



Palaeolatitudinal distribution of the Ediacaran macrobiota


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Abstract: Macrofossils of the late Ediacaran Period (*c.* 579–539 Ma) document diverse, complex multicellular eukaryotes, including early animals, prior to the Cambrian radiation of metazoan phyla. To investigate the relationships between environmental perturbations, biotic responses and early metazoan evolutionary trajectories, it is vital to distinguish between evolutionary and ecological controls on the global distribution of Ediacaran macrofossils. The contributions of temporal, palaeoenvironmental and lithological factors in shaping the observed variations in assemblage taxonomic composition between Ediacaran macrofossil sites are widely discussed, but the role of palaeogeography remains ambiguous. Here we investigate the influence of palaeolatitude on the spatial distribution of Ediacaran macrobiota through the late Ediacaran Period using two leading palaeogeographical reconstructions. We find that overall generic diversity was distributed across all palaeolatitudes. Among specific groups, the distributions of candidate ‘Bilateral’ and Frondomorph taxa exhibit weakly statistically significant and statistically significant differences between low and high palaeolatitudes within our favoured palaeogeographical reconstruction, respectively, whereas Algal, Tubular, Soft-bodied and Biomineralizing taxa show no significant difference. The recognition of statistically significant palaeolatitudinal differences in the distribution of certain morphogroups highlights the importance of considering palaeolatitudinal influences when interrogating trends in Ediacaran taxon distributions.

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The Ediacaran macrobiota evidence a diverse assortment of macroscopic organisms that occupied the global oceans during the *c.* 40 myr interval prior to the Phanerozoic Eon (*c.* 579–539 Ma; e.g. Xiao and Laflamme 2009). The fossils document protists, algae, bacterial colonies and the first recognizable animals (e.g. Fedonkin *et al.* 2007; Grazhdankin and Gerdes 2007; Liu *et al.* 2014; Bobrovskiy *et al.* 2018*a, b*; Kolesnikov *et al.* 2018; Xiao *et al.* 2020) and yield evidence for ecological innovations, including metazoan-grade surface locomotion (e.g. Ivantsov and Malakhovskaya 2002; Liu *et al.* 2010), grazing (Ivantsov 2013), predation (Hua *et al.* 2003), sexual reproduction (Droser and Gehling 2008; Mitchell *et al.* 2015), macroscopic skeletonization/biomineralization (e.g. Wood 2018) and shallow burrowing (e.g. Chen *et al.* 2019; Xiao *et al.* 2019). Understanding late Ediacaran evolutionary drivers is therefore crucial in studies of early animal evolution.

Despite challenges in determining the precise phylogenetic position of many Ediacaran taxa (summarized in Dunn and Liu 2019), considerable progress has been made in investigating patterns in the temporal and environmental distribution of Ediacaran macrofossils. Global-scale studies have recognized distinct biotic assemblages within the Ediacaran macrobiota (Waggoner 2003; Boag *et al.* 2016; Muscente *et al.* 2019). These – the Avalon, White Sea, Nama and, most recently, Miaohé assemblages – are frequently discussed in publications exploring the evolutionary and ecological trajectories of organisms, and their underlying drivers, across the Ediacaran–Cambrian transition (e.g. Darroch *et al.* 2018; Wood *et al.* 2019). Although the

constitution of these biotic assemblages appears robust, even when updated with recent fossil discoveries (Boag *et al.* 2016; Muscente *et al.* 2019), the relative influence of the underlying factors shaping their spatial and temporal distribution remain unresolved.

On a local to regional scale, there is compelling evidence for an association between certain Ediacaran macrofossil taxa and specific shallow marine facies (e.g. Grazhdankin 2004; Gehling and Droser 2013; Reid *et al.* 2020). Furthermore, redox conditions are recognized to control the presence or absence of fossils – and, by inference, the original organisms – within some successions (Hall *et al.* 2013; Wood *et al.* 2015; Cui *et al.* 2016; Sperling *et al.* 2016; Tostevin *et al.* 2016; Bowyer *et al.* 2020), while the degree of water column stratification, and/or salinity, can also be correlated to the occurrence of particular fossils, within some localities (Duda *et al.* 2020). Together, these findings suggest that palaeoenvironmental conditions exerted a strong control on the composition and ecology of shallow marine Ediacaran macrofossil assemblages. The broad-scale community ecology of deeper water Ediacaran palaeocommunities has been shown to be more resistant to local variations in the palaeoenvironment (Mitchell and Kenchington 2018; Mitchell *et al.* 2019) than that of shallow water communities (Mitchell *et al.* 2020).

Radiometric dating appears to support a broad temporal pattern in the distribution of biotic assemblages, with the Avalon assemblage (*c.* 574–556 Ma; Noble *et al.* 2015; Rooney *et al.* 2020; Matthews *et al.* 2021) being older than the White Sea (*c.* 558–550 Ma; Martin *et al.* 2000) and Nama (<550 Ma; e.g. Narbonne *et al.* 1997) assemblages, although some overlap is recognized (Boag *et al.*

2016). This temporal pattern raises the possibility that the biotic assemblages record a broad-scale evolutionary trajectory (e.g. [Grazhdankin 2014](#)), which, in turn, implies that transitions between each assemblage may reflect evolutionary events – for example, an ecological ‘second wave’ ([Droser *et al.* 2017](#)) or a late Ediacaran mass extinction (e.g. [Laflamme *et al.* 2013](#); [Darroch *et al.* 2015, 2018](#)). Still other suggestions have proposed that taphonomic modes may exert some control over fossil assemblage compositions on a global ([Narbonne 2005](#)) or local ([Narbonne *et al.* 2014](#)) scale.

The position of continental land masses shaped the distribution of benthic marine taxa in both the modern and Phanerozoic oceans – for example, by influencing the location of provincial faunas, latitudinal biodiversity gradients, and the tempo and mode of biotic recoveries following mass extinctions (e.g. [Valentine and Moores 1972](#); [Whittington and Hughes 1972](#); [Mannion *et al.* 2014](#); [Saupe *et al.* 2020](#)). Furthermore, palaeogeography exerts a first-order control on ocean circulation (and thus local redox conditions; e.g. [Bowyer *et al.* 2017](#)) and weathering fluxes ([Godd ris *et al.* 2014](#)), both of which are known to affect the global spatial distribution and composition of biotic communities (e.g. [Saupe *et al.* 2020](#)). The relationship between palaeogeography and late Ediacaran fossil distributions has been contemplated by a number of researchers ([McMenamin 1982](#); [Waggoner 1999, 2003](#); [Meert and Lieberman 2008](#); [Laflamme *et al.* 2013](#); [Zakrevskaya 2019](#)), who have approached the topic in a variety of different ways. Some workers have attempted to utilize the modern geographical distribution of the Ediacaran macrobiota to constrain past palaeogeographical reconstructions (e.g. [Waggoner 1999](#); [Meert and Lieberman 2008](#); [Zakrevskaya 2019](#); although notably not [Waggoner 2003](#)), based on assumptions that similar taxonomic assemblages would have been geographically closely spaced, or that biomineralizers were likely to have favoured low, warmer palaeolatitudes. Attempts to tackle the inverse problem – using palaeogeographical knowledge to provide insights into the distribution and potential evolutionary trajectories of Ediacaran taxa – are complicated by considerable uncertainty regarding late Neoproterozoic palaeogeographical reconstructions (e.g. [Meridith *et al.* 2017](#); [Evans 2020](#)). However, to draw quantitative comparisons between the competing influences of tectonics, palaeogeography, environment and evolution on observed Ediacaran biotic assemblages, we must consider this palaeogeographical approach.

Discussions regarding the relative importance of age, palaeo-environment (including water depth and sedimentary environment), palaeogeography and lithology/taphonomy in dictating the distribution of Ediacaran macrofossils have tended to favour evolutionary and environmental processes as the dominant controls on assemblage composition ([Laflamme *et al.* 2013](#); [Grazhdankin 2014](#); [Boag *et al.* 2016](#); [Muscente *et al.* 2019](#)). However, these studies generally agree that (1) these factors are not mutually exclusive and (2) attempts to determine the relative influence of different factors are hindered by the uneven global coverage of available well-dated fossil-bearing sections. Previous studies have considered the influence of palaeogeography on broad-scale Ediacaran morphogroups ([Laflamme *et al.* 2013](#)), but by grouping localities within the aforementioned biotic assemblages (effectively viewing them as evolutionary biozones), they are unable to deconvolve palaeogeographical and evolutionary signals.

There has been no previous attempt to explore the palaeolatitudinal distribution of Ediacaran macrofossils quantitatively from the perspective of trying to identify and test the global spatial patterns of evolutionary trajectories. Acknowledging the problems inherent with attempting to reconstruct past global biodiversity patterns from irregularly sampled fossil sites (e.g. [Vilhena and Smith 2013](#)), we here compile a comprehensive database of the known spatial and temporal occurrence of global late Ediacaran macrofossils. We analyse our data using two prominent palaeogeographical reconstructions for the late Ediacaran to investigate the broad-scale

palaeolatitudinal influence on the distribution of the Ediacaran macrobiota.

Materials and methods

Data collation

Data for 167 Ediacaran macrofossil genera that fulfilled certain criteria were compiled from 31 modern fossil localities ([Fig. 1, Supplementary File 2](#)). Microfossil taxa, taphomorphs and simple radial impressions were excluded (see [Supplementary File 1](#) for details of taxon selection). For each genus, we recorded the age range (compiled from consideration of the ages of all the global sections in which the taxon occurs), the original ‘composition’ (i.e. biomineralized, organic-walled, agglutinated or soft-bodied), the morphogroup (expanding the scheme outlined in the supplementary information of [Erwin *et al.* 2011](#); see also [Laflamme *et al.* 2013](#)), and a broader morphogroup/clade ‘Type’ (defined as Algal, Bilateral, Radial, Frondomorph, Erniettomorph, Protist, Tubular, Miscellaneous) (see [Supplementary File 1](#) for further details). For the ‘Type’, we consider the bilateral symmetry of *Dickinsonia* specimens from South Australia (e.g. [Gold *et al.* 2015](#); [Evans *et al.* 2017](#)) to justify classification of the Dickinsoniomorpha as ‘Bilateral’ in this study (although see [Ivantsov *et al.* 2020](#) for alternative views; [Supplementary File 1](#)). Our Bilateral ‘Type’ grouping therefore consists of genera assigned to the Bilateralomorpha, Dickinsoniomorpha and Kimberellomorpha morphogroups. We recognize that some of these groups may include phylogenetically disparate lineages and so we are mindful that trends arising from them are interpreted with this phylogenetic disparity in mind.

To focus on temporal trends rather than the Avalon, White Sea, Nama and Miaohu biotic assemblages identified by previous studies, we assessed the taxa within 10 myr time bins of >581, 580–571, 570–561, 560–551 and 550–539 Ma (the latter being slightly longer to encompass recently revised radiometric dates from terminal Ediacaran sections; [Linnemann *et al.* 2019](#)).

Palaeogeographical reconstructions

There remains much debate surrounding the palaeogeographical position of major Precambrian cratons during the Ediacaran Period (e.g. [Pisarevsky *et al.* 2008](#); [Meridith *et al.* 2017](#)). Palaeogeographical reconstructions rely heavily on several assumptions, including that Neoproterozoic plate tectonic systems operated as they do in the modern day ([Evans 2003](#); [Stern 2018](#)). They also draw on different data types in their construction, including geological, kinematic and palaeomagnetic data. Several previous studies addressing Ediacaran macrofossil distributions and palaeogeography have sought to plot fossil distributions on a range of competing palaeogeographical reconstructions to identify those reconstructions that are most consistent with the assumed palaeobiological preconceptions. Although this approach has precedent, it carries considerable risk of circular reasoning when attempting to interpret the controls on fossil distribution. Other studies have simply chosen well-cited palaeogeographical reconstructions (e.g. those of [Scotese 2001](#); [Smith 2001](#); or [Li *et al.* 2013](#)), often without explicit explanation of why those reconstructions were chosen over the alternatives.

There are two broad categories of palaeogeographical reconstructions: continental drift style models and full-plate tectonic models (see [Meridith *et al.* 2021](#) for an overview). Continental drift style reconstructions only model the kinematic evolution of the continental crust, whereas full-plate tectonic models, in addition to the motion of continents, also explicitly model the evolution of plate boundaries and tectonic plates through time. Both categories

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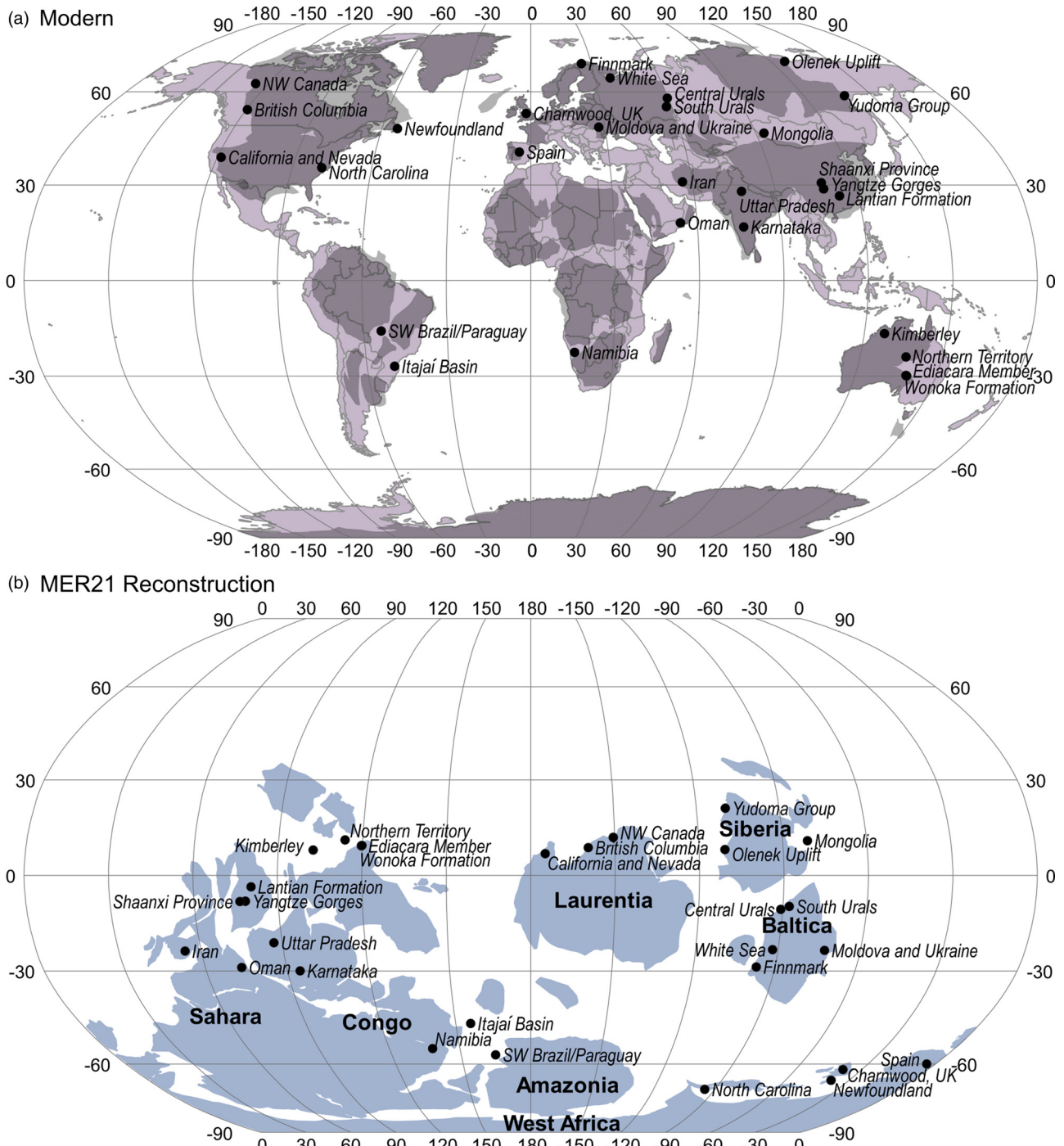


Fig. 1. Precambrian cratons (bold text) and the locations of Ediacaran fossil sites included in this study (italic text) plotted on (a) the modern global map (cratons shaded) and (b) the *Meredith et al. (2021)* palaeogeographical reconstruction at 555 Ma.

of model are underpinned by similar data types representing different lines of evidence, with the significance of each line dependent on the time being modelled. For example, during the Mesozoic and Cenozoic the seafloor spreading history of the ocean basins and hotspot tracks are the principal controls on plate motion (e.g. *Seton et al. 2012*). In the pre-Jurassic (including our study period, the Ediacaran), the emphasis is, by contrast, on the palaeomagnetic and geological record preserved on continents, including data such as the metamorphic history of orogens, the inception ages of rift basins, and the ages and geochemical make-up of dykes and volcanic rocks emblematic of arc assemblages (e.g. *Domeier and Torsvik 2019*).

Palaeomagnetic data are used in both categories of model to constrain the drift and absolute (latitudinal) position of continents at

each time step. Comparably, geological data are used to constrain key tectonic events, such as ocean basin opening and closure, and terrane migration. However, the constant recycling and reworking of the Earth's lithosphere invites competing interpretations of the data that become more prevalent as we move further back in time, when there is both less data and no effective method to constrain the absolute palaeolongitude. Contradictory palaeomagnetic data in the Ediacaran (e.g. *Abrajevitch and Van der Voo 2010*) have led to hypotheses suggesting that an equatorial magnetic field was present and recorded within some rocks or, alternatively, large-scale true polar wander occurred during this time period.

The key difference between the continental drift and full-plate models is that, in the latter, the geological data are explicitly modelled in the form of plate boundaries, whereas in the former they

are used to inform decisions without being explicitly modelled. Because the geological data are explicitly modelled in full-plate reconstructions, models within this category must fully integrate both geological and palaeomagnetic data into a self-consistent framework that is congruent with the basic principles of plate tectonics (Gurnis *et al.* 2012). Although this integration is possible within continental drift style models, it is not explicitly demonstrated by them.

We use two models in our analysis: one continental drift and one full-plate reconstruction. Our favoured reconstruction is presented in Merdith *et al.* (2021), hereon referred to as the MER21 reconstruction. The MER21 reconstruction is a full-plate reconstruction from 1 Ga to the present day, meaning that it explicitly defines plate boundaries and tectonic plates. As a result of uncertainties within the literature surrounding continent positions during the Ediacaran (e.g. Pisarevsky *et al.* 2008), we have also plotted all our data on the widely used model of Scotese (2001) (hereafter SCO01) (Supplementary Figs 13–22). The SCO01 reconstruction is a continental drift model that has been used in Phanerozoic and Ediacaran studies investigating ancient biodiversity and palaeogeographical distributions (e.g. Opdyke and Wilkinson 1990; Laflamme *et al.* 2013; Saupe *et al.* 2020). There are few first-order differences between the two models from the late Paleozoic to the present day; however, the differences are more evident in the Ediacaran (see Supplementary Fig. 1) and are driven primarily by the selection of different palaeomagnetic data between the two models (cf. Pisarevsky *et al.* 2008). Importantly, both the MER21 and SCO01 models omit contradictory palaeomagnetic poles from their analysis and do not infer true polar wander during this time. Plotting our data on both the MER21 and SCO01 models allows us to compare our findings between them and to consider the level of confidence we can place in the observed patterns.

Data processing and analysis

Each locality was plotted onto a modern world map in QGIS (Fig. 1a). These points were then exported to the GPlates software package (www.gplates.org; Müller *et al.* 2018), which was used to extract continent configurations and localities for both the MER21 and SCO01 models halfway through each of our time bins for analysis (i.e. at 575, 565, 555 and 545 Ma) (Fig. 1b; Supplementary Fig. 1b, c).

Data were extracted from the database and plotted against the coordinates in QGIS to allow data visualization and the exploration of both temporal trends and patterns in individual morphogroup distributions over the entire late Ediacaran interval (for our code, see Supplementary File 3). The plot for 555 Ma was chosen to visualize data pertaining to the whole interval (>581–539 Ma) because most of the taxa are found in the latter half of the late Ediacaran and thus the craton and terrane placement at 555 Ma is representative of the majority of the data presented. The environmental setting (dominant lithology and nearshore v. offshore depositional environment) was also documented for each locality.

Hierarchical cluster analysis was performed using R and the package *ape* (Paradis and Schliep 2018) to produce a dendrogram showing the similarity in genus-level assemblage composition between localities with more than six genera (this number was chosen to optimize support for measures of similarity; Supplementary Fig. 23). The *hclust* function was used to perform average-linkage clustering (following Boag *et al.* 2016). Cophenetic correlation was used to test whether the dendrogram provided a reliable interpretation of the observed data.

Palaeolatitudes were divided into two 45° bands for statistical tests to ensure both that the errors in palaeolatitude were smaller than the bins, and that sufficient sample sizes could be acquired to perform statistical analyses (with one exception: overall taxa

against localities, where 20° bands provided sufficient sample sizes). χ^2 tests, which take into account non-uniform sampling between groups, were used to assess differences in taxon distribution between the low and high palaeolatitudinal bins. We divided the same data into 20° palaeolatitudinal bands when plotting our data as graphs to aid data visualization. Kruskal–Wallis statistical tests were used to assess the temporal trends alongside the plots, comparing the distribution of sites with the distribution of taxonomic diversity through time (following Chiarenza *et al.* 2019).

Results

The results described in this section refer to the distribution of Ediacaran macrofossils in the MER21 reconstruction unless stated otherwise. Discussion of the results plotted on the SCO01 reconstruction, as well as comparisons with the MER21 results, can be found in Supplementary File 1. Although we only discuss distributions by Types (broad groupings of taxa; see Methods and Supplementary File 1) in the main text, figures showing the distribution of taxa arranged within the more granular morphogroups are presented in Supplementary Figures 5, 7 and 8.

Overall diversity through time

The distribution of fossil Types through time (Fig. 2) reveals very low taxonomic diversity in the oldest (pre-581 Ma) time bin (just two recognizable Types – Algal and Protist – alongside members of the Miscellaneous group), spread across two localities located at broadly equatorial latitudes (the Lantian Formation and Kimberley; pie charts with bold green rims in the top left reconstruction in Fig. 2). In the next 10 myr interval (580–571 Ma), three different localities (the Nadaleen Formation, NW Canada, Finnmark and Newfoundland) include taxa belonging to two new Types (Frondomorphs, which dominate, and Tubular taxa, represented by recently described putative SiO₂ biomineralizing tubular taxa from Finnmark; Moczydłowska *et al.* 2021), as well as a putative member of the ‘Sponge’ morphogroup (*Thectardis*; Sperling *et al.* 2011). The positioning of these localities implies that Frondomorphs and protistan forms are found across low (<45°) and high (>45°) palaeolatitudes by this time.

Between 570 and 561 Ma, taxonomic diversity in Avalonia (Charnwood, UK, and Newfoundland) increases (from 10 to 25 genera), with the first record of taxa representative of the ‘Cnidarian’ morphogroup (Liu *et al.* 2014), although Frondomorphs continue to dominate the distribution at those sites. The two low-latitude sites reported within this time bin (the Itajaí Basin and the Wonoka Formation of South Australia) both currently exhibit a very low diversity biota (one taxon, the likely protist *Palaeopascichnus*; Antcliffe *et al.* 2011).

Between 560 and 551 Ma, the diversity of both Types and genera increases dramatically (from 25 to 110 genera), with a corresponding increase in the number of localities (from four to 13; Supplementary Figs 3 and 4). This increase primarily occurs at lower palaeolatitudes (which exhibit 107 taxa across 11 localities), while higher palaeolatitudes remain less diverse (eight taxa across two localities; Fig. 2, inset, and Fig. 3; Supplementary Fig. 6). All eight assessed fossil Types are found during this interval and no single group appears to have been proportionally dominant. Several neighbouring sites in close palaeogeographical proximity have markedly different patterns of diversity, such as the Ediacara Member and the Northern Territories in Australia, possibly due to different environmental and preservational conditions (Boag *et al.* 2016; Muscente *et al.* 2018), or variations in the extent of the outcrop area that has been subjected to palaeobiological investigation (Allison and Briggs 1993).

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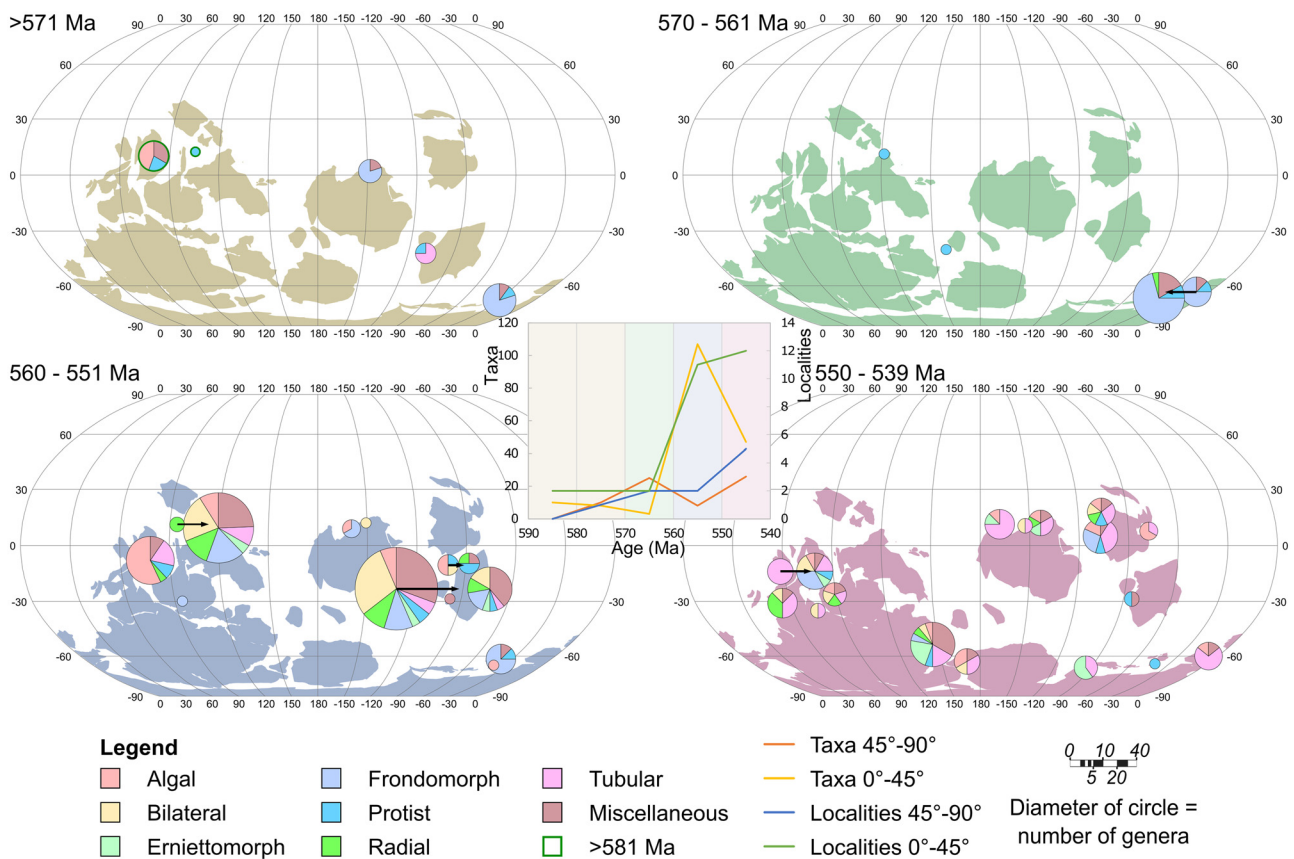


Fig. 2. Distribution of fossil Types with each locality presented as a pie chart centred on its palaeolocation (black arrows indicate the palaeolocation for instances where the pie charts have been moved to avoid overlap with neighbouring sites) and each palaeogeographical map plotted at the mid-point of each time bin (Precambrian cratons are colour-coded for each bin). Pie charts are scaled to represent the number of genera within each Type, with the circle area equivalent to the total number of genera at each locality. Inset: graph comparing the distribution of Ediacaran fossil sites within two latitudinal bands (high and low latitude) with the distribution of taxa throughout the late Ediacaran in each latitudinal band. The ‘second wave’ ecological radiation of macrofossil taxa (Droser *et al.* 2017) appears as a significant increase in taxonomic diversity at low latitudes (yellow line) at *c.* 560 Ma. However, this increase is coupled with a significant increase in the number of documented fossil localities at low latitudes (green line). The apparent difference in the magnitude of this ‘radiation’ at high and low latitudes may therefore be a function of the increased availability of exposure of that age. Conversely, the dip in generic diversity observed at *c.* 550 Ma is coupled with a further increase in the number of low-latitude localities available. However, the decrease in diversity is not significant enough to be statistically distinguished as a true biotic signal (Table 1). A weakly significant Kruskal–Wallis result is observed when comparing high-latitude taxa against high-latitude localities; $p = 0.093$ (Table 1).

In the final *c.* 10 myr of the Ediacaran Period, the diversity of the macrobiota decreases to 60 taxa, despite an increase in the number of sampled localities to 17 (Fig. 2, inset; Supplementary Figs 3–4).

This apparent dip in generic diversity (consistent with Laflamme *et al.* 2013; Darroch *et al.* 2015; Muscente *et al.* 2018) appears to be restricted to lower palaeolatitudes, despite these regions actually

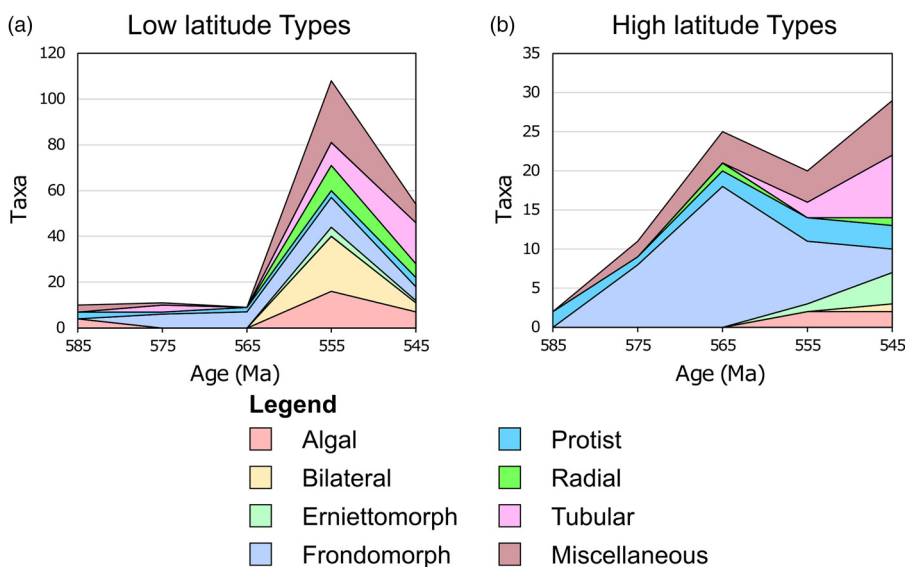


Fig. 3. Stacked area chart showing the variation in overall Ediacaran macrobiota generic diversity by Type at (a) low and (b) high palaeolatitudes through the late Ediacaran on the MER21 reconstruction. The apparent dip in diversity in the final time bin is observed at low, but not high, palaeolatitudes. Bilateral Type taxa are observed only at low palaeolatitudes when they first appear (560–551 Ma) and just one taxon within this group occurs at high palaeolatitudes in the youngest time bin. Frondomorphs constitute a high proportion of the diversity at high palaeolatitudes, particularly between 570 and 561 Ma, with a significant χ^2 result obtained when comparing Frondomorph taxa against non-Frondomorph taxa at low and high palaeolatitudes ($p < 0.001$; Table 1).

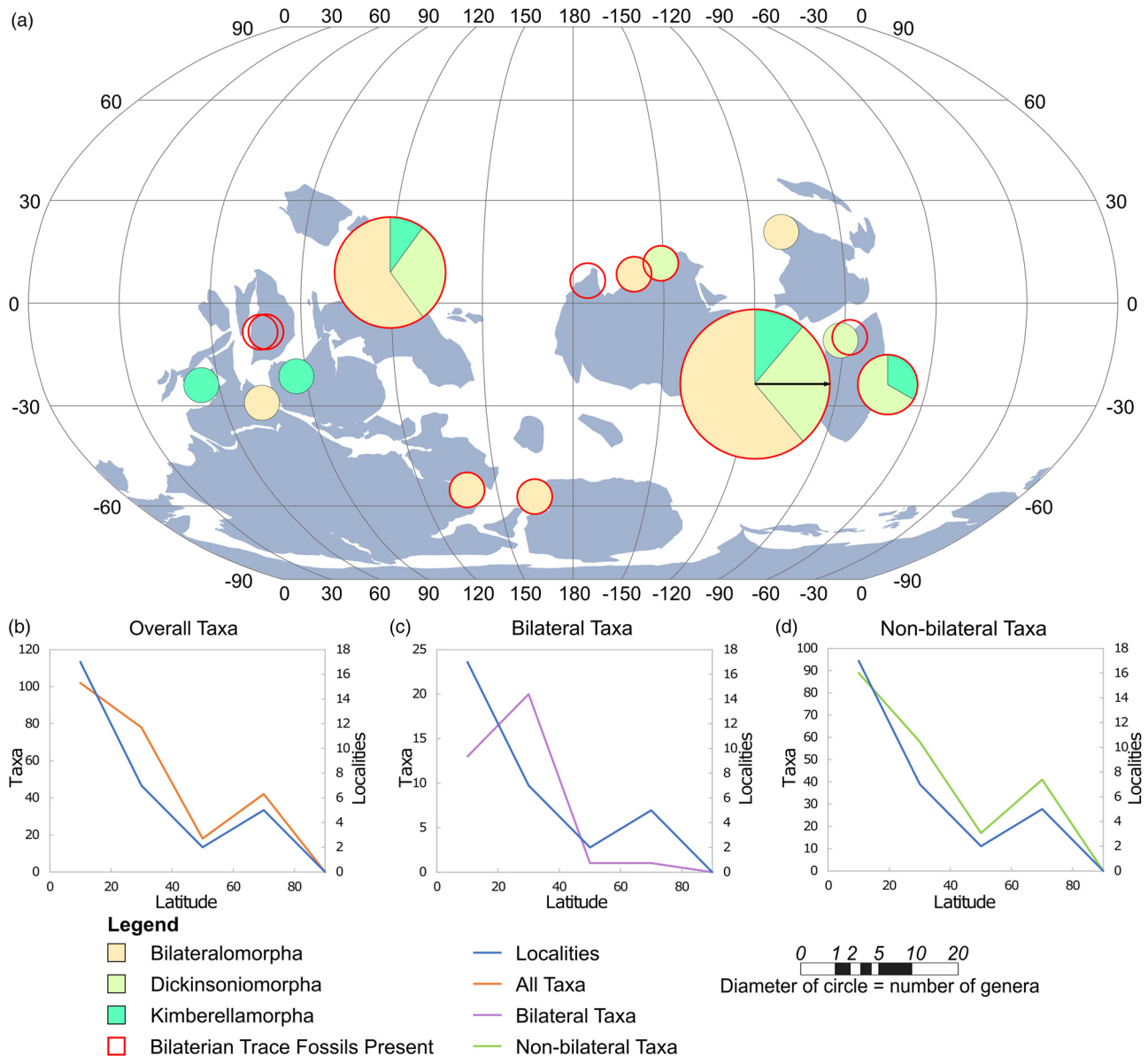


Fig. 4. Global distribution of late Ediacaran Bilateral Type fossils. (a) Bilateral body fossils presented as pie charts featuring the relative proportion of constituent morphogroups, with red outlines indicating the presence of bilaterian trace fossils, centred over the locality at which they are found at 555 Ma (black arrows indicate the palaeolocation where necessary). The area of the pie charts is equivalent to the total number of genera at each locality. Almost all Bilateral body fossils occur at low palaeolatitudes, within 30° of the Equator, with only *Namacalathus* (recently considered a candidate lophotrochozoan; Shore *et al.* 2021) and inferred bilaterian trace fossils found at higher latitudes in the youngest time bin (in Namibia and SW Brazil). Graphs comparing the distribution of Ediacaran fossil localities for all time (blue) with the distribution of (b) all taxa, (c) Bilateral Type taxa and (d) non-Bilateral taxa. All Bilateral taxa included in part (c) are found between 560 and 539 Ma. The distributions of all taxa and non-Bilateral taxa closely follow those of the localities. Bilateral taxa show a marked deviation above the locality trend at low palaeolatitudes and below the locality trend at high palaeolatitudes, with a weakly significant χ^2 result when comparing Bilateral taxa against non-Bilateral taxa at low and high latitudes ($p = 0.013$; Table 1).

seeing an increase in the number of known fossil sites (decreasing to 47 taxa across 12 localities). At high palaeolatitudes, taxonomic diversity increases (to 26 taxa across five localities; Fig. 2, inset, and Fig. 3; Supplementary Fig. 6). This latest Ediacaran time bin sees a sizeable proportion of Tubular taxa, which occur at 15 of the 17 documented fossil localities.

The overall diversity (of all Ediacaran macrobiota taxa) broadly tracks the number of localities across palaeolatitudes, with greater numbers of taxa and localities at low latitudes (Fig. 4b). A Kruskal–Wallis test to determine whether the distribution in taxon diversity is significantly different from the distribution of localities across 20° palaeolatitudinal bands (with the null hypothesis being that they follow the same distribution) revealed a weakly significant difference (KW test, $p = 0.094$; Table 1). When the data are normalized to the sampling intensity (i.e. the latitudinal distribution of localities), no

obvious difference between low and high latitudes is recovered (Supplementary Fig. 9a), suggesting that the weak significance of the Kruskal–Wallis test may be a result of under-sampling of the data, resulting in a lack of power in the statistical tests.

Kruskal–Wallis tests of whether the distribution in taxon diversity through time is significantly different from the distribution of localities through time, with the null hypothesis being that they follow the same distribution, revealed a significant difference for all taxa through time across all palaeolatitudes (KW test, $p = 0.047$; Table 1), suggesting that the sampling intensity may not fully explain the taxon distribution (Supplementary Fig. 3). When testing our two latitudinal bands individually, there was no significant difference between low palaeolatitude localities and taxa (KW test, $p = 0.169$; Table 1), which suggests that the low palaeolatitude temporal trends in taxon diversity, which encapsulate the apparent

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Table 1. Key statistical results for the MER21 reconstruction (results for the SCO01 reconstruction are presented in *Supplementary Table 3*)

Test type	Comparison	χ^2	<i>p</i>
Kruskal–Wallis	Localities–Taxa	3.938	0.047
Kruskal–Wallis	Low-latitude localities–low-latitude Taxa	1.889	0.169
Kruskal–Wallis	High-latitude localities–high-latitude Taxa	2.827	0.093
Kruskal–Wallis	Low-latitude Taxa–high-latitude Taxa	0.276	0.599
Kruskal–Wallis	Low-latitude localities–high-latitude localities	2.098	0.148
Kruskal–Wallis	Overall Taxa–localities (20° bands)	2.810	0.094
χ^2	Algal–non-Algal	3.327	0.068
χ^2	Bilateral–non-Bilateral	6.183	0.013
χ^2	Frondomorph–non-Frondomorph	16.572	<0.001
χ^2	Tubular–non-Tubular	0.096	0.757
χ^2	Soft-bodied–non-Soft-bodied	0.002	0.967
χ^2	Biom mineralizing and Organic Template–Soft and Agglutinating	1.372	0.241
χ^2	Miscellaneous–non-Miscellaneous	2.835E-30	1

Significant and weakly significant *p*-value results in bold. Significant and weakly significant *p*-values for Kruskal–Wallis tests are <0.05 and between 0.05 and 0.10, respectively. Significant and weakly significant *p*-values for χ^2 tests on Types are corrected to 0.007 and 0.014 using the Bonferroni correction, respectively. χ^2 tests test whether there is a significant difference between the distributions of the selected taxonomic groups at low and high palaeolatitudes.

latest Ediacaran radiation and ensuing diversity dip (Figs 2 and 3; *Supplementary Fig. 6*), cannot be distinguished from sampling bias. At high palaeolatitudes, diversity remains relatively constant throughout the studied interval, with no obvious radiation or diversity dip (Figs 2 and 3, *Supplementary Fig. 6*). A weakly significant difference is observed at high palaeolatitudes (KW test, $p = 0.093$; *Table 1*), which could be due to increased sampling effort from one locality (Newfoundland). Newfoundland has a very large spatial extent for sampling and therefore more sampled taxa with respect to the other high-latitude localities, perhaps resulting in the peak in diversity between 570 and 561 Ma (*Supplementary Fig. 6*).

Frondomorph fossils across all time display a significant χ^2 test ($\chi^2(1, N = 195) = 16.572, p < 0.001$; *Table 1*; testing Frondomorph taxa against non-Frondomorph taxa at low and high palaeolatitudes, with the null hypothesis that they follow the same distribution), probably due to the diverse populations of such fossils reported from the high palaeolatitude UK and Newfoundland localities (Fig. 3). Algal taxa and Tubular taxa do not display a significant relationship ($\chi^2(1, N = 195) = 3.327, p = 0.068$ and $\chi^2(1, N = 195) = 0.096, p = 0.757$, respectively; *Table 1*), whilst Bilateral taxa display a weakly significant relationship (see Bilateral taxa below), and all other Types are too poorly sampled to perform valid χ^2 tests. The Bonferroni-corrected *p*-value for 5% significance is 0.007 for the χ^2 tests performed for taxa on the MER21 reconstruction (*Table 1*).

Bilateral taxa

Bilateral Type (Bilateralomorpha, Dickinsoniomorpha and Kimberellomorpha) body fossils occur almost entirely within low palaeolatitudes (all 26 Bilateral taxa occur at low palaeolatitudes and only one occurs at high palaeolatitudes; Figs 3 and 4a, c; *Supplementary Figs 10 and 11*). However, trace fossils interpreted to have been produced by bilaterian taxa, and *Namacalathus* (recently interpreted as a potential lophotrochozoan; *Shore et al. 2021*), are found at higher palaeolatitudes in locations that sample the youngest time bin (Namibia and SW Brazil/Paraguay). A χ^2 test was performed to examine how Bilateral and non-Bilateral taxa behave at low and high palaeolatitudes, with the null hypothesis that they follow the same distribution. The relationship between these variables is weakly significant, ($\chi^2(1, N = 195) = 6.183, p = 0.013$, where a 5% significance level is given by 0.007 with the Bonferroni correction and 10% by 0.014) (*Table 1*). Bilateral taxa are found entirely at low latitudes in the time bin of their first occurrence (560–551 Ma; Fig. 3; *Supplementary Fig. 10*) and are more likely to be found at low palaeolatitudes throughout the late Ediacaran (Fig. 4). Even

accounting for the uneven distribution of localities across latitudes, there are more Bilateral taxa at lower palaeolatitudes than would be expected by chance (*Supplementary Fig. 9b*).

Biom mineralizers and tubular fossils

Other than the recent reports of silica biomineralizing tubular taxa from Finnmark (*Moczyłowska et al. 2021*), organisms with a biomineralized skeleton, and all other tubular taxa, are observed only between 560 and 539 Ma. The latest Ediacaran distribution of tubular, biomineralizing and organic template taxa is global, spanning equatorial to almost polar latitudes ($\chi^2(1, N = 195) = 0.096, p = 0.757$ for tubular taxa compared with non-tubular taxa and $\chi^2(1, N = 195) = 1.372, p = 0.241$ for biomineralizing and organic template taxa compared with soft or agglutinating taxa, when testing the taxa across high and low palaeolatitudes, with the null hypothesis that they follow the same distribution) (*Table 1*; Fig. 5; *Supplementary Fig. 12*). These results appear to indicate a rapid and global radiation of these organisms during the last two time bins. Eight of the 20 sites that contain tubular organisms do not contain biomineralizing organisms. All 12 sites containing proposed biomineralizing organisms contain biomineralizing tubular genera.

The distribution of taxa by body composition (biomineralizing, organic template and soft-bodied; Fig. 5b–d) shows no significant difference between high and low palaeolatitudes that is distinguishable from the locality sampling density: the palaeolatitudinal distribution of taxon diversity broadly follows the distribution of fossil localities (*Supplementary Fig. 9d–f*). The distribution of biomineralizing organisms is dominated by that of tubular taxa. χ^2 tests reveal no significant difference between soft-bodied taxa and non-soft-bodied taxa at low and high palaeolatitudes ($\chi^2(1, N = 195) = 0.002, p = 0.967$; *Table 1*). Biomineralizing and organic template taxa were grouped together as the data were not numerous enough to perform valid statistical tests on individual body compositions.

Similarity dendrograms

An average-linkage dendrogram for localities with more than six taxa, along with the palaeolatitudinal band they fall within for both the MER21 and SCO01 reconstructions, the dominant lithology, and the depositional setting, are presented in *Figure 6a*. Cophenetic correlation for the dendrogram is high (0.804), indicating that the original data are reliably grouped (*Sokal and Rohlf 1962*). The older Lantian Formation and algae-dominated Miaohe Member sit apart from the rest of the localities, followed by three separate branch

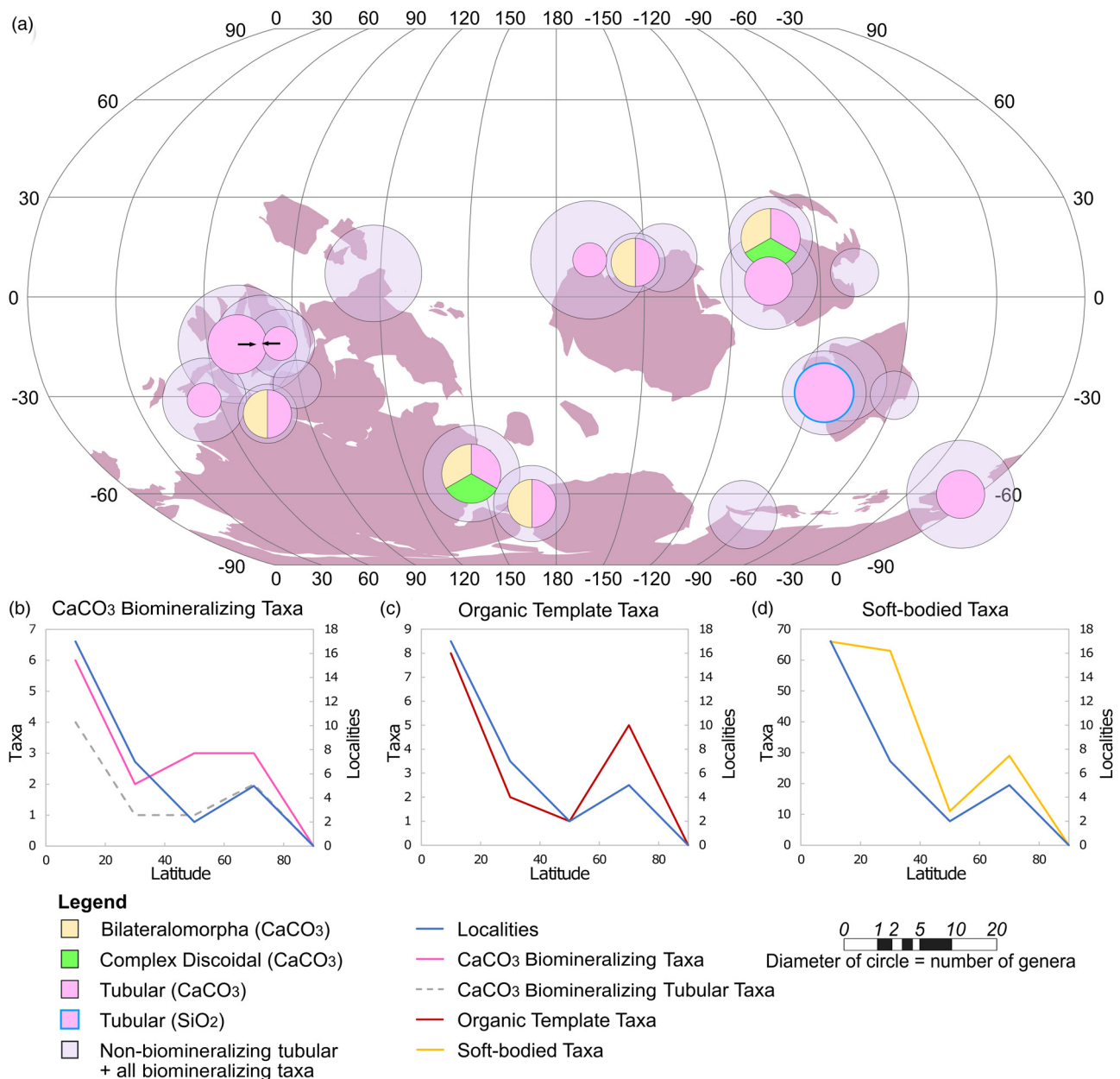


Fig. 5. Global distribution of biomineralizing and tubular Ediacaran taxa. **(a)** Tubular fossils and all other biomineralizing fossils (faint circles), with pie charts of only biomineralizing organisms overlain (solid circles), centred over the locality at which they are found at 545 Ma (black arrows indicate the palaeolocation where necessary). Pie charts and circles are scaled to represent the number of genera within each morphogroup, with the circle area being equivalent to the total number of genera at each locality. A global distribution is observed for both tubular and biomineralizing organisms between 550 and 539 Ma. Biomineralizing organisms are dominated by tubular taxa and are often found alongside non-biomineralizing tubular organisms. Graphs comparing the distribution of Ediacaran fossil sites for all time (blue lines) with the distribution of **(b)** CaCO₃ biomineralizing taxa, **(c)** Organic Template taxa; and **(d)** Soft-bodied taxa. The latitudinal distributions of each group of taxa broadly follow those of the localities, with a significant proportion of the CaCO₃ biomineralizing taxa comprising tubular taxa (grey dotted line). Soft-bodied taxa deviate from the locality distribution at low palaeolatitudes, seemingly as a result of the higher number of Bilateral taxa than expected (Fig. 4c). All CaCO₃ biomineralizing and organic template taxa (b–c) are found between 550 and 539 Ma. None of the taxonomic groupings in parts (b–d) show a statistically significant deviation between high and low latitudes.

clusters that almost recapitulate the three traditional biotic assemblages identified by Waggoner (2003). Some mixing between the White Sea and Nama assemblages is present, with the Olenek Uplift (traditionally a ‘White Sea assemblage’ locality) grouping within the Nama cluster, consistent with recent suggestions that the Olenek Uplift has affinities with the Nama assemblage (e.g. Bykova *et al.* 2020). No separate Miaohe cluster (see Muscente *et al.* 2019) is observed. This difference may be a result of our analysis grouping individual formations within combined geographical locations (by contrast, Muscente *et al.* 2019 analysed data at the Formation scale) or due to our taxon occurrence database including more recent fossil discoveries.

In the MER21 reconstruction, there is some grouping of sites in the same palaeolatitudinal band within the sub-branches of the main clusters (e.g. the two high-latitude Avalonian localities of Newfoundland and Charnwood, UK). All the White Sea sites are found at low palaeolatitudes, which may indicate a degree of provinciality. However, at a first-order scale, no obvious difference arises between the low- and high-palaeolatitude distributions to explain the taxonomic composition of late Ediacaran macrofossil assemblages. The SCO01 reconstruction similarly shows little evidence for palaeolatitudinal groupings. Deep marine depositional settings tend to group closely together – for example, in the Avalon branch. In terms of lithology, it is notable that diverse fossil-bearing

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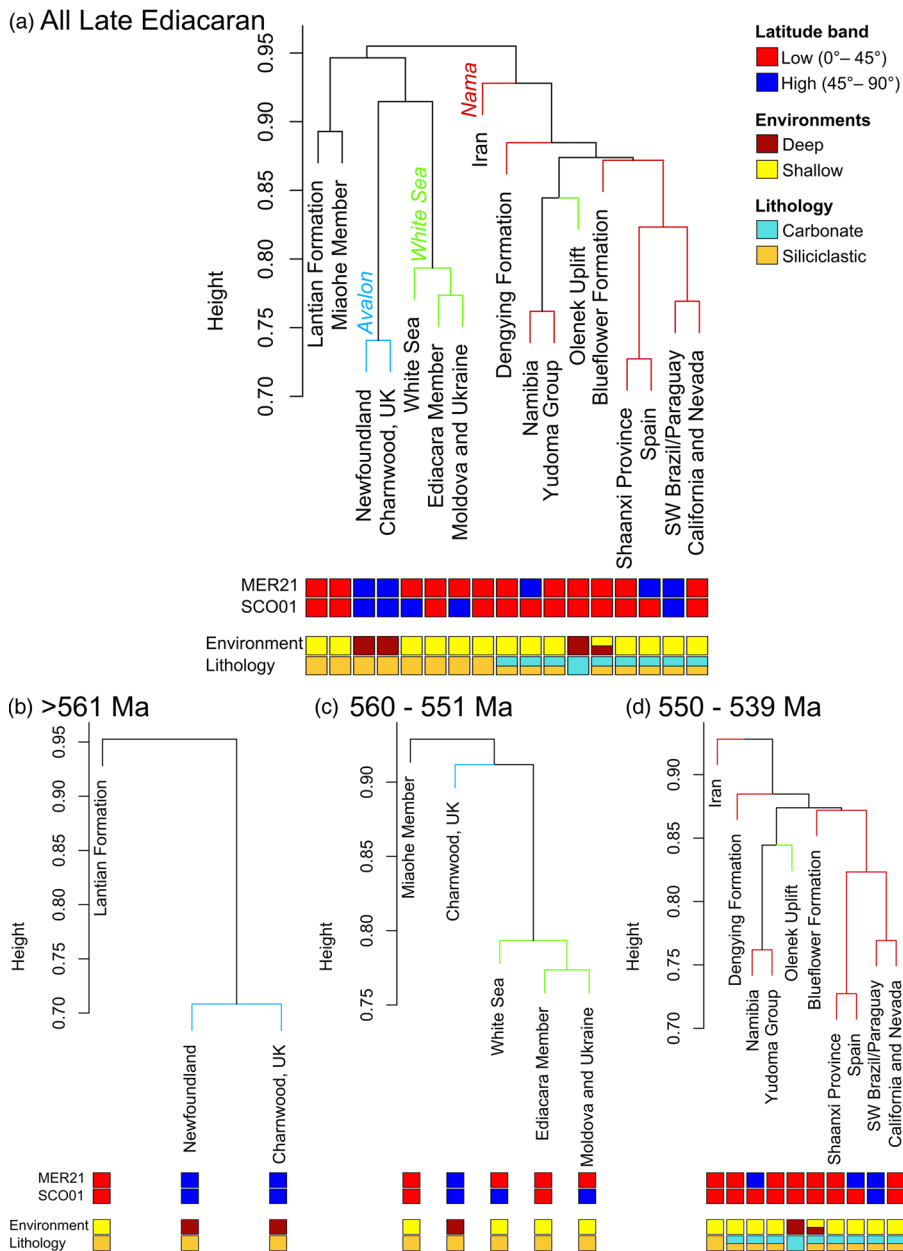


Fig. 6. Average-linkage dendrograms for localities with more than six Ediacaran macrofossil taxa, including the presence or absence of bilaterian trace fossils for (a) the whole time interval, and divided into three time bins: (b) >561 Ma; (c) 560–551 Ma and (d) 550–539 Ma. Also shown are the corresponding 45° latitudinal bands for each locality during the time bin in which fossils were preserved for the MER21 and SCO01 reconstructions; the ‘environment’ (shallow or deep marine); and the dominant fossil-bearing lithology (carbonate or siliciclastic; see [Supplementary Information 1](#) for further information). The height (*y*-axis) represents the taxonomic dissimilarity using the average-linkage method. High cophenetic correlation coefficients of 0.804, 0.994, 0.933, and 0.739 for parts (a–d), respectively, indicate reliable groupings of the original datapoints. Localities previously recognized to belong to the Avalon (blue), White Sea (green) and Nama (red) assemblages (following the colour scheme from [Muscente *et al.* 2019](#)) tend to cluster together. However, one site (Olenek Uplift), typically considered to belong to the White Sea assemblage, lies within the Nama cluster in the branch to the right of part (a) and in part (d). Some grouping of palaeolatitudes is present within sub-branches in the MER21 reconstruction in parts (a) and (b). However, age and assemblage, as well as environment, appear to exert greater control on the branches. When considering individual time bins in parts (b–d), both environment and palaeolatitude could feasibly explain the clustering within the oldest two time bins, but there is no clear relationship between these variables and sub-clusters in part (d). Alternative dendrograms with different filters on the number of taxa per locality included can be found in [Supplementary Figure 23](#).

carbonate lithologies lie within the Nama assemblage cluster and within the final 10 myr time bin, regardless of the palaeolatitudinal band they fall within ([Fig. 6d](#)).

When considering the assemblages by time bin, the sub-dendrograms ([Fig. 6b–d](#)) reveal that the palaeolatitudinal distribution of taxa on the MER21 reconstruction correlates with the clusters of assemblage similarity in an identical way to environment for the pre-561 and 560–551 Ma time bins. This correlation suggests that, once age is no longer a consideration, the roles played by palaeolatitude and depositional environment in shaping the assemblage composition are difficult to deconvolve.

Discussion

Overall distribution

The broad-scale late Ediacaran temporal trends in biodiversity identified in previous studies include a major diversification in genera and morphogroups at *c.* 560 Ma ([Droser *et al.* 2017](#)) and a decline in diversity going into the latest Ediacaran time bin ([Darroch *et al.* 2018](#)). Although our data recognize that the overall diversity

through time exhibits a statistically significant difference from the locality trends, consistent with either or both of these patterns ([Fig. 2](#), inset; [Supplementary Fig. 3](#)), these trends are only observed at low latitudes, where it is not possible to statistically distinguish sampling biases from taxonomic trends ([Supplementary Fig. 6](#)). Our study provides a greater discrimination of patterns in pre-561 Ma data than previous studies (most of which combine the *c.* 20 myr Avalon assemblage into one data point) and reveals an increase in taxonomic diversity (increasing to 25 taxa globally; [Supplementary Fig. 3](#)) over the 580–561 Ma interval (with this diversity restricted to a small number of Types). However, we note that only six localities have been sampled within this interval.

Modern day biodiversity follows a broad latitudinal biodiversity gradient, consisting of a tropical peak and a poleward decline in species diversity ([Fischer 1981](#); [Stevens 1989](#)), although there is a dip in species richness within 10° of the Equator ([Saedi *et al.* 2019](#)). Such latitudinal gradients have been observed during other time periods throughout the Phanerozoic (e.g. [Jablonski *et al.* 2006](#); [Mittelbach *et al.* 2007](#); [Mannion *et al.* 2014](#); although see [Jones *et al.* 2021](#)), where they can vary in gradient or magnitude,

potentially in response to the dominant climatic regime (Mannion *et al.* 2014). Our raw data appear to indicate a latitudinal difference in biodiversity during the late Ediacaran, with the highest diversity at lower palaeolatitudes, but because this pattern broadly mirrors the number of available fossil sites across palaeolatitudes, with poor sampling particularly at higher palaeolatitudes, it is indistinguishable from sampling biases. When normalized against the number of fossil localities, the latitudinal difference in biodiversity across palaeolatitudes appears flat (Supplementary Fig. 9a). Therefore, the Ediacaran macrobiota overall do not appear to have exhibited a significant difference between low and high palaeolatitudes in either of the palaeogeographical reconstructions considered (Table 1; Supplementary Table 3).

Although the data are sparse in the early part of the late Ediacaran, our maps potentially reveal insights into the ecology of key macroscopic groups. Frondomorph-dominated sites appear in both low- and high-palaeolatitude locations within the earliest time bins, consistent with previous suggestions that they may have utilized water-borne dispersal to become widely distributed as part of their reproductive strategy (Darroch *et al.* 2013; Mitchell *et al.* 2015). Protistan taxa are also present at high and low palaeolatitudes. Alternatively, the global distribution of Protists and/or Frondomorphs could indicate that they had a considerable, as yet unrecognized, evolutionary history prior to their first appearance in this study. There are few shallow marine environments pre-561 Ma (four of eight localities present: the Lantian Formation, Finnmark, the Wonoka Formation and the Itajai Basin; the latter two currently have only one described taxon) or carbonate-dominated successions (one of eight localities is carbonate: the Wonoka Formation; the Nadaleen Formation, NW Canada, is mixed siliciclastic and carbonate lithologies and the rest are all siliciclastic). Differences in community composition among these sites could therefore result from their recording distinct environments and ecosystems, but it is difficult to make meaningful direct comparisons when the environments are so unevenly sampled.

The results from the sub-dendrograms, divided by time bin (Fig. 6b–d), indicate that much of the clustering within the main dendrogram (Fig. 6a) is driven by the age of the sites. Within the sub-dendrograms, environment and lithology appear to exert an important control on the clusters in all time bins, with palaeolatitude seemingly less influential. Future work is required to decouple the respective importance of palaeolatitude from these environmental, ecological and taphonomic factors.

Bilateral taxa

Our raw body fossil data reveal a weakly significant signal, indicating that Bilateral taxa exhibit higher diversity at lower palaeolatitudes (Fig. 4), hinting at a potential latitudinal biodiversity difference for this group. The pattern is observed in all three Bilateral Type morphogroups (Bilateralomorpha, Dickinsoniomorpha and Kimberellomorpha; although the data are not sufficient to perform χ^2 tests on the individual morphogroups), even after the data have been normalized to account for variations in localities/sampling (Supplementary Fig. 11). The pattern appears most distinct at the first appearance of Bilateral taxa, between 560 and 551 Ma (Supplementary Fig. 10), and may indicate a low-latitude origin for Bilateral Type taxa. By 550–539 Ma, candidate bilaterian trace fossils and the candidate lophotrochozoan *Namacalathus* are present over a wider palaeolatitudinal range, including at high-palaeolatitude sites from modern day Brazil and Namibia.

Our data appear to suggest that Bilateral Type taxa evolved later than the other taxon Types considered in this study (Fig. 3), consistent with phylogenetic expectations that bilaterians should evolve later than non-bilaterian metazoans (Erwin *et al.* 2011; dos Reis *et al.* 2016; Budd and Mann 2020). We recognize that our

Bilateral grouping is a crude proxy for phylogenetic affinity rather than a direct record of evolutionary relationships, and that it incorporates some taxa with a contentious bilaterian affinity (e.g. *Dickinsonia*; see Sperling and Vinther 2010), while omitting taxa that may have been true bilaterians (e.g. tubular taxa recently compared to annelids; Yang *et al.* 2020). Nevertheless, our data warrant further investigation to explore a potential palaeolatitudinal control on this important step in metazoan evolution.

Body composition and tubes

Organic-walled, biomineralizing and tubular taxa had a widespread palaeolatitudinal distribution at the end of the late Ediacaran on both of the palaeocontinental reconstructions considered (Fig. 5; Supplementary Fig. 19). Such a global distribution challenges the notion that early biomineralization was preferentially restricted to lower palaeolatitudes. This restriction is thought to exist because modern biomineralization and carbonate production are favoured in warmer conditions due to the lower solubility of calcium carbonate at higher temperatures (e.g. Tucker 1992). Consequently, some previous studies of Ediacaran taxon distribution have proposed that the presence of biomineralizing taxa could indicate deposition at low palaeolatitudes (e.g. Zakrevskaya 2019). Carbonates can and do form at higher latitudes, both in warm water settings if the temperatures are suitable and in cool water conditions if the ocean chemistry is favourable. Even microbialites have been reported from deep marine settings in the Jurassic (Dromart *et al.* 1994). As such, it is important to consider the uniformitarian possibility that certain Ediacaran carbonate-bearing successions could have been cool water settings, until evidence is found to the contrary.

CaCO₃ biomineralizing, organic template, agglutinating and soft-bodied tubular taxa are globally distributed from their first appearance between 560 and 551 Ma, suggesting that they may have experienced a rapid global radiation. This result contrasts with that of Waggoner (2003, fig. 5), who recognized a latitudinal diversity gradient for tubular organisms (although that study included only seven tubular taxa, whereas recent discoveries allow us to consider 28). It has been proposed that *Cloudina* may have been composed of an organic skeleton (Yang *et al.* 2020), as opposed to biomineralized calcium carbonate. *Cloudina* is widely distributed, found at 11 of 12 sites recorded to contain biomineralizing taxa. Only three low palaeolatitude sites (the western USA, Iran and the Dengying Formation) have *Cloudina* as the only biomineralizing taxon present and so, even if *Cloudina* specifically is found to have been non-biomineralized, our reported global distribution of biomineralizing taxa would remain unchanged. In such a scenario, biomineralizing tubular taxa would become less prominent, present at only four of the remaining nine sites.

Comparison with the SCO01 reconstruction

There are three key differences between taxon distributions in the SCO01 and MER21 reconstructions. First, the distribution of localities in the SCO01 reconstruction is more evenly spread between high and low palaeolatitudes, resulting in more similar overall taxon patterns through time in both latitudinal bands, including an apparent increase at c. 560 Ma and a subsequent decrease at c. 550 Ma (note that the Kruskal–Wallis tests remain weakly significant for high latitudes and non-significant at low latitudes), and no significant Frondomorph signal (Supplementary Table 3). Second, the SCO01 distribution of both Bilateral taxa and biomineralizers is global, so no significant difference is found between the low- and high-palaeolatitude groups. Third, significant and weakly significant χ^2 signals are observed for the palaeolatitudinal distributions of Soft-bodied and Algal taxa, respectively (Supplementary Table 3), probably due to diversity peaks at lower

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latitudes for algae, biomineralizing and organic template taxa (for further details, see [Supplementary File 1](#)). We favour the MER21 reconstruction because of its self-consistent framework and greater dependence on multiple lines of evidence, which we consider to provide a more accurate reflection of Ediacaran palaeogeography. However, we acknowledge that further data are required to better constrain these reconstructions and to refine our currently coarse distinctions between latitudinal bands.

Comparisons with previous studies

[Boag et al. \(2016\)](#) suggest that the differences in diversity between the Avalon assemblage (i.e. the first two time bins in our [Fig. 2](#)) and those in the White Sea assemblage (c. 560–551 Ma) arise from differences in the depth of deposition of the available outcrops. Although most of the localities plotted on the maps between 580 and 561 Ma are offshore, and the majority of the younger localities were deposited in shallow settings ([Supplementary Fig. 2](#)), there are some exceptions and more granular consideration of the data ([Fig. 6b–d](#)) reveals that palaeolatitude could contribute to these differences.

Previous hierarchical cluster analyses ([Boag et al. 2016](#); [Muscente et al. 2019](#)) clearly distinguish the three ‘traditional’ biotic assemblages. The dendrogram produced here ([Fig. 6a](#)) separates the Avalon assemblage, but mixes one locality from the White Sea assemblage (Olenek Uplift) into the Nama assemblage. This mixing may result from the increased number of taxa used in this study or from recent discoveries in units such as the Dengying Formation, which contain taxa known from both the classic Nama and White Sea assemblages ([Xiao et al. 2021](#)). Alternatively, the presence of tubular taxa, more typical of Nama assemblages, in the Olenek Uplift may result in its placement within our dendrogram. The Miaohu cluster ([Muscente et al. 2019](#)), comprising the Olenek Uplift and units from South China and Ukraine/Moldova, is not identified as a discrete cluster here, although we note differences in the way our studies have grouped data from global localities. The dendrogram presented by [Zakrevskaya \(2019\)](#) has few branches in common with those in [Figure 6a](#), probably reflecting both their different cluster analysis methodology and their far smaller taxonomic dataset (46 taxa and 13 localities). The sensitivity of these hierarchical cluster analyses (both within this study and others) to the criteria of inclusion (e.g. the minimum number of taxa, see [Supplementary Fig. 23](#)) limits their utility in drawing strong conclusions regarding the similarity of fossil assemblage compositions.

The global distribution of biomineralizers observed in this study contrasts with that of [Zakrevskaya \(2019\)](#), who predicts a tropical distribution of biomineralizing organisms by assuming that biomineralization was favoured at tropical temperatures. Ediacaran global temperatures are poorly constrained (though see [Meng et al. 2011](#)), but a higher global temperature than today could feasibly have favoured biomineralizing organisms across a wide palaeolatitudinal range.

Conclusions

This study considers the distribution of the Ediacaran macrobiota between high and low palaeolatitudes through time. In addition to factors such as depth, lithology and age, palaeolatitude is found to have exerted a significant control on the distribution of certain Ediacaran macrofossil taxa groups. Bilateral taxa (the group containing the most promising candidate bilaterian taxa among the Ediacaran macrobiota) demonstrate a weakly significant latitudinal difference in their distribution on the MER21 palaeocontinental reconstruction, being more abundant at low palaeolatitudes. The low palaeolatitude distribution of Bilateral taxa may

indicate a possible temperature dependence and/or a low-latitude ‘cradle’ for bilaterian evolution, and warrants further investigation. The relatively late appearance of Bilateral forms after frondose and candidate cnidarian and poriferan forms, noted by previous researchers (e.g. [Laflamme et al. 2013](#)), may alternatively be a function of a paucity of low palaeolatitude sites in the critical 570–561 Ma interval. All other taxa, including biomineralizing taxa, are distributed at both high and low palaeolatitudes, with no significant latitudinal difference observed between low and high palaeolatitudes in the overall diversity of Ediacaran macrofossil taxa.

Our analyses support the work of previous researchers ([Boag et al. 2016](#); [Muscente et al. 2019](#)) in suggesting that age, palaeoenvironment, taphonomy and palaeolatitude all probably played a part in shaping the distribution of Ediacaran macrofossil taxa. We consider it likely that age exerts a high-level control on assemblage similarity and we recognize that, at local to regional scales, palaeoenvironment exhibits a strong relationship with the presence or absence of certain taxa (e.g. [Grazhdankin 2004](#); [Gehling and Droser 2013](#); [Reid et al. 2020](#)). However, our results indicate that palaeolatitude may also impart organism-specific influences on the distribution of Ediacaran macrobiota. The palaeolatitudinal distribution of late Ediacaran taxa should therefore not be overlooked in studies investigating the controls on taxon occurrence in space and time.

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Data availability All data generated or analysed during this study are included in this published article (and its [supplementary](#) information files).

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References

- Abrajevitch, A. and Van der Voo, R. 2010. Incompatible Ediacaran paleomagnetic directions suggest an equatorial geomagnetic dipole hypothesis. *Earth and Planetary Science Letters*, **293**, 164–170, <https://doi.org/10.1016/j.epsl.2010.02.038>
- Allison, P.A. and Briggs, D.E.G. 1993. Paleolatitudinal sampling bias, Phanerozoic species diversity, and the end-Permian extinction. *Geology*, **21**, 65–68, [https://doi.org/10.1130/0091-7613\(1993\)021<0065:PSBPSD>2.3.CO;2](https://doi.org/10.1130/0091-7613(1993)021<0065:PSBPSD>2.3.CO;2)
- Antcliffe, J.B., Gooday, A.J. and Brasier, M.D. 2011. Testing the protozoan hypothesis for Ediacaran fossils: a developmental analysis of *Palaeopascichnus*. *Palaentology*, **54**, 1157–1175, <https://doi.org/10.1111/j.1475-4983.2011.01058.x>
- Boag, T.H., Darroch, S.A.F. and Laflamme, M. 2016. Ediacaran distributions in space and time: testing assemblage concepts of earliest macroscopic body fossils. *Paleobiology*, **42**, 574–594, <https://doi.org/10.1017/pab.2016.20>
- Bobrovskiy, I., Hope, J.M., Ivantsov, A., Nettersheim, B.J., Hallmann, C. and Brocks, J.J. 2018 a. Ancient steroids establish the Ediacaran fossil *Dickinsonia* as one of the earliest animals. *Science*, **361**, 1246–1249, <https://doi.org/10.1126/science.aat7228>
- Bobrovskiy, I., Hope, J.M., Krasnova, A., Ivantsov, A.Y. and Brocks, J.J. 2018b. Molecular fossils from organically preserved Ediacara biota reveal

Distribution of the Ediacaran macrobiota

- Merdith, A.S., Williams, S.E. *et al.* 2021. Extending full-plate tectonic models into deep time: linking the Neoproterozoic and the Phanerozoic. *Earth Science Reviews*, **214**, 103477, <https://doi.org/10.1016/j.earscirev.2020.103477>
- Mitchell, E.G. and Kenchington, C.G. 2018. The utility of height for the Ediacaran organisms of Mistaken Point. *Nature Ecology & Evolution*, **2**, 1218–1222, <https://doi.org/10.1038/s41559-018-0591-6>
- Mitchell, E.G., Kenchington, C.G., Liu, A.G., Matthews, J.J. and Butterfield, N.J. 2015. Reconstructing the reproductive mode of an Ediacaran macro-organism. *Nature*, **524**, 343–346, <https://doi.org/10.1038/nature14646>
- Mitchell, E.G., Harris, S. *et al.* 2019. The importance of neutral over niche processes in structuring Ediacaran early animal communities. *Ecology Letters*, **22**, 2028–2038, <https://doi.org/10.1111/ele.13383>
- Mitchell, E.G., Bobkov, N. *et al.* 2020. The influence of environmental setting on the community ecology of Ediacaran organisms. *Interface Focus*, **10**, 20190109, <https://doi.org/10.1098/rsfs.2019.0109>
- Mittelbach, G.G., Schemske, D.W. *et al.* 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**, 315–331, <https://doi.org/10.1111/j.1461-0248.2007.01020.x>
- Moczydłowska, M., Kear, B.P., Snitting, D., Liu, L., Lazor, P. and Majka, J. 2021. Ediacaran metazoan fossils with siliceous skeletons from the Digermulen Peninsula of Arctic Norway. *Journal of Paleontology*, **95**, 440–475, <https://doi.org/10.1017/jpa.2020.105>
- Müller, R.D., Cannon, J. *et al.* 2018. GPlates: building a virtual Earth through deep time. *Geochemistry, Geophysics, Geosystems*, **19**, 2243–2261, <https://doi.org/10.1029/2018GC007584>
- Muscente, A., Boag, T.H., Bykova, N. and Schiffbauer, J.D. 2018. Environmental disturbance, resource availability, and biologic turnover at the dawn of animal life. *Earth-Science Reviews*, **177**, 248–264, <https://doi.org/10.1016/j.earscirev.2017.11.019>
- Muscente, A.D., Bykova, N. *et al.* 2019. Ediacaran biozones identified with network analysis provide evidence for pulsed extinctions of early complex life. *Nature Communications*, **10**, 911, <https://doi.org/10.1038/s41467-019-08837-3>
- Narbonne, G.M. 2005. The Ediacara biota: Neoproterozoic origin of animals and their ecosystems. *Annual Review of Earth and Planetary Sciences*, **33**, 421–442, <https://doi.org/10.1146/annurev.earth.33.092203.122519>
- Narbonne, G.M., Saylor, B.Z. and Grotzinger, J.P. 1997. The youngest Ediacaran fossils from southern Africa. *Journal of Paleontology*, **71**, 953–967, <https://doi.org/10.1017/S0022336000035940>
- Narbonne, G.M., Laflamme, M., Trusler, P.W., Dalrymple, R.W. and Greentree, C. 2014. Deep-water Ediacaran fossils from Northwestern Canada: taphonomy, ecology, and evolution. *Journal of Paleontology*, **88**, 207–223, <https://doi.org/10.1666/13-053>
- Noble, S.R., Condon, D.J., Carney, J.N., Wilby, P.R., Pharaoh, T.C. and Ford, T.D. 2015. U–Pb geochronology and global context of the Charnian Supergroup, UK: constraints on the age of key Ediacaran fossil assemblages. *GSA Bulletin*, **127**, 250–265, <https://doi.org/10.1130/B31013.1>
- Opdyke, B.N. and Wilkinson, B.H. 1990. Paleolatitude distribution of Phanerozoic marine ooids and cements. *Palaogeography, Palaeoclimatology, Palaeoecology*, **78**, 135–148, [https://doi.org/10.1016/0031-0182\(90\)90208-0](https://doi.org/10.1016/0031-0182(90)90208-0)
- Paradis E. and Schliep K. 2018. Ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, **35**, 526–528, <https://doi.org/10.1093/bioinformatics/bty633>
- Pisarevsky, S.A., Murphy, J.B., Cawood, P.A. and Collins, A.S. 2008. Late Neoproterozoic and early Cambrian palaeogeography: models and problems. *Geological Society, London, Special Publications*, **294**, 9–31, <https://doi.org/10.1144/SP294.2>
- Reid, L.M., Holmes, J.D., Payne, J.L., Garcia-Bellido, D.C. and Jago, J.B. 2020. Taxa, turnover and taphofacies: a preliminary analysis of facies-assemblage relationships in the Ediacara Member (Flinders Ranges, South Australia). *Australian Journal of Earth Sciences*, **67**, 905–914, <https://doi.org/10.1080/08120099.2018.1488767>
- Rooney, A.D., Cantine, M.D. *et al.* 2020. Calibrating the coevolution of Ediacaran life and environment. *PNAS*, **117**, 16824–16830, <https://doi.org/10.1073/pnas.2002918117>
- Saeedi, H., Costello, M.J., Warren, D. and Brandt, A. 2019. Latitudinal and bathymetrical species richness patterns in the NW Pacific and adjacent Arctic Ocean. *Scientific Reports*, **9**, 1–10, <https://doi.org/10.1038/s41598-019-45813-9>
- Saupe, E.E., Qiao, H. *et al.* 2020. Extinction intensity during Ordovician and Cenozoic glaciations explained by cooling and palaeogeography. *Nature Geoscience*, **13**, 65–70, <https://doi.org/10.1038/s41561-019-0504-6>
- Scotese, C.R. 2001. *Atlas of Earth History, Volume 1, Paleogeography*. PALEOMAP Project, Arlington, TX, www.scotese.com
- Seton, M., Müller, R.D. *et al.* 2012. Global continental and ocean basin reconstructions since 200 Ma. *Earth-Science Reviews*, **113**, 212–270, <https://doi.org/10.1016/j.earscirev.2012.03.002>
- Shore, A.J., Wood, R.A., Butler, I.B., Zhuravlev, A.Y., McMahon, S., Curtis, A. and Bowyer, F.T. 2021. Ediacaran metazoan reveals lophotrochozoan affinity and deepens root of Cambrian explosion. *Science Advances*, **7**, eabf2933, <https://doi.org/10.1126/sciadv.abf2933>
- Smith, A.G. 2001. Paleomagnetically and tectonically based global maps for Vendian to mid-Ordovician time. In: Zhuravlev, A.Y. (ed.) *The Ecology of the Cambrian Radiation*. Columbia University Press, New York, 11–46.
- Sokal, R.R. and Rohlf, F.J. 1962. The comparison of dendrograms by objective methods. *Taxon*, **11**, 33–40, <https://doi.org/10.2307/1217208>
- Sperling, E.A. and Vinther, J. 2010. A placozoan affinity for *Dickinsonia* and the evolution of late Proterozoic metazoan feeding modes. *Evolution & Development*, **12**, 201–209, <https://doi.org/10.1111/j.1525-142X.2010.00404.x>
- Sperling, E.A., Peterson, K.J. and Laflamme, M. 2011. Rangeomorphs, *Thectardis* (Porifera?) and dissolved organic carbon in the Ediacaran oceans. *Geobiology*, **9**, 24–33, <https://doi.org/10.1111/j.1472-4669.2010.00259.x>
- Sperling, E.A., Carbone, C., Strauss, J.V., Johnston, D.T., Narbonne, G.M. and Macdonald, F.A. 2016. Oxygen, facies, and secular controls on the appearance of Cryogenian and Ediacaran body and trace fossils in the Mackenzie Mountains of northwestern Canada. *GSA Bulletin*, **128**, 558–575, <https://doi.org/10.1130/B31329.1>
- Stern, R.J. 2018. The evolution of plate tectonics. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, **376**, 20170406, <https://doi.org/10.1098/rsta.2017.0406>
- Stevens, G.C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *The American Naturalist*, **133**, 240–256, <https://doi.org/10.1086/284913>
- Tostevin, R., Wood, R.A. *et al.* 2016. Low-oxygen waters limited habitable space for early animals. *Nature Communications*, **7**, 12818, <https://doi.org/10.1038/ncomms12818>
- Tucker, M.E. 1992. The Precambrian–Cambrian boundary: seawater chemistry, ocean circulation and nutrient supply in metazoan evolution, extinction and biomineralization. *Journal of the Geological Society, London*, **149**, 655–668, <https://doi.org/10.1144/gsjgs.149.4.0655>
- Valentine, J.W. and Moores, E.M. 1972. Global tectonics and the fossil record. *The Journal of Geology*, **80**, 167–184, <https://doi.org/10.1086/627723>
- Vilhena, D.A. and Smith, A.B. 2013. Spatial bias in the marine fossil record. *PLoS One*, **8**, e74470, <https://doi.org/10.1371/journal.pone.0074470>
- Waggoner, B. 1999. Biogeographic analyses of the Ediacara biota: a conflict with paleotectonic reconstructions. *Paleobiology*, **25**, 440–458, <https://doi.org/10.1017/S0094837300020315>
- Waggoner, B. 2003. The Ediacaran biotas in space and time. *Integrative and Comparative Biology*, **43**, 104–113, <https://doi.org/10.1093/icb/43.1.104>
- Whittington, H.B. and Hughes, C.P. 1972. Ordovician geography and faunal provinces deduced from trilobite distribution. *Philosophical Transactions of the Royal Society of London. B*, **263**, 235–278, <https://doi.org/10.1098/rstb.1972.0001>
- Wood, R. 2018. Exploring the drivers of early biomineralization. *Emerging Topics in Life Sciences*, **2**, 201–212, <https://doi.org/10.1042/ETLS20170164>
- Wood, R.A., Poulton, S.W. *et al.* 2015. Dynamic redox conditions control late Ediacaran metazoan ecosystems in the Nama Group, Namibia. *Precambrian Research*, **261**, 252–271, <https://doi.org/10.1016/j.precamres.2015.02.004>
- Wood, R., Liu, A.G. *et al.* 2019. Integrated records of environmental change and evolution challenge the Cambrian explosion. *Nature Ecology & Evolution*, **3**, 528–538, <https://doi.org/10.1038/s41559-019-0821-6>
- Xiao, S. and Laflamme, M. 2009. On the eve of animal radiation: phylogeny, ecology and evolution of the Ediacara biota. *Trends in Ecology & Evolution*, **24**, 31–40, <https://doi.org/10.1016/j.tree.2008.07.015>
- Xiao, S., Chen, Z., Zhou, C. and Yuan, X. 2019. Surfing in and on microbial mats: oxygen-related behavior of a terminal Ediacaran bilaterian animal. *Geology*, **47**, 1054–1058, <https://doi.org/10.1130/G46474.1>
- Xiao, S., Gehling, J.G., Evans, S.D., Hughes, I.V. and Droser, M.L. 2020. Probable benthic macroalgae from the Ediacara Member, South Australia. *Precambrian Research*, **350**, 105903, <https://doi.org/10.1016/j.precamres.2020.105903>
- Xiao, S., Chen, Z., Pang, K., Zhou, C. and Yuan, X. 2021. The Shibantan Lagerstätte: insights into the Proterozoic–Phanerozoic transition. *Journal of the Geological Society, London*, **178**, <https://doi.org/10.1144/jgs2020-135>
- Yang, B., Steiner, M., Schiffbauer, J.D., Selly, T., Wu, X., Zhang, C. and Liu, P. 2020. Ultrastructure of Ediacaran cloninids suggests diverse taphonomic histories and affinities with non-biomineralized annelids. *Scientific Reports*, **10**, 535, <https://doi.org/10.1038/s41598-019-56317-x>
- Zakrevskaya, M.A. 2019. Paleobiogeographic analysis of the assemblages of Late Vendian macrofossils. *Stratigraphy and Geological Correlation*, **27**, 603–611, <https://doi.org/10.1134/S0869593819050095>