood basalt volcanism (Hodgin *et al.*, 2021) in sharpening or accelerating late-Ediacaran turnover should be dismissed altogether. Rather, the weight of evidence suggests that such episodic phenomena exerted at most second-order control on an incremental

biotic transition (Fig. 6A). This exposes a paradox at the heart of Ediacaran ‘catastrophe’ proposals: there are no signatures in the Ediacaran record of extrinsic geological events fundamentally and permanently resetting macroevolutionary dynamics. That is, *contra* Evans *et al.* (2022, p. 1), there is no evidence for an Ediacaran mass extinction acting as a ‘significant step in the evolutionary trajectory of life on this planet’ (Fig. 6B). Even in a scenario where Ediacaran ‘catastrophes’ did happen, their superimposition on remarkably steady macroecological and macroevolutionary trends would raise the intriguing possibility that geological happenstance was, to a first approximation, immaterial to the assembly of the Phanerozoic biosphere (Butterfield, 2011).

The abiotic drivers of well-studied Phanerozoic mass extinctions, such as the Permo-Triassic (P-Tr) or Cretaceous–Paleogene (K-Pg) events, can be described as feedforward (Bogart, 1980; Chakrabarty, 2016), rather than feedback elements with respect to the course of evolutionary history: external controls that ‘set’ the conditions for drastic biotic changes from without, remaining unaffected by the cascading consequences of the changes themselves. Since they are removed from evolutionary and ecological feedback loops, mass extinction drivers like asteroids and supervolcanoes introduce consequences that could not be predicted based on their internal dynamics. With respect to the course of the history of life, they can thus be conceptualised as ‘random’ or ‘chancy’ (Gould, 1994).

Accordingly, at least some Phanerozoic mass extinctions unexpectedly reset macroevolutionary trajectories (Raup & Sepkoski, 1982) with previously ecologically dominant groups, such as non-avian dinosaurs or ammonites, disappearing in one fell swoop. *Vice versa*, previously marginal taxa diversified spectacularly in the aftermath as a consequence of changed biogeochemical baselines or release from negative ecological interactions (Hull, 2015). Sweeping the board clean of well-established functional types, life-history strategies, and trophic levels typically allows for the evolution of

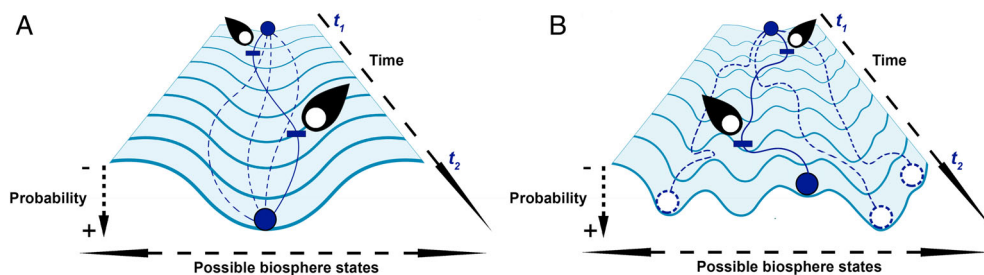


Fig. 6. Alternative probability landscapes of biosphere states through time. (A) In this landscape, over time strong self-reinforcing biotic feedbacks create a probability landscape increasingly skewed towards a single peak. In this landscape, ‘contingent’ feedforward influences are always of insufficient magnitude to deviate macroevolutionary trajectories permanently away from the observed biosphere state at t_2 . Under this scenario, the realised state at t_2 coincides with the range of possible states. (B) A rugged landscape of possible biosphere states: internal self-reinforcing feedbacks are weak and impart only second-order control, with first-order control exerted by feedforward elements. In this scenario, extrinsic contingencies can tip macroevolutionary dynamics towards multiple alternative ‘stable state’ outcomes at t_2 . Blue lines denote realised (continuous) and possible (dashed) macroevolutionary trajectories, with the timing of geobiologically significant ‘contingencies’ (asteroid icons) indicated by superimposed blue bars. Realised biosphere states at t_2 are indicated by blue circles, possible biosphere states by empty circles with dashed outlines.

radically new actors and attendant morphologies. The Triassic radiation of diverse upright, marine, and flying diapsids from sprawling and ecologically marginal ancestors was not presaged by evolutionary trends during the Permian (Benton, 2010; Kelley & Pyenson, 2015). Similarly, the post K-Pg replacement of marine reptiles, ammonites, and non-acanthomorph fishes by marine mammals and acanthomorphs marked at once a reset of marine food webs and a sharp break with previous macroevolutionary trends (Friedman, 2010; Robertson *et al.*, 2013). The lasting effects of Phanerozoic mass extinctions reverberate in the phylogenetic breadth, biogeography, and macroecology of survivors, drawing evolutionary trajectories that deviate from a simple extrapolation of pre-existing tendencies (Fig. 6B; Hull, 2015).

The aftermath of putative Ediacaran catastrophes appears starkly different. Neither the White Sea–Nama nor the end-Nama extinctions take the form of radical biotic resets. Neither heralds a protracted recovery period dominated by ‘strange ecosystems’ witnessing the re-evolution of pre-extinction-like complexity (Hull, 2015; Eden *et al.*, 2022), and no abrupt decreases in morphospace occupancy appear to punctuate the history of the Ediacaran Biota (Shen *et al.*, 2008). The most compelling case against portrayals of the Ediacaran Biota as an evolutionary anomaly or failed experiment (Tarhan *et al.*, 2018; Dunn & Liu, 2019) has to do precisely with such continuity (Wood *et al.*, 2019). Virtually all critical trends in the assembly of Phanerozoic ecologies – including escalations in bioturbation, biomineralisation, niche partitioning, habitat heterogeneity, suspension feeding, motility, and behavioural and sensory complexity – continue essentially unimpeded across presumed Ediacaran mass extinction ‘boundaries’, and their initiation does not coincide with them (Butterfield, 2007, 2011; Carbone & Narbonne, 2014; Droser *et al.*, 2017; Mángano & Buatois, 2017; Tarhan *et al.*, 2018; Wood *et al.*, 2019; Cribb *et al.*, 2019; Cracknell *et al.*, 2021; Xiao

et al., 2021; Eden *et al.*, 2022; Bowyer *et al.*, 2022; Nelson *et al.*, 2022). Bilaterians – arguably the chief architects of late-Ediacaran ecological restructuring – offer a case in point. This group likely appeared in the Avalon well before either Ediacaran ‘mass extinction’ (Dunn *et al.*, 2022), first rose to obvious ecological significance in the White Sea interlude (Droser *et al.*, 2017), and continued on a consistent trajectory of diversification in the Nama, developing vertical burrowing prior to the base of the Cambrian (Xiao *et al.*, 2021; Carbone & Narbonne, 2014; Darroch *et al.*, 2021; Turk *et al.*, 2022).

The empirical fit of the ‘Savannah Hypothesis’ and other models centred on habitat heterogeneity as an evolutionary stimulus for motility and targeted resource acquisition (Budd & Jensen, 2017; Droser *et al.*, 2017; Mitchell *et al.*, 2020; Xiao *et al.*, 2021) suggests that the Ediacaran Biota itself fostered the conditions that made its bilaterian takeover an ecological inevitability. The pre-metazoan Neoproterozoic benthos was, to a first approximation, spatially isotropic (Fig. 7A): in the absence of both macroscopic carcasses (Budd & Jensen, 2017) and zooplanktonic export of clumped organic carbon (Butterfield, 1997), a homogenous distribution of resources would have been the norm. Further, any anisotropies down the sediment column (e.g. in granularity and nutrient or oxygen distribution) were made all but ecologically inaccessible by matgrounds (e.g. Menon *et al.*, 2016; Gehling & Droser, 2018). *Contra* Martinez & Sprecher (2020), benthic environments are hence not in themselves anisotropic. Rather, anisotropy is chiefly a biotic property, first imposed by animals (Fig. 7).

This metazoan imposition of spatial anisotropy on the Ediacaran–Cambrian benthos may best be understood as a two-step process, with the first naturally conducive to the second. Two-dimensional isotropy was broken first (Fig. 7B); sessile Ediacarans introduced heterogeneities in organic carbon distribution, local oxygen concentrations,

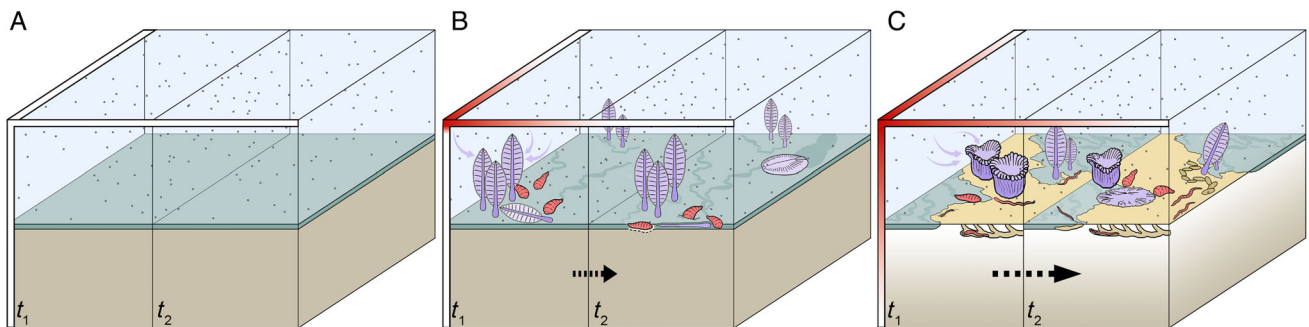


Fig. 7. The Ediacaran establishment of benthic anisotropy. (A) The pre-metazoan benthos; (B) the Ediacaran Biota before the advent of vertical burrowing; (C) the bilaterian-dominated ‘Wormworld’. Each box (A–C) is divided into two domains (t_1 and t_2) representing short-term ($\sim 10^2$ – 10^3 s) environmental change. The increasing magnitude of temporal anisotropy (B, C) is illustrated by the dashed arrows between t_1 and t_2 . The magnitude and spread of anisotropy in the three spatial dimensions is indicated by the coloured bars along the respective axes. ‘Ediacarans’ are marked in violet; bilaterians in red. Violet arrows indicate the withdrawal and concentration of suspended organic carbon (black dots) by suspension-feeding Ediacarans. Green denotes bacterial mats, light blue is the water column, and sandy is the sediment column. The colour gradient in the sediment column in C indicates inflow of oxygen and nutrients *via* matground removal and bioturbation, represented by bilaterian burrows.

and topography to matground ecologies (Budd & Jensen, 2017; Droser *et al.*, 2017; Tarhan *et al.*, 2018; Mitchell *et al.*, 2020). Later, the rise of bilaterian burrowing opened up and expanded vertical anisotropy (Fig. 7C; Budd & Jensen, 2017; Mángano & Buatois, 2017).

In linking these two phases in the animal construction of benthic heterogeneity, a third form of anisotropy – in time, rather than space – may have been crucial. As noted by Martinez & Sprecher (2020), radial symmetry can only accommodate slow locomotion, accompanied by low Reynolds numbers and a corresponding predominance of viscous over inertial forces. Where the disadvantages of slow locomotion may be minimal in a homogenous world with continuous and rarefied resource supplies, its drawbacks become evident in settings characterised by patchy, time-limited resources. As predicted by optimal foraging theory, home range sizes in animals are positively related to rate of movement, and inversely related to resource density and renewal rates (Ford, 1983). In the case of Ediacaran organic carbon hotspots, availability in time would have been limited not only by sediment burial and overgrowth by matgrounds, but also by competition with other grazers, decomposers, or scavengers (Gehling & Droser, 2018; Budd & Jensen, 2017; Mitchell *et al.*, 2020). Hence, all else being equal, selective pressures on members of these guilds would have favoured faster locomotion, translating into increased dominance of inertial over viscous forces.

In this context, the acquisition of bilaterian-type motility may have provided a twofold advantage. First, directing movement along an elongated anteroposterior axis helps to reduce drag (e.g. Beklemishev 1969; Wainwright 1988), which increases non-linearly with speed. Second, under an inertial regime bilaterian locomotion offers a significant manoeuvrability advantage. Streamlining a body plan in one direction only allows for faster changeovers and more precise steering of locomotion through the generation of instantaneous ‘pushing’ surfaces, including in upper sediment layers and around the sediment–water interface (Holló & Novák, 2012). These mechanical advantages are pertinent even to a purely two-dimensional, pre-burrowing world. As such, they may have fostered the evolution of the bilaterian bauplan in its initial phase.

However, bilaterality comes with a package of exaptations bound to introduce three-dimensional anisotropy (Martinez & Sprecher, 2020) into benthic ecologies. The presence of an anteroposterior axis allows for the segregation of the mouth and anus at or near opposite poles, ejecting waste in an animal’s wake rather than in its path. This removes an obvious impediment to substrate penetration and allows feeding to be coupled to effective locomotion through sediment (Holland, 2015). The secondary reacquisition of bilaterality by a radial ancestor in infaunal sea urchins offers a case in point (Saucède, Mooi & David, 2003). Distributing musculature along the bilaterian anteroposterior axis enables peristalsis – the transmission of waves of muscle contraction parallel to the direction of motion. Peristalsis underpins burrowing in disparate extant bilaterians and is inferred

to have been present already in White Sea tracemakers (Dorgan, 2018; Evans *et al.*, 2020). Moreover, the reduced cross section offered by an elongated anteroposterior axis minimises friction per unit of body mass, lending itself to efficient sediment penetration (Holló & Novák, 2012). These innovations explain why bilaterians, rather than coelenterate-grade animals, have a near-monopoly on deep burrowing and global sediment mixing (Holland, 2015).

With the advent of shallow burrowing (Gehling & Droser, 2018; Budd & Jensen, 2017), bilaterian locomotion coupled to faster access to ephemeral resources a capacity to stave off their sequestration by substrates. That is, by enabling sediment penetration burrowing extended the time-frame in which resource hotspots remained within reach of bilaterians to the post-burial phase (Fig. 7B). In doing so, it offered a twofold response to temporal anisotropy. In accordance with the idea of a cascading amplification of bioturbation (Herringshaw *et al.*, 2017; Budd & Jensen, 2017; Cribb *et al.*, 2019), the ensuing escalation of two-dimensional anisotropy and its expansion into the three-dimensional realm may have been self-sustaining within a very broad parameter space. As Ediacaran ‘whale falls’ (Budd & Jensen, 2017) or other carbon hotspots on matgrounds conceivably became the focus of greater competition as bilaterians became more ecologically prevalent, shallow burrowing may also have provided a means to access resources sheltered from epifaunal competitors. Computational and robotic simulations (Hayes, 2003; reviewed in Carbone & Narbonne, 2014) indicate that selective pressures for feeding efficiency would be expected to promote progressive increases in ichnofossil complexity to maximise the surface area to path length ratio. The driver for this trend is the necessity to maximise the harvesting of resources concentrated around the sediment–water interface (as in grazing, scavenging, or superficial deposit-feeding) while minimising the time and energy spent foraging. This theoretical scenario matches palaeontological evidence for progressively tighter and more organised meanders in bilaterian ichnofossils, and the eventual appearance of vertical burrowing amid escalating resource competition among surface-dwelling tracemakers (Carbone & Narbonne, 2014).

The spatial anisotropies of the bilaterian Umwelt are necessarily mirrored at the neuroanatomical level. Bilaterians naturally tend to encounter stimuli along the direction of motion. This promotes the packing of receptors and associated neural units at the rear of the animal in a self-amplifying process, whereby increased clustering of neurons begets further packing of sensors at close range (Martinez & Sprecher, 2020). The origins of bilaterian central nervous systems and cephalisation may best be understood by situating this feedback process in a competitive scenario, where the ability to confront anisotropies offers an increasingly critical fitness advantage. In this light, the Ediacaran escalation of motility and sensory complexity documented by Carbone & Narbonne (2014), and the subsequent Cambrian explosion of bilaterian behaviours (McIlroy & Brasier, 2017) are predictable from first principles given two-dimensional

anisotropy and a non-limiting supply rate of evolutionary novelties. This model is consistent with the seemingly irrepressible amplification and diversification of the bilaterian presence across Ediacaran ‘mass extinction’ boundaries. Moreover, it agrees with evolutionary–developmental evidence suggesting that nerve cords and condensed anterior portions of the nervous systems evolved convergently at the base of several major bilaterian phyla, which most likely diverged during the late Ediacaran (Dunn *et al.*, 2014; Gavilán, Perea-Atienza & Martínez, 2016; Martín-Durán *et al.*, 2018; Martín-Durán & Hejnol, 2021).

If the anisotropic scenario is correct, the demise of the Ediacaran Biota as a distinctive grade of ecological organisation – an essentially two-dimensional benthic realm, coupled to inconspicuous or absent infaunal, nektonic, and possibly zooplanktonic components (Butterfield, 1997) – may also have been predictable from first principles. The plausibility of this scenario can be tested from a phylogenetic angle. Sessile and radially lobate Ediacarans may define a grade of organisation spanning the eumetazoan stem-group (Dunn *et al.*, 2018; Evans, Droser & Erwin, 2021). If so, early stem-group bilaterians and their last common ancestor with cnidarians were most likely coelenterate-like rather than bilaterian-like (Manuel, 2009; Hejnol & Pang, 2016; Butterfield, 2020), and – in accordance with the ichnofossil record (Liu, McLroy & Brasier, 2010; Menon, McLroy & Brasier, 2013) – the origin of focussed, polarised bilaterian-type locomotion postdated that of the Ediacaran Biota in the Avalon assemblage. If so, the anisotropies established in the Biota itself would emerge as credible drivers of bilaterian origins and innovation. This scenario would be reinforced by evidence for multiple, independent origins of bilaterian-like locomotion among Ediacaran animals, including dickinsoniomorphs, ‘bilateralomorphs’, and *bona fide* bilaterians. Indirect support comes from the evolutionary–developmental evidence for convergent origins of a through-gut and neural centralisation among extant bilaterians (Hejnol & Martindale, 2008; Hejnol & Pang, 2016; Gavilán *et al.*, 2016; Cannon *et al.*, 2016; Nielsen, Brunet & Arendt, 2018; Nielsen, 2019; Martín-Durán & Hejnol, 2021; but see Kapli & Telford, 2020). *Vice versa*, evidence for a bilaterian-like eumetazoan common ancestor (Finnerty, 2003) coupled with a derived status for Ediacarans (e.g. as total-group cnidarians; Butterfield, 2020) would sideline the ecological importance of the Ediacaran Biota in the construction of the bilaterian bauplan. At present, the weight of the evidence suggests that at least some Ediacarans did populate the eumetazoan stem-group (Dunn *et al.*, 2018, 2019a,b, 2021; Hoyal Cuthill & Han, 2018; Runnegar, 2022). However, disentangling the topology of Ediacaran interrelationships, in addition to their broad placement in the animal tree of life, remains crucial.

The context independence of the principles of macroscopic motion, optimal foraging theory, and information-processing architectures raise the possibility that the disruption of isotropy is a universal requirement for the emergence of bilaterian-type locomotion and neural centralisation. If so, the Ediacaran Biota was the polar opposite of

an anomaly in the evolution of complex life (Tarhan *et al.*, 2018; Dunn & Liu, 2019). Rather, it is hard to envisage how anything comparable to the Phanerozoic biosphere could have developed in the absence of the Biota or a functional equivalent thereof. Valuable and ephemeral resource hotspots in an otherwise uniform world may have been indispensable for focussed, directional movement and its cascade of behavioural innovations to arise in the first place. With the imposition of two-dimensional and temporal anisotropy on the Ediacaran benthos the stage for the Cambrian Explosion may have been all but set, in line with the inconsequentiality of proposed Ediacaran mass extinctions. By the same token, the popular notion of Ediacaran catastrophes ‘liberating’ vacant niches for the Cambrian Explosion (Hsu *et al.*, 1985) arguably rests on a misconception. Niches do not exist in an abiotic vacuum, and in both ecological and phylogenetic terms the Ediacaran Biota was almost certainly much more of a cradle than a roadblock for the Cambrian Explosion. Once stripped of its macrobiota and attendant richness of TOS and heterogenous matgrounds, Neoproterozoic oceans offered very little on which a hypothetical metazoan radiation could have been engineered and sustained. Large-scale analyses of temporal co-occurrence in fossil taxa (Hoyal Cuthill, Guttenberg & Budd, 2020) underscore this point, contradicting ‘vacant-ecospace’ narratives. Mass extinctions and comparable ‘mass radiations’ – including the Cambrian Explosion – are generally decoupled, and radiations may themselves precipitate quick turnover as niches are forged and dismantled by evolving organisms. It is such destructive creation, rather than creative destruction (Hoyal Cuthill *et al.*, 2020), that may best explain the decline and fall of the Ediacarans.

VII. CONCLUSIONS

- (1) The long fuse of the Cambrian Explosion was lit on the Ediacaran benthos. Far from being an ecological impediment, the Ediacaran Biota at the height of its diversity probably fostered the evolution of the eumetazoan engineers that would ultimately precipitate its downfall.
- (2) The impacts of bioturbation, predation, biomineralisation, and the creation of new habitats by early bilaterians all deserve further investigation as possible drivers of terminal Ediacaran turnover, which increasingly emerges as more protracted than traditionally assumed.
- (3) Catastrophic abiotic events analogous to those that precipitated Phanerozoic mass extinctions may have accelerated or amplified late-Ediacaran turnover, but the patterns and tempo of end-Neoproterozoic biotic change suggest that they were largely immaterial to the structuring of the Phanerozoic biosphere.
- (4) The ‘destructive creation’ accompanying the diversification of crown-group eumetazoans and the decline of the Ediacaran Biota finds no true parallels in the subsequent 539 million years. Explanations centred on Phanerozoic

analogues fail to recognise the Ediacaran hourglass neck as a macroecological and macroevolutionary revolution, terraforming marine ecosystems past irreversible tipping points.

(5) The implications of end-Neoproterozoic extinction dynamics are far-reaching. Instead of representing historical accidents, the fall of the Ediacarans and the emergence of Phanerozoic ecosystems hint at a key role for endogenous, self-sustaining eco-evolutionary cascades in shaping the history of the biosphere.

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IX. REFERENCES

- ÁLVARO, J. J., CORTIJO, I., JENSEN, S., MUS, M. M. & PALACIOS, T. (2020). *Cloudina*-microbial reef resilience to substrate instability in a Cadomian retro-arc basin of the Iberian Peninsula. *Precambrian Research* **336**, 105479.
- BAL, T. L., STORER, A. J. & JURGENSEN, M. F. (2018). Evidence of damage from exotic invasive earthworm activity was highly correlated to sugar maple dieback in the Upper Great Lakes region. *Biological Invasions* **20**(1), 151–164.
- BECKER-KERBER, B., PACHECO, M. L. A. F., RUDNITZKI, I. D., GALANTE, D., RODRIGUES, F. & DE MORAES LEME, J. (2017). Ecological interactions in *Cloudina* from the Ediacaran to Brazil: implications for the rise of animal biomineralization. *Scientific Reports* **7**(1), 1–11.
- BEKLEMISHEV, V. N. (1969). *Principles of Comparative Anatomy of Invertebrates*. The University of Chicago Press, Chicago.
- BENGTSON, S. & ZHAO, Y. (1992). Predatorial borings in late Precambrian mineralized exoskeletons. *Science* **257**(5068), 367–369.
- BENTON, M. J. (2010). The origins of modern biodiversity on land. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**(1558), 3667–3679.
- BOAG, T. H., DARROCH, S. A. & LAFLAMME, M. (2016). Ediacaran distributions in space and time: testing assemblage concepts of earliest macroscopic body fossils. *Paleobiology* **42**(4), 574–594.
- BOAG, T. H., STOCKEY, R. G., ELDER, L. E., HULL, P. M. & SPERLING, E. A. (2018). Oxygen, temperature and the deep-marine stenothermal cradle of Ediacaran evolution. *Proceedings of the Royal Society B* **285**(1893), 20181724.
- BOGART, D. H. (1980). Feedback, feedforward, and feedwithin: strategic information in systems. *Behavioral Science* **25**(4), 237–249.
- BOND, D. P. & GRASBY, S. E. (2017). On the causes of mass extinctions. *Palaogeography, Palaeoclimatology, Palaeoecology* **478**, 3–29.
- BOWYER, F. T., ZHURAVLEV, A. Y., WOOD, R., SHIELDS, G. A., ZHOU, Y., CURTIS, A., POULTON, S. W., CONDON, D. J., YANG, C. & ZHU, M. (2022). Calibrating the temporal and spatial dynamics of the Ediacaran-Cambrian radiation of animals. *Earth-Science Reviews* **225**, 103913.
- BRASIER, M. (2009). *Darwin's Lost World: The Hidden History of Animal Life*. Oxford University Press, Oxford.
- BRASIER, M. D. (1992). Global Ocean—atmosphere change across the Precambrian—Cambrian transition. *Geological Magazine* **129**(2), 161–168.
- BUATOIS, L. A. & MÁNGANO, M. G. (2018). The other biodiversity record: innovations in animal-substrate interactions through geologic time. *GSA Today* **28**(10), 4–10.
- BUATOIS, L. A., MÁNGANO, M. G., MINTER, N. J., ZHOU, K., WISSHAK, M., WILSON, M. A. & OLEA, R. A. (2020). Quantifying ecospace utilization and ecosystem engineering during the early Phanerozoic—the role of bioturbation and bioerosion. *Science Advances* **6**(33), eabb0618.
- BUDD, G. E. & JENSEN, S. (2017). The origin of the animals and a ‘Savannah’ hypothesis for early bilaterian evolution. *Biological Reviews* **92**(1), 446–473.
- BUTTERFIELD, N. J. (1997). Plankton ecology and the Proterozoic-Phanerozoic transition. *Paleobiology* **23**(2), 247–262.
- BUTTERFIELD, N. J. (2006). Hooking some stem-group ‘worms’: fossil lophotrochozoans in the Burgess Shale. *BioEssays* **28**(12), 1161–1166.
- BUTTERFIELD, N. J. (2007). Macroevolution and macroecology through deep time. *Palaentology* **50**(1), 41–55.
- BUTTERFIELD, N. J. (2009). Oxygen, animals and oceanic ventilation: an alternative view. *Geobiology* **7**(1), 1–7.
- BUTTERFIELD, N. J. (2011). Animals and the invention of the Phanerozoic Earth system. *Trends in Ecology & Evolution* **26**(2), 81–87.
- BUTTERFIELD, N. J. (2015a). Proterozoic photosynthesis—a critical review. *Palaentology* **58**(6), 953–972.
- BUTTERFIELD, N. J. (2015b). The neoproterozoic. *Current Biology* **25**(19), R859–R863.
- BUTTERFIELD, N. J. (2020). Constructional and functional morphology of Ediacaran rangemorphs. *Geological Magazine* **159**(7), 1148–1159.
- CAI, Y., CORTIJO, I., SCHIFFBAUER, J. D. & HUA, H. (2017). Taxonomy of the late Ediacaran index fossil *Cloudina* and a new similar taxon from South China. *Precambrian Research* **298**, 146–156.
- CAI, Y., XIAO, S., LI, G. & HUA, H. (2019). Diverse biomineralizing animals in the terminal Ediacaran Period herald the Cambrian explosion. *Geology* **47**(4), 380–384.
- CAIRNS, J. JR. (2004). Ecological tipping points: a major challenge for experimental sciences. *Asian Journal of Experimental Sciences* **18**(1), 1–16.
- CANNON, J. T., VELLUTINI, B. C., SMITH, J., RONQUIST, F., JONDELIUS, U. & HEJNOL, A. (2016). Xenacoelomorpha is the sister group to Nephrozoa. *Nature* **530**(7588), 89–93.
- CARBONE, C. & NARBONNE, G. M. (2014). When life got smart: the evolution of behavioral complexity through the Ediacaran and Early Cambrian of NW Canada. *Journal of Paleontology* **88**(2), 309–330.
- CARBONE, C. A., NARBONNE, G. M., MACDONALD, F. A. & BOAG, T. H. (2015). New Ediacaran fossils from the uppermost Blueflower Formation, Northwest Canada: disentangling biostratigraphy and paleoecology. *Journal of Paleontology* **89**(2), 281–291.
- CHAKRABARTY, D. (2016). Humanities in the Anthropocene: the crisis of an enduring Kantian fable. *New Literary History* **47**(2), 377–397.
- CHEN, W., CAI, Y., LIANG, D. & WANG, X. (2022). Two tubular fossil assemblages from the terminal Ediacaran Dengying Formation in southern Shaanxi Province of South China. *Precambrian Research* **378**, 106762.
- CHEN, Z., CHEN, X., ZHOU, C., YUAN, X. & XIAO, S. (2018). Late Ediacaran trackways produced by bilaterian animals with paired appendages. *Science Advances* **4**(6), eaa06691.
- CHEN, Z., ZHOU, C., YUAN, X. & XIAO, S. (2019). Death march of a segmented and trilobate bilaterian elucidates early animal evolution. *Nature* **573**(7774), 412–415.
- CHERRY, L. B., GILLEAUDEAU, G. J., GRAZHDANKIN, D. V., ROMANIELLO, S. J., MARTIN, A. J. & KAUFMAN, A. J. (2022). A diverse Ediacaran assemblage survived under low-oxygen conditions. *Nature Communications* **13**(1), 7306.
- COLLINS, A. G. (1998). Evaluating multiple alternative hypotheses for the origin of Bilateria: an analysis of 18S rRNA molecular evidence. *Proceedings of the National Academy of Sciences* **95**(26), 15458–15463.
- CONWAY MORRIS, S. (1993). Ediacaran-like fossils in Cambrian Burgess Shale-type faunas of North America. *Palaentology* **36**(3), 593–635.
- CRACKNELL, K., GARCÍA-BELLIDO, D. C., GEHLING, J. G., ANKOR, M. J., DARROCH, S. A. & RAHMAN, I. A. (2021). Pentaradial eukaryote suggests expansion of suspension feeding in white sea-aged Ediacaran communities. *Scientific Reports* **11**(1), 4121.
- CRIBB, A. T., KENCHINGTON, C. G., KOESTER, B., GIBSON, B. M., BOAG, T. H., RACICOT, R. A., MOCKE, H., LAFLAMME, M. & DARROCH, S. A. (2019). Increase in metazoan ecosystem engineering prior to the Ediacaran–Cambrian boundary in the Nama Group, Namibia. *Royal Society Open Science* **6**(9), 190548.
- CRIBB, A. T., VAN DE VELDE, S. J., BERELSON, W. M., BOTTJER, D. J. & CORSETTI, F. A. (2023). Ediacaran–Cambrian bioturbation did not extensively oxygenate sediments in shallow marine ecosystems. *Geobiology* **21**, 1–19.
- CROOKS, J. A. (2002). Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* **97**(2), 153–166.
- CUNNINGHAM, J. A., LIU, A. G., BENGTSON, S. & DONOGHUE, P. C. (2017). The origin of animals: can molecular clocks and the fossil record be reconciled? *BioEssays* **39**(1), 1–12.
- DAL CORSO, J., BERNARDI, M., SUN, Y., SONG, H., SEYFULAH, L. J., PRETO, N., GIANOLLA, P., RUFFELL, A., KUSTATSCHER, E., ROGGI, G., MERICCO, A., HOHN, S., SCHMIDT, A. R., MARZOLI, A., NEWTON, R. J., ET AL. (2020). Extinction and dawn of the modern world in the Carnian (Late Triassic). *Science Advances* **6**(38), eaba0099.

- DARROCH, S. A., BOAG, T. H., RACICOT, R. A., TWEEDT, S., MASON, S. J., ERWIN, D. H. & LAFLAMME, M. (2016). A mixed Ediacaran-metazoan assemblage from the Zaris Sub-basin, Namibia. *Palaogeography, Palaeoclimatology, Palaeoecology* **459**, 198–208.
- DARROCH, S. A., CRIBB, A. T., BUATOIS, L. A., GERMS, G. J., KENCHINGTON, C. G., SMITH, E. F., MOCKE, H., O'NEIL, G. R., SCHIFFBAUER, J. D., MALONEY, K. M., RACICOT, R. A., TURK, K. A., GIBSON, B. M., ALMOND, J., KOESTER, B., *ET AL.* (2021). The trace fossil record of the Nama Group, Namibia: exploring the terminal Ediacaran records of the Cambrian explosion. *Earth-Science Reviews* **212**, 103435.
- DARROCH, S. A., GIBSON, B. M., SYVERSEN, M., RAHMAN, I. A., RACICOT, R. A., DUNN, F. S., GUTARRA, S., SCHINDLER, E., WEHRMANN, A. & LAFLAMME, M. (2022). The life and times of *Pteridinium simplex*. *Paleobiology* **48**, 527–556.
- DARROCH, S. A., GUTARRA, S., MASAKI, H., OLARU, A., GIBSON, B. M., DUNN, F. S., MITCHELL, E. G., RACICOT, R. A., BURZYNSKI, G. & RAHMAN, I. A. (2023a). The rangeomorph *Pectinifrons abyssalis*: hydrodynamic function at the dawn of animal life. *iScience* **26**, 105989.
- DARROCH, S. A., SMITH, E. F., LAFLAMME, M. & ERWIN, D. H. (2018). Ediacaran extinction and Cambrian explosion. *Trends in Ecology & Evolution* **33**(9), 653–663.
- DARROCH, S. A., SPERLING, E. A., BOAG, T. H., RACICOT, R. A., MASON, S. J., MORGAN, A. S., TWEEDT, S., MYROU, P., JOHNSTON, D. T., ERWIN, D. H. & LAFLAMME, M. (2015). Biotic replacement and mass extinction of the Ediacara biota. *Proceedings of the Royal Society B: Biological Sciences* **282**(1814), 20151003.
- DARROCH, S. A. F., SMITH, E. F., NELSON, L. L., CRAFFEY, M., SCHIFFBAUER, J. D. & LAFLAMME, M. (2023b). Causes and consequences of end-Ediacaran extinction: an update. *Cambridge Prisms: Extinction* **1**, e15.
- DEBRENNE, F. & ZHURAVLEV, A. Y. (1997). Cambrian food web: a brief review. *Geobios* **30**, 181–188.
- DOHRMANN, M. & WÖRHEIDE, G. (2013). Novel scenarios of early animal evolution—is it time to rewrite textbooks? *Integrative and Comparative Biology* **53**(3), 503–511.
- DORGAN, K. M. (2018). Kinematics of burrowing by peristalsis in granular sands. *Journal of Experimental Biology* **221**(10), jeb167759.
- DOS REIS, M., THAWORNWATTANA, Y., ANGELIS, K., TELFORD, M. J., DONOGHUE, P. C. & YANG, Z. (2015). Uncertainty in the timing of origin of animals and the limits of precision in molecular timescales. *Current Biology* **25**(22), 2939–2950.
- DROSER, M. L., TARHAN, L. G. & GEHLING, J. G. (2017). The rise of animals in a changing environment: global ecological innovation in the late Ediacaran. *Annual Review of Earth and Planetary Sciences* **45**, 593–617.
- DUNN, C. W., GIRIBET, G., EDGECOMBE, G. D. & HEJNOL, A. (2014). Animal phylogeny and its evolutionary implications. *Annual Review of Ecology, Evolution, and Systematics* **45**, 371–395.
- DUNN, F. S., KENCHINGTON, C. G., PARRY, L. A., CLARK, J. W., KENDALL, R. S. & WILBY, P. R. (2022). A crown-group cnidarian from the Ediacaran of Charnwood Forest, UK. *Nature Ecology & Evolution* **6**(8), 1095–1104.
- DUNN, F. S. & LIU, A. G. (2019). Viewing the Ediacaran biota as a failed experiment is unhelpful. *Nature Ecology & Evolution* **3**(4), 512–514.
- DUNN, F. S., LIU, A. G. & DONOGHUE, P. C. (2018). Ediacaran developmental biology. *Biological Reviews* **93**(2), 914–932.
- DUNN, F. S., LIU, A. G. & GEHLING, J. G. (2019a). Anatomical and ontogenetic reassessment of the Ediacaran frond *Arborea arborea* and its placement within total group Eumetazoa. *Palaentology* **62**(5), 851–865.
- DUNN, F. S., LIU, A. G., GRAZHDANKIN, D. V., VIXSEBOXSE, P., FLANNERY-SUTHERLAND, J., GREEN, E., HARRIS, S., WILBY, P. R. & DONOGHUE, P. C. (2021). The developmental biology of *Charnia* and the eumetazoan affinity of the Ediacaran rangeomorphs. *Science Advances* **7**(30), eabe0291.
- DUNN, F. S., WILBY, P. R., KENCHINGTON, C. G., GRAZHDANKIN, D. V., DONOGHUE, P. C. & LIU, A. G. (2019b). Anatomy of the Ediacaran rangeomorph *Charnia masoni*. *Papers in Palaentology* **5**(1), 157–176.
- EDEN, R., MANICA, A. & MITCHELL, E. G. (2022). Metacommunity analyses show an increase in ecological specialisation throughout the Ediacaran period. *PLoS Biology* **20**(5), e3001289.
- ELLIOTT, D. A., TRUSLER, P. W., NARBONNE, G. M., VICKERS-RICH, P., MORTON, N., HALL, M., HOFFMANN, K. H. & SCHNEIDER, G. I. (2016). *Ermetia* from the late Ediacaran Nama Group, Namibia. *Journal of Paleontology* **90**(6), 1017–1026.
- ERWIN, D. H. & VALENTINE, J. W. (2013). *The Cambrian Explosion*. Roberts and Company, Genwodd Village, Colorado.
- EVANS, S. D., DROSER, M. L. & ERWIN, D. H. (2021). Developmental processes in Ediacara macrofossils. *Proceedings of the Royal Society B* **288**(1945), 20203055.
- EVANS, S. D., HUGHES, I. V., GEHLING, J. G. & DROSER, M. L. (2020). Discovery of the oldest bilaterian from the Ediacaran of South Australia. *Proceedings of the National Academy of Sciences* **117**(14), 7845–7850.
- EVANS, S. D., TU, C., RIZZO, A., SURPRENANT, R. L., BOAN, P. C., McCANDLESS, H., MARSHALL, N., XIAO, S. & DROSER, M. L. (2022). Environmental drivers of the first major animal extinction across the Ediacaran White Sea-Nama transition. *Proceedings of the National Academy of Sciences* **119**(46), e2207475119.
- FABRICIUS, K. E., GENIN, A. & BENAYAHU, Y. (1995). Flow-dependent herbivory and growth in zooxanthellae-free soft corals. *Limnology and Oceanography* **40**(7), 1290–1301.
- FEDONKIN, M. A. & WAGGONER, B. M. (1997). The Late Precambrian fossil *Kimberella* is a mollusc-like bilaterian organism. *Nature* **388**(6645), 868–871.
- FINNERTY, J. R. (2003). The origins of axial patterning in the metazoa: how old is bilateral symmetry? *International Journal of Developmental Biology* **47**(7–8), 523–529.
- FORD, R. G. (1983). Home range in a patchy environment: optimal foraging predictions. *American Zoologist* **23**(2), 315–326.
- FRELICH, L. E., HALE, C. M., REICH, P. B., HOLDSWORTH, A. R., SCHEU, S., HENEGHAN, L. & BOHLEN, P. J. (2006). Earthworm invasion into previously earthworm-free temperate and boreal forests. In *Biological Invasions Belowground: Earthworms as Invasive Species*, pp. 35–45. Springer, Dordrecht.
- FRIEDMAN, M. (2010). Explosive morphological diversification of spiny-finned teleost fishes in the aftermath of the end-Cretaceous extinction. *Proceedings of the Royal Society B: Biological Sciences* **277**(1688), 1675–1683.
- GAVILÁN, B., PEREA-ATIENZA, E. & MARTINEZ, P. (2016). Xenacoelomorpha: a case of independent nervous system centralization? *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**(1685), 20150039.
- GEHLING, J. G. (1999). Microbial mats in terminal Proterozoic siliciclastics; Ediacaran death masks. *Palaos* **14**(1), 40–57.
- GEHLING, J. G. & DROSER, M. L. (2013). How well do fossil assemblages of the Ediacara Biota tell time? *Geology* **41**(4), 447–450.
- GEHLING, J. G. & DROSER, M. L. (2018). Ediacaran scavenging as a prelude to predation. *Emerging Topics in Life Sciences* **2**(2), 213–222.
- GIBSON, B. M., RAHMAN, I. A., MALONEY, K. M., RACICOT, R. A., MOCKE, H., LAFLAMME, M. & DARROCH, S. A. (2019). Gregarious suspension feeding in a modular Ediacaran organism. *Science Advances* **5**(6), eaaw0260.
- GOULD, S. J. (1994). The evolution of life on the earth. *Scientific American* **271**(4), 84–91.
- GRAZHDANKIN, D. (2004). Patterns of distribution in the Ediacaran biotas: facies versus biogeography and evolution. *Paleobiology* **30**(2), 203–221.
- GRAZHDANKIN, D. (2014). Patterns of evolution of the Ediacaran soft-bodied biota. *Journal of Paleontology* **88**(2), 269–283.
- HAGADORN, J. W., FEDO, C. M. & WAGGONER, B. M. (2000). Early Cambrian Ediacaran-type fossils from California. *Journal of Paleontology* **74**(4), 731–740.
- HAGADORN, J. W. & WAGGONER, B. (2000). Ediacaran fossils from the southwestern Great Basin, United States. *Journal of Paleontology* **74**(2), 349–359.
- HAN, J., CAI, Y., SCHIFFBAUER, J. D., HUA, H., WANG, X., YANG, X., UESUGI, K., KOMIYA, T. & SUN, J. I. E. (2017). A Cloudina-like fossil with evidence of asexual reproduction from the lowest Cambrian, South China. *Geological Magazine* **154**(6), 1294–1305.
- HAN, J., ZHANG, Z., LIU, J. & SHU, D. (2007). Evidence of priapulid scavenging from the Early Cambrian Chengjiang deposits, Southern China. *Palaos* **22**(6), 691–694.
- HAYES, B. (2003). Computing science: In search of the Optimal Scumsucking Bottomfeeder. *American Scientist* **91**(5), 392–396.
- HEJNOL, A. & MARTINDALE, M. Q. (2008). Acoel development indicates the independent evolution of the bilaterian mouth and anus. *Nature* **456**(7220), 382–386.
- HEJNOL, A. & PANG, K. (2016). Xenacoelomorpha's significance for understanding bilaterian evolution. *Current Opinion in Genetics & Development* **39**, 48–54.
- HERRINGSHAW, L. G., CALLOW, R. H. & McILROY, D. (2017). Engineering the Cambrian explosion: the earliest bioturbators as ecosystem engineers. *Geological Society, London, Special Publications* **448**(1), 369–382.
- HODGIN, E. B., NELSON, L. L., WALL, C. J., BARRÓN-DÍAZ, A. J., WEBB, L. C., SCHMITZ, M. D., FIKE, D. A., HAGADORN, J. W. & SMITH, E. F. (2021). A link between rift-related volcanism and end-Ediacaran extinction? Integrated chemostratigraphy, biostratigraphy, and U-Pb geochronology from Sonora, Mexico. *Geology* **49**(2), 115–119.
- HÖGSTRÖM, A., JENSEN, S., PALACIOS, T. & EBBESTAD, J. O. R. (2013). New information on the Ediacaran-Cambrian transition in the Vestertana Group, Finnmark, northern Norway, from trace fossils and organic-walled microfossils. *Norwegian Journal of Geology* **93**, 95–106.
- HOLLAND, P. W. (2015). Did homeobox gene duplications contribute to the Cambrian explosion? *Zoological Letters* **1**(1), 1–8.
- HOLLÓ, G. & NOVÁK, M. (2012). The manoeuvrability hypothesis to explain the maintenance of bilateral symmetry in animal evolution. *Biology Direct* **7**(1), 1–7.
- HONG, H., ZHE, C. & XUNLAI, Y. (2007). The advent of mineralized skeletons in Neoproterozoic Metazoa—new fossil evidence from the Gaojianshan Fauna. *Geological Journal* **42**(3–4), 263–279.
- HOYAL CUTHILL, J. F. (2022). Ediacaran survivors in the Cambrian: suspicions, denials and a smoking gun. *Geological Magazine* **159**, 1–10.
- HOYAL CUTHILL, J. F., GUTTENBERG, N. & BUDD, G. E. (2020). Impacts of speciation and extinction measured by an evolutionary decay clock. *Nature* **588**, 1–6.
- HOYAL CUTHILL, J. F. & HAN, J. (2018). Cambrian petalonamid Stromatoveris phylogenetically links Ediacaran biota to later animals. *Palaentology* **61**(6), 813–823.

- HSU, K. J., OBERHÄNSLI, H., GAO, J. Y., SHU, S., HAIHONG, C. & KRÄHENBÜHL, U. (1985). 'Strangelove Ocean' before the Cambrian explosion. *Nature* **316**(6031), 809–811.
- HUA, H., PRATT, B. R. & ZHANG, L. Y. (2003). Borings in *Cloudina* shells: complex predator-prey dynamics in the terminal Neoproterozoic. *Palaios* **18**(4–5), 454–459.
- HUANG, K., CHENG, M., ALGEO, T. J., HU, J., WANG, H., ZHANG, Z., DODD, M. S., WU, Y., GUO, W. & LI, C. (2022). Interaction of Shibanian Biota and environment in the terminal Ediacaran Ocean: evidence from I/(Ca+ Mg) and sulfur isotopes. *Precambrian Research* **379**, 106814.
- HULL, P. (2015). Life in the aftermath of mass extinctions. *Current Biology* **25**(19), R941–R952.
- IVANTSOV, A. & ZAKREVSAYA, M. (2022). *Dickinsonia*: mobile and adhered. *Geological Magazine* **159**(7), 1118–1133.
- IVANTSOV, A. Y., NARBONNE, G. M., TRUSLER, P. W., GREENTREE, C. & VICKERS-RICH, P. (2016). Elucidating *Ernie*: new insights from exceptional specimens in the Ediacaran of Namibia. *Lethaia* **49**(4), 540–554.
- IVANTSOV, A. Y. & ZAKREVSAYA, M. (2023). Body plan of *Dickinsonia*, the oldest mobile animals. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 1–14.
- IVANTSOV, A. Y. & ZAKREVSAYA, M. A. (2021a). Symmetry of Vendobionta (Late Precambrian Metazoa). *Paleontological Journal* **55**(7), 717–726.
- IVANTSOV, A. Y. & ZAKREVSAYA, M. A. (2021b). Trilobozoa, precambrian tri-radial organisms. *Paleontological Journal* **55**, 727–741.
- JENSEN, S., DROSER, M. L. & GEHLING, J. G. (2006). A critical look at the Ediacaran trace fossil record. In *Neoproterozoic Geobiology and Paleobiology*, pp. 115–157. Springer, Dordrecht.
- JENSEN, S., GEHLING, J. G. & DROSER, M. L. (1998). Ediacara-type fossils in Cambrian sediments. *Nature* **393**(6685), 567–569.
- JENSEN, S. & RUNNEGAR, B. N. (2005). A complex trace fossil from the Spitskop Member (terminal Ediacaran–? Lower Cambrian) of southern Namibia. *Geological Magazine* **142**(5), 561–569.
- KAPLI, P. & TELFORD, M. J. (2020). Topology-dependent asymmetry in systematic errors affects phylogenetic placement of Ctenophora and Xenacoelomorpha. *Science Advances* **6**(50), eabc5162.
- KARATAYEV, A. Y., BURLAKOVA, L. E. & PADILLA, D. K. (2002). Impacts of zebra mussels on aquatic communities and their role as ecosystem engineers. In *Invasive Aquatic Species of Europe. Distribution, Impacts and Management*, pp. 433–446. Springer, Dordrecht.
- KELLEY, N. P. & PYENSON, N. D. (2015). Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene. *Science* **348**(6232), aaa3716.
- KENCHINGTON, C. G., DUNN, F. S. & WILBY, P. R. (2018). Modularity and overcompensatory growth in Ediacaran rangeomorphs demonstrate early adaptations for coping with environmental pressures. *Current Biology* **28**(20), 3330–3336.
- LAAKSO, T. A., SPERLING, E. A., JOHNSTON, D. T. & KNOLL, A. H. (2020). Ediacaran reorganization of the marine phosphorus cycle. *Proceedings of the National Academy of Sciences* **117**(22), 11961–11967.
- LAFLAMME, M. (2022). Lifting the veil on the oldest-known animals. *Nature* **609**, 904–905.
- LAFLAMME, M., DARROCH, S. A., TWEEDT, S. M., PETERSON, K. J. & ERWIN, D. H. (2013). The end of the Ediacara biota: extinction, biotic replacement, or Cheshire Cat? *Gondwana Research* **23**(2), 558–573.
- LAUMER, C. E., GRUBER-VODICKA, H., HADFIELD, M. G., PEARSE, V. B., RIESGO, A., MARIONI, J. C. & GIRIBET, G. (2018). Support for a clade of Placozoa and Cnidaria in genes with minimal compositional bias. *eLife* **7**, e36278.
- LEME, J. M., VAN ITEN, H. & SIMÕES, M. G. (2022). A new conulariid (Cnidaria, Scyphozoa) from the terminal Ediacaran of Brazil. *Frontiers in Earth Sciences* **10**, 77746.
- LI, D., ZHANG, X., HU, D., LI, D., ZHANG, G., ZHANG, X., LING, H.-F., XU, Y. & SHEN, Y. (2020a). Multiple S-isotopic constraints on paleo-redox and sulfate concentrations across the Ediacaran-Cambrian transition in South China. *Precambrian Research* **349**, 105500.
- LI, Z., CAO, M., LOYD, S. J., ALGEO, T. J., ZHAO, H., WANG, X., ZHAO, L. & CHEN, Z.-Q. (2020b). Transient and stepwise ocean oxygenation during the late Ediacaran Shuram Excursion: insights from carbonate $\delta^{238}\text{U}$ of northwestern Mexico. *Precambrian Research* **344**, 105741.
- LINNMANN, U., OVTCHAROVA, M., SCHALTEGGER, U., GÄRTNER, A., HAUTMANN, M., GEYER, G., VICKERS-RICH, P., RICH, T., PLESSEN, B., HOFMANN, M., ZIEGER, J., KRAUSE, R., KRIESFELD, L. & SMITH, J. (2019). New high-resolution age data from the Ediacaran–Cambrian boundary indicate rapid, ecologically driven onset of the Cambrian explosion. *Terra Nova* **31**(1), 49–58.
- LIU, A. G., MCLLOY, D. & BRASIER, M. D. (2010). First evidence for locomotion in the Ediacara biota from the 565 Ma Mistaken Point Formation, Newfoundland. *Geology* **38**(2), 123–126.
- MÁNGANO, M. G. & BUATOIS, L. A. (2017). The Cambrian revolutions: trace-fossil record, timing, links and geobiological impact. *Earth-Science Reviews* **173**, 96–108.
- MANUEL, M. (2009). Early evolution of symmetry and polarity in metazoan body plans. *Comptes Rendus Biologies* **332**(2–3), 184–209.
- MARSHALL, C. R. (2006). Explaining the Cambrian 'explosion' of animals. *Annual Review of Earth and Planetary Sciences* **34**, 355–384.
- MARTÍN-DURÁN, J. M. & HEJNOL, A. (2021). A developmental perspective on the evolution of the nervous system. *Developmental Biology* **475**, 181–192.
- MARTÍN-DURÁN, J. M., PANG, K., BØRVE, A., LÊ, H. S., FURU, A., CANNON, J. T., JONDELIUS, U. & HEJNOL, A. (2018). Convergent evolution of bilaterian nerve cords. *Nature* **553**(7686), 45–50.
- MARTINEZ, P. & SPRECHER, S. G. (2020). Of circuits and brains: the origin and diversification of neural architectures. *Frontiers in Ecology and Evolution* **8**, 82.
- MATSUZAKI, S. I. S., USIO, N., TAKAMURA, N. & WASHITANI, I. (2009). Contrasting impacts of invasive engineers on freshwater ecosystems: an experiment and meta-analysis. *Oecologia* **158**(4), 673–686.
- MCLLOY, D. & BRASIER, M. D. (2017). Ichnological evidence for the Cambrian explosion in the Ediacaran to Cambrian succession of Tanafjord, Finnmark, northern Norway. *Geological Society, London, Special Publications* **448**(1), 351–368.
- MCMAHON, W., LIU, A., TINDAL, B. & KLEINHANS, M. (2020). Ediacaran life close to land: coastal and shoreface habitats of the Ediacaran macrobiota in the central and southern Flinders Ranges, South Australia. *Journal of Sedimentary Research* **90**(11), 1463–1499.
- MCMENAMIN, M. A. (1986). The garden of Ediacara. *Palaios* **1**, 178–182.
- MEERT, J. G. & LIEBERMAN, B. S. (2008). The Neoproterozoic assembly of Gondwana and its relationship to the Ediacaran–Cambrian radiation. *Gondwana Research* **14**(1–2), 5–21.
- MEHRA, A. & MALOOF, A. (2018). Multiscale approach reveals that *Cloudina* aggregates are detritus and not in situ reef constructions. *Proceedings of the National Academy of Sciences* **115**(11), E2519–E2527.
- MENON, L. R., MCLLOY, D. & BRASIER, M. D. (2013). Evidence for Cnidaria-like behavior in ca. 560 Ma Ediacaran *Aspidella*. *Geology* **41**(8), 895–898.
- MENON, L. R., MCLLOY, D., LIU, A. G. & BRASIER, M. D. (2016). The dynamic influence of microbial mats on sediments: fluid escape and pseudofossil formation in the Ediacaran Longmyndian Supergroup, UK. *Journal of the Geological Society* **173**(1), 177–185.
- MITCHELL, E. G., BOBKOV, N., BYKOVA, N., DHUNGANA, A., KOLESNIKOV, A. V., HOGARTH, I. R., LIU, A. G., MUSTILL, T. M. R., SOZONOV, N., ROGOV, V. I., XIAO, S. & GRAZHANKIN, D. V. (2020). The influence of environmental setting on the community ecology of Ediacaran organisms. *Interface Focus* **10**(4), 20190109.
- MITCHELL, E. G., HARRIS, S., KENCHINGTON, C. G., VIXSEBOXSE, P., ROBERTS, L., CLARK, C., DENNIS, A., LIU, A. G. & WILBY, P. R. (2019). The importance of neutral over niche processes in structuring Ediacaran early animal communities. *Ecology Letters* **22**(12), 2028–2038.
- MUSCENTE, A. D., BOAG, T. H., BYKOVA, N. & SCHIFFBAUER, J. D. (2018). Environmental disturbance, resource availability, and biologic turnover at the dawn of animal life. *Earth-Science Reviews* **177**, 248–264.
- MUSCENTE, A. D., BYKOVA, N., BOAG, T. H., BUATOIS, L. A., MÁNGANO, M. G., ELEISH, A., PRABHU, A., PAN, F., MEYER, M. B., SCHIFFBAUER, J. D., FOX, P., HAZEN, R. M. & KNOLL, A. H. (2019). Ediacaran biozones identified with network analysis provide evidence for pulsed extinctions of early complex life. *Nature Communications* **10**(1), 911.
- NARBONNE, G. M. (2005). The Ediacara biota: Neoproterozoic origin of animals and their ecosystems. *Annual Review of Earth and Planetary Sciences* **33**, 421–442.
- NELSON, L. L., RAMEZANI, J., ALMOND, J. E., DARROCH, S. A., TAYLOR, W. L., BRENNER, D. C., FUREY, R. P., TURNER, M. & SMITH, E. F. (2022). Pushing the boundary: a calibrated Ediacaran–Cambrian stratigraphic record from the Nama Group in northwestern Republic of South Africa. *Earth and Planetary Science Letters* **580**, 117396.
- NIELSEN, C. (2019). Blastopore fate: amphistomy, protostomy or deuterostomy. In *eLS*. John Wiley & Sons Ltd, Chichester.
- NIELSEN, C., BRUNET, T. & ARENDT, D. (2018). Evolution of the bilaterian mouth and anus. *Nature Ecology & Evolution* **2**(9), 1358–1376.
- OJI, T., DORNOS, S. Q., YADA, K., HASEGAWA, H., GONCHIGDORJ, S., MOCHIZUKI, T., TAKAYANAGI, H. & IRYU, Y. (2018). Penetrative trace fossils from the late Ediacaran of Mongolia: early onset of the agronomic revolution. *Royal Society Open Science* **5**(2), 172250.
- PARK, T. Y. S., JUNG, J., LEE, M., LEE, S., ZHEN, Y. Y., HUA, H., WARREN, L. V. & HUGHES, N. C. (2021). Enduring evolutionary embellishment of cloudinids in the Cambrian. *Royal Society Open Science* **8**(12), 210829.
- PARRY, L. A., BOGGIANI, P. C., CONDON, D. J., GARWOOD, R. J., LEME, J. D. M., MCLLOY, D., BRASIER, M. D., TRINIDADE, R., CAMPANHA, G. A. C., PACHECO, M. L. A. F., DINIZ, C. Q. C. & LIU, A. G. (2017). Ichnological evidence for meiofaunal bilaterians from the terminal Ediacaran and earliest Cambrian of Brazil. *Nature Ecology & Evolution* **1**(10), 1455–1464.

- PATERSON, J. R., GEHLING, J. G., DROSER, M. L. & BICKNELL, R. D. (2017). Rheotaxis in the Ediacaran epibenthic organism *Parvancorina* from South Australia. *Scientific Reports* **7**(1), 1–9.
- PENNY, A. M., WOOD, R., CURTIS, A., BOWYER, F., TOSTEVIN, R. & HOFFMAN, K. H. (2014). Ediacaran metazoan reefs from the Nama Group, Namibia. *Science* **344**(6191), 1504–1506.
- PISANI, D., PETT, W., DOHRMANN, M., FEUDA, R., ROTA-STABELLI, O., PHILIPPE, H., LARTILLOT, N. & WÖRHEIDE, G. (2015). Genomic data do not support comb jellies as the sister group to all other animals. *Proceedings of the National Academy of Sciences* **112**(50), 15402–15407.
- RAHMAN, I. A., DARROCH, S. A., RACICOT, R. A. & LAFLAMME, M. (2015). Suspension feeding in the enigmatic Ediacaran organism *Tribrachidium* demonstrates complexity of Neoproterozoic ecosystems. *Science Advances* **1**(10), e1500800.
- RAUP, D. M. & SEPKOSKI, J. J. JR. (1982). Mass extinctions in the marine fossil record. *Science* **215**(4539), 1501–1503.
- RHOADS, D. C. & YOUNG, D. K. (1970). The influence of deposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research* **28**, 150–178.
- ROBERTSON, D. S., LEWIS, W. M., SHEEHAN, P. M. & TOON, O. B. (2013). K-Pg extinction patterns in marine and freshwater environments: the impact winter model. *Journal of Geophysical Research: Biogeosciences* **118**(3), 1006–1014.
- ROONEY, A. D., CANTINE, M. D., BERGMANN, K. D., GÓMEZ-PÉREZ, I., AL BALOUSHI, B., BOAG, T. H., BUSCH, J. F., SPERLING, E. A. & STRAUSS, J. V. (2020). Calibrating the coevolution of Ediacaran life and environment. *Proceedings of the National Academy of Sciences* **117**(29), 16824–16830.
- RUNNEGAR, B. (2022). Following the logic behind biological interpretations of the Ediacaran biotas. *Geological Magazine* **159**(7), 1093–1117.
- SAHNEY, S. & BENTON, M. J. (2008). Recovery from the most profound mass extinction of all time. *Proceedings of the Royal Society B: Biological Sciences* **275**(1636), 759–765.
- SAHOO, S. K., PLANAVSKY, N. J., JIANG, G., KENDALL, B., OWENS, J. D., WANG, X., SHI, X., ANBAR, A. D. & LYONS, T. W. (2016). Oceanic oxygenation events in the anoxic Ediacaran Ocean. *Geobiology* **14**(5), 457–468.
- SAUCÈDE, T., MOOI, R. & DAVID, B. (2003). Combining embryology and paleontology: origins of the anterior-posterior axis in echinoids. *Comptes Rendus Palevol* **2**(6–7), 399–412.
- SAVAZZI, E. (2012). A reassessment of the lower Cambrian psammocoral *Spatangopsis costata*. *Paleontological Research* **16**(2), 159–170.
- SCHIFFBAUER, J. D. (2022). Paleontology: Paleogastronomy in the Ediacaran. *Current Biology* **32**(4), R1343–R1345.
- SCHIFFBAUER, J. D., HUNTLEY, J. W., O'NEIL, G. R., DARROCH, S. A., LAFLAMME, M. & CAI, Y. (2016). The latest Ediacaran Wormworld fauna: setting the ecological stage for the Cambrian Explosion. *GSA Today* **26**(11), 4–11.
- SCHULTZ, D. T., HADDOCK, S. H., BREDESON, J. V., GREEN, R. E., SIMAKOV, O. & ROKHSAR, D. S. (2023). Ancient gene linkages support ctenophores as sister to other animals. *Nature* **618**, 110–117.
- SEILACHER, A. (1989). Vendozoa: organismic construction in the Proterozoic biosphere. *Lethaia* **22**(3), 229–239.
- SELLY, T., SCHIFFBAUER, J. D., JACQUET, S. M., SMITH, E. F., NELSON, L. L., ANDREASEN, B. D., HUNTLEY, J. W., STRANGE, M. A., O'NEIL, G. R., THATER, C. A., BYKOVA, N., STEINER, M., YANG, B. & CAI, Y. (2020). A new cloudinid fossil assemblage from the terminal Ediacaran of Nevada, USA. *Journal of Systematic Palaeontology* **18**(4), 357–379.
- SHEN, B., DONG, L., XIAO, S. & KOWALEWSKI, M. (2008). The Avalon explosion: evolution of Ediacara morphospace. *Science* **319**(5859), 81–84.
- SHU, D. G., CONWAY MORRIS, S., HAN, J., LI, Y., ZHANG, X. L., HUA, H., ZHANG, Z.-F., LIU, J.-N., GUO, J.-F., YAO, Y. & YASUI, K. (2006). Lower Cambrian vendobionts from China and early diploblast evolution. *Science* **312**(5774), 731–734.
- SILVA, F. B. D., MUSCHNER, V. C. & BONATTO, S. L. (2007). Phylogenetic position of placozoa based on large subunit (LSU) and small subunit (SSU) rRNA genes. *Genetics and Molecular Biology* **30**, 127–132.
- SPERLING, E. A. & VINTNER, J. (2010). A placozoan affinity for Dickinsonia and the evolution of late Proterozoic metazoan feeding modes. *Evolution & Development* **12**(2), 201–209.
- SUAREZ, P. A. & LEYS, S. P. (2022). The sponge pump as a morphological character in the fossil record. *Paleobiology* **48**, 446–461.
- TARHAN, L. G., DROSER, M. L., COLE, D. B. & GEHLING, J. G. (2018). Ecological expansion and extinction in the late Ediacaran: weighing the evidence for environmental and biotic drivers. *Integrative and Comparative Biology* **58**(4), 688–702.
- TARHAN, L. G., DROSER, M. L., GEHLING, J. G. & DZAUGIS, M. P. (2015). Taphonomy and morphology of the Ediacara form genus *Aspidella*. *Precambrian Research* **257**, 124–136.
- TARHAN, L. G., MYROW, P. M., SMITH, E. F., NELSON, L. L. & SADLER, P. M. (2020). Infaunal augurs of the Cambrian explosion: an Ediacaran trace fossil assemblage from Nevada, USA. *Geobiology* **18**(4), 486–496.
- TOPPER, T., BETTS, M. J., DORJNAMJAA, D., LI, G., LI, L., ALTANSHAGAI, G., ENKHBAATAR, B. & SKOVSTED, C. B. (2022). Locating the BACE of the Cambrian: Bayan Gol in southwestern Mongolia and global correlation of the Ediacaran–Cambrian boundary. *Earth-Science Reviews* **229**, 104017.
- TOSTEVIN, R., CLARKSON, M. O., GANGL, S., SHIELDS, G. A., WOOD, R. A., BOWYER, F., PENNY, A. M. & STIRLING, C. H. (2019). Uranium isotope evidence for an expansion of anoxia in terminal Ediacaran oceans. *Earth and Planetary Science Letters* **506**, 104–112.
- TURK, K. A., MALONEY, K. M., LAFLAMME, M. & DARROCH, S. A. (2022). Paleontology and ichnology of the late Ediacaran Nasep–Huns transition (Nama Group, southern Namibia). *Journal of Paleontology* **96**(4), 753–769.
- TYRRELL, T. (1999). The relative influences of nitrogen and phosphorus on oceanic primary production. *Nature* **400**(6744), 525–531.
- VAN DE VELDE, S., MILLS, B. J., MEYSMAN, F. J., LENTON, T. M. & POULTON, S. W. (2018). Early Palaeozoic Ocean anoxia and global warming driven by the evolution of shallow burrowing. *Nature Communications* **9**(1), 1–10.
- VANNIER, J., CALANDRA, I., GAILLARD, C. & ŻYLIŃSKA, A. (2010). Priapulid worms: pioneer horizontal burrowers at the Precambrian–Cambrian boundary. *Geology* **38**(3), 711–714.
- VAZIRI, S. H., MAJIDIFARD, M. R. & LAFLAMME, M. (2018). Diverse assemblage of Ediacaran fossils from Central Iran. *Scientific Reports* **8**(1), 5060.
- VICKERS-RICH, P., IVANTSOV, A. Y., TRUSLER, P. W., NARBONNE, G. M., HALL, M., WILSON, S. A., GREENTREE, C., FEDONKIN, M. A., ELLIOTT, D. A., HOFFMANN, K. H. & SCHNEIDER, G. I. (2013). Reconstructing Ranges: new discoveries from the Ediacaran of southern Namibia. *Journal of Paleontology* **87**(1), 1–15.
- WAGGONER, B. (2003). The Ediacaran biotas in space and time. *Integrative and Comparative Biology* **43**(1), 104–113.
- WAINWRIGHT, S. A. (1988). *Axis and Circumference*. Harvard University Press, Cambridge.
- WANG, X. P., CHEN, Z., PANG, K., ZHOU, C. M., XIAO, S., WAN, B. & YUAN, X. L. (2021). Dickinsonia from the Ediacaran Dengying formation in the Yangtze gorges area, South China. *Palaeworld* **30**(4), 602–609.
- WARREN, L. V., QUAGLIO, F., SIMÕES, M. G., GAUCHER, C., RICCOMINI, C., POIRÉ, D. G., FREITAS, B. T., BOGGIANI, P. C. & SIAL, A. N. (2017). *Cloudina-Corumbella-Namacalathus* association from the Itapucumi Group, Paraguay: increasing ecosystem complexity and tiering at the end of the Ediacaran. *Precambrian Research* **298**, 79–87.
- WEBER, B., STEINER, M. & ZHU, M. Y. (2007). Precambrian–Cambrian trace fossils from the Yangtze platform (South China) and the early evolution of bilaterian lifestyles. *Palaogeography, Palaeoclimatology, Palaeoecology* **254**(12), 328–349.
- WEI, W., CHEN, X., LING, H. F., WU, F., DONG, L. H., PAN, S., JING, Z. & HUANG, F. (2023). Vanadium isotope evidence for widespread marine oxygenation from the late Ediacaran to early Cambrian. *Earth and Planetary Science Letters* **602**, 117942.
- WHELAN, N. V., KOCOT, K. M. & HALANYCH, K. M. (2015). Employing phylogenomics to resolve the relationships among cnidarians, ctenophores, sponges, placozoans, and bilaterians. *Integrative and Comparative Biology* **55**(6), 1084–1095.
- WOOD, R. & CURTIS, A. (2015). Extensive metazoan reefs from the Ediacaran Nama Group, Namibia: the rise of benthic suspension feeding. *Geobiology* **13**(2), 112–122.
- WOOD, R., LIU, A. G., BOWYER, F., WILBY, P. R., DUNN, F. S., KENCHINGTON, C. G., HOYAL CUTHILL, J. F., MICHELL, E. G. & PENNY, A. (2019). Integrated records of environmental change and evolution challenge the Cambrian Explosion. *Nature Ecology & Evolution* **3**(4), 528–538.
- WOOD, R. & ZHURAVLEV, A. Y. (2012). Escalation and ecological selectivity of mineralogy in the Cambrian radiation of skeletons. *Earth-Science Reviews* **115**(4), 249–261.
- XIANG, L., SCHOEPPER, S. D., ZHANG, H., CAO, C. Q. & SHEN, S. Z. (2018). Evolution of primary producers and productivity across the Ediacaran–Cambrian transition. *Precambrian Research* **313**, 68–77.
- XIAO, S., CHEN, Z., PANG, K., ZHOU, C. & YUAN, X. (2021). The Shibantan Lagerstätte: insights into the Proterozoic–Phanerozoic transition. *Journal of the Geological Society* **178**(1), jgs2020-135.
- YANG, B., STEINER, M., ZHU, M., LI, G., LIU, J. & LIU, P. (2016). Transitional Ediacaran–Cambrian small skeletal fossil assemblages from South China and Kazakhstan: implications for chronostratigraphy and metazoan evolution. *Precambrian Research* **285**, 202–215.

- YANG, C., ROONEY, A. D., CONDON, D. J., LI, X. H., GRAZHDANKIN, D. V., BOWYER, F. T., HU, C., MACDONALD, F. A. & ZHU, M. (2021). The tempo of Ediacaran evolution. *Science Advances* **7**(45), eabi9643.
- YANG, Q., MA, J., SUN, X. & CONG, P. (2007). Phylochronology of early metazoans: combined evidence from molecular and fossil data. *Geological Journal* **42**(3–4), 281–295.
- ZHANG, F., XIAO, S., ROMANIELLO, S. J., HARDISTY, D., LI, C., MELEZHIK, V., POKROVSKY, B., CHENG, M., SHI, W., LENTON, T. M. & ANBAR, A. D. (2019). Global marine redox changes drove the rise and fall of the Ediacara biota. *Geobiology* **17**(6), 594–610.
- ZHAO, Y., VINTHER, J., LI, Y. J., WEI, F., HOU, X. G. & CONG, P. (2022). An early Cambrian mackenziiid reveals links to modular Ediacaran macro-organisms. *Papers in Palaeontology* **8**(1), e1412.
- ZHU, M., LU, M., ZHANG, J., ZHAO, F., LI, G., AIHUA, Y., ZHAO, X. & ZHAO, M. (2013). Carbon isotope chemostratigraphy and sedimentary facies evolution of the Ediacaran Doushantuo formation in western Hubei, South China. *Precambrian Research* **225**, 7–28.
- ZHURAVLEV, A. Y. & WOOD, R. A. (2018). The two phases of the Cambrian Explosion. *Scientific Reports* **8**(1), 1–10.

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