The palaeolatitudinal distribution of the Ediacaran macrobiota

Catherine E. Boddy¹, Emily G. Mitchell², Andrew Merdith³⁴, and Alexander G. Liu¹

¹: Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EQ, U.K.
²: Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, U.K.
³: Laboratoire de Géologie de Lyon : Terre, Planète, Environnement, UMR CNRS 5276, Université Claude Bernard, Lyon1, 2, rue Raphaël Dubois, 69622 Villeurbanne Cedex, France
⁴: School of Earth and Environment, University of Leeds, Woodhouse, Leeds, LS2 9JT, U.K.

Abstract

Macrofossils of the late Ediacaran Period (~579–539 Ma) document diverse, complex multicellular eukaryotes, including early animals, prior to the Cambrian radiation of metazoan phyla. To investigate causal relationships between environmental perturbations, biotic responses, and early metazoan evolutionary trajectories, it is vital to distinguish between evolutionary and ecological controls on global Ediacaran macrofossil distribution. The contributions of temporal, palaeoenvironmental and lithological factors in shaping observed variation 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 palaeogeographic reconstructions. We find that overall generic diversity was distributed across all palaeolatitudes. Amongst 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 palaeogeographic reconstruction, respectively, whilst Algal, Tubular, Soft-bodied and Biomineralising taxa show no significant difference. 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.

Introduction

The Ediacaran macrobiota evidence a diverse assortment of macroscopic organisms that occupied the global oceans during the ~40 million-year interval prior to the Phanerozoic Eon (~579–539 Ma; e.g. Xiao and Laflamme, 2009). The fossils document protists, algae, bacterial colonies, and the first recognisable animals (e.g. Fedonkin et al., 2007; Grazhdankin and Gerdes, 2007; Liu et al., 2014; Bobrovskiy et al., 2018a, 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 skeletonisation/biomineralisation (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 for the study of early animal evolution.

Despite challenges in determining the precise phylogenetic position of many Ediacaran taxa (summarised in Dunn and Liu, 2019), considerable progress has been made investigating
patterns in the temporal and environmental distribution of Ediacaran macrofossils. Global-scale studies have recognised 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 Miaohe 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 & Droser, 2013; Reid et al., 2020). Furthermore, redox conditions are recognised to control the presence or absence of fossils, and by inference original organisms, within some successions (Hall et al., 2013; Wood et al., 2015; Sperling et al., 2016; Cui 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 (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 variation in 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 (~574–556 Ma; Noble et al., 2015; Rooney et al., 2020; Matthews et al., 2021) being older than the White Sea assemblage (~558–550 Ma; Martin
et al., 2000), and the Nama assemblage (<550 Ma; e.g. Narbonne et al., 1997), although some overlap is recognised (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 valid 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 at a global (Narbonne, 2005) or local scale (Narbonne et al., 2014).

The position of continental landmasses shaped the distribution of benthic marine taxa in 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. Whittington & Hughes, 1972; Valentine & Moores, 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 (Goddéris et al., 2014), both of which are known to affect the 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 multiple authors (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 utilise the modern geographic distribution of the Ediacaran macrobiota to constrain past palaeogeographic reconstructions (e.g. Waggoner, 1999; Meert and Lieberman, 2008; Zakrevskaya, 2019; though notably not Waggoner, 2003), based on assumptions that similar taxonomic assemblages would have been geographically closely spaced, or that biomineralisers were likely to have favoured low, warmer, palaeolatitudes. Attempts to tackle the inverse problem—using palaeogeographic knowledge to provide insight
into the distribution and potential evolutionary trajectories of Ediacaran taxa—are complicated by considerable uncertainty regarding late Neoproterozoic palaeogeographic reconstructions (e.g. Merdith et al., 2017; Evans, 2020). However, in order to draw quantitative comparisons between the competing influences of tectonics, palaeogeography, environment, and evolution on observed Ediacaran biotic assemblages, we must consider this palaeographic approach.

Discussions regarding the relative importance of age, palaeoenvironment (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, those studies generally agree that: 1) those factors are not mutually exclusive; and 2) attempts to determine the relative influence of different factors are hindered by 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 those as evolutionary biozones), they are unable to de-convolve palaeogeographic and evolutionary signals. There have been no previous attempts to explore the palaeolatitudinal distribution of Ediacaran macrofossils quantitatively, from the perspective of trying to identify and test the 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 & 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 palaeogeographic 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 not considered (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 global sections in which the taxon occurs), original ‘composition’ (i.e. biomineralised, organic-walled, agglutinated or soft-bodied), 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 (though 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 Kimberellamorpha morphogroups. We recognise 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.

In order to focus on temporal trends rather than the Avalon, White Sea, Nama and Miaohe biotic assemblages identified by previous studies, we assessed the taxa within 10 Myr time-bins of >581 Ma, 580–571 Ma, 570–561 Ma, 560–551 Ma, and 550–539 Ma (the latter being slightly longer to encompass recently revised radiometric dates from terminal Ediacaran sections; Linnemann et al., 2019).
There remains much debate surrounding the palaeogeographic position of major Precambrian
cratons during the Ediacaran Period (e.g. Pisarevsky et al., 2008; Merdith et al., 2017).

Palaeogeographic 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 upon 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 palaeogeographic reconstructions, to identify those reconstructions that are
most consistent with assumed palaeobiological preconceptions. While 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 palaeogeographic
reconstructions (for example those of Scotese, 2001; Smith, 2001; or Li et al., 2013), often
without explicit explanation of why those reconstructions were chosen over alternatives.

There are two broad categories of palaeogeographic reconstructions: continental-drift style
models, or full-plate tectonic models (see Merdith et al., 2021 for an overview). The former
category model only the kinematic evolution of continental crust, whereas the latter, in addition
to the motion of continents, also explicitly model the evolution of plate boundaries and tectonic
plates through time. Both types 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 instead
on the palaeomagnetic and geological record preserved on continents, including data such as the metamorphic history of orogens, inception ages of rift basins, and ages and geochemical makeup of dykes and volcanic rocks emblematic of arc assemblages (e.g. Domeier and Torsvik, 2019). Palaeomagnetic data are used in both categories of models 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 Earth’s lithosphere invites competing interpretations of the data that become more prevalent as one moves further back in time, because there are both fewer data, and no effective methods to constrain absolute palaeolongitude. Moreover, contradictory palaeomagnetic data in the Ediacaran (e.g. Abrajevitch and Van der Voo, 2010) have led to hypotheses suggesting 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, while 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). While this integration is possible within continental-drift style models, it is not explicitly demonstrated by them.

In our analysis we use two models: 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. Due to
uncertainties within the literature surrounding continent positions during the Ediacaran (e.g. Pisarevsky et al., 2008), we have also plotted all of our data on the widely used model of Scotese (2001) (hereafter SCO01) (Supp. Figs 13–22). The SCO01 reconstruction is a continental-drift model that has been used in Phanerozoic and Ediacaran studies investigating ancient biodiversity and palaeogeographic 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-Palaeozoic to present; however, in the Ediacaran the differences are more evident (see Supp. Fig. 1), and are driven primarily by selection of different palaeomagnetic data between the two models (c.f. 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 permits comparison of our findings between them, and consideration of the level of confidence we can place in observed patterns.

Data processing and analysis

Each locality was plotted on to a modern world map in QGIS (Fig. 1a). These points were exported to the GPplates 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 half-way through each of our time-bins for analysis (i.e. at 575 Ma, 565 Ma, 555 Ma, and 545 Ma) (Fig. 1b, Supp. Fig. 1b–c).

Data were extracted from the database and plotted against the coordinates in QGIS to permit data visualisation and 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 visualise data pertaining to the
whole interval (>581–539 Ma), since 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 for the majority of data presented. The environmental setting (dominant lithology and nearshore versus offshore depositional environment) was also documented for each locality.

Hierarchical cluster analysis was performed using R and 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 optimise support for measures of similarity; Supp. 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 provides 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). Chi-squared 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 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 otherwise stated. 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 Supp. Figs 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 recognisable 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, Finnmark and Newfoundland) include taxa belonging to two new Types (Frondomorphs, which dominate, and Tubular taxa, represented by recently described putative SiO₂ biominalising tubular taxa from Finnmark; Moczydłowska et al., 2021), as well as a putative member of the ‘Sponge’ morphogroup (Thecтарdis; Sperling et al., 2011). The positioning of these localities across low (< 45°) and high (> 45°) palaeoaltitudes is consistent with a global distribution for Frondomorphs and protistan forms by this point.

Between 570–561 Ma, taxonomic diversity in Avalonia (Charnwood, U.K., and Newfoundland) increased (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 (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 560–551 Ma, the diversity of both Types and genera dramatically increases (from 25 to 110 genera), with a corresponding increase in the number of localities (from 4 to 13; Supp. Figs 3–4). This increase occurs primarily at lower palaeolatitudes (which exhibit 107 taxa across 11 localities), whilst higher palaeolatitudes remain less diverse (8 taxa across 2 localities; Figs 2 inset and 3, Supp. 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 palaeogeographic 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 variation in the extent of outcrop area that has been subjected to palaeobiological investigation (Allison and Briggs, 1993).

In the final ~10 Myr of the Ediacaran Period, the diversity of the macrobiota declines to 60 taxa despite an increase in the number of sampled localities to 17 (Fig. 2 inset, Supp. Figs 3–4). This apparent dip in generic diversity (consistent with Laflamme et al., 2013; Darroch et al., 2015; Muscente et al., 2018), appears restricted to lower palaeolatitudes despite those regions actually 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 5 localities; Figs 2 inset and 3, Supp. Figs 6). This latest Ediacaran time-bin sees a sizeable proportion of Tubular taxa, which occur at 15 of the 17 documented fossil localities.

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 to the distribution of localities across 20° palaeolatitudinal bands (with the null hypothesis being that they follow the same distribution) revealed a weakly-significant difference ($KW \text{ test, } p = 0.094$; Table 1). When the data are normalised to sampling intensity
(i.e. the latitudinal distribution of localities), no obvious difference between low and high latitudes is recovered (Supp. 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 to 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 locality distribution may not fully explain the taxon distribution (Supp. Fig. 3). When testing our two latitudinal bands individually, there is 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 latest Ediacaran radiation and ensuing diversity dip (Figs 2–3, Supp. 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 2–3, Supp. 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, resulting in a peak in diversity between 570–561 Ma (Supp. Fig. 6). Frondomorph fossils across all time display a significant chi-squared test (\( \chi^2(1, N = 195) = 16.572, p << 0.001 \), Table 1, testing Frondomorph taxa against non-Frondomorph taxa in low and high palaeolatitudes, with the null hypothesis that they follow the same distribution), likely due to the diverse populations of such fossils reported from high-palaeolatitude U.K. 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) and all other Types are too poorly sampled to perform valid chi-squared
tests. The Bonferroni-corrected $p$-value for 5% significance is 0.007 for the chi-squared tests
performed for taxa on the MER21 reconstruction (Table 1).

Bilateral Taxa

Bilateral Type (Bilateralomorpha, Dickinsoniomorpha and Kimberellamorpha) body fossils
occur almost entirely within low palaeolatitudes (all 26 Bilateral taxa occur at low
palaeolatitudes, only 1 occurs at high palaeolatitudes; Figs 3, 4a,c; Supp. Figs 10, 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 chi-squared 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 was weakly-significant, ($\chi^2(1, N = 195)$
$= 6.183, p = 0.013$, where a 5% significance level is given by 0.007 with 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, Supp. Fig. 10) and were 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 (Supp. Fig. 9b).

Biomineralisers and Tubular fossils

Other than the recent reports of silica biomineralising tubular taxa from Finnmark
(Moczydłowska et al., 2021), organisms with a biomineralised skeleton, and all other tubular
taxa, are observed only between 560–539 Ma. The latest Ediacaran distribution of tubular, biomineralising, 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 biomineralising 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, Supp. 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 biomineralising organisms. All 12 sites containing proposed biomineralising organisms contain biomineralising tubular genera.

The distribution of taxa by body composition (biomineralising, 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 (Supp. Fig. 9d–f). The distribution of biomineralising organisms is dominated by that of tubular taxa. Chi-squared 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). Biomineralising 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, dominant lithology, and depositional setting, is presented in Fig. 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 Miaohé Member sit apart from the rest of the localities, followed by three separate branch 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 Miaohé cluster (see Muscente et al., 2019) is observed. This may be a result of our analysis grouping individual formations within combined geographical locations (in contrast, Muscente et al. 2019 analysed data at a 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 (for example, the two high-latitude Avalonian localities of Newfoundland and Charnwood, U.K.). All White Sea sites are found at low palaeolatitudes, which may indicate a degree of provinciality. However, at a first-order scale, no obvious difference between the low and high palaeolatitude distributions arises 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 all 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 Ma and 560–551 Ma time-bins. This correlation suggests that once age is taken out of the equation, the
roles played by palaeolatitude and depositional environment in shaping assemblage composition are difficult to deconvolve.

**Discussion**

*Overall distribution*

Broad-scale late Ediacaran temporal trends in biodiversity identified in previous studies include a major diversification in genera and morphogroups ~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 recognise that overall diversity through time exhibits a statistically significant difference to the locality trends, consistent with either or both of these patterns (Fig. 2 inset; Supp. Fig. 3), these trends are only observed at low latitudes, where it is not possible to statistically distinguish sampling biases from taxonomic trends (Supp. Fig. 6). Our study provides greater discrimination of patterns in data pre-561 Ma than previous studies (most of which combine the ~20 Myr Avalon assemblage into one datapoint), and reveals an increase in taxonomic diversity (from 14 to 25 taxa globally, Supp. 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 animal 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; Saeedi 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, though 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 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 normalised against the number of fossil
localities, the latitudinal biodiversity difference across palaeolatitudes appears flat (Supp. 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 palaeogeographic
reconstructions considered (Table 1; Supp. Table 3).

Although the data are sparse in the early part of the late Ediacaran, our maps potentially reveal
insight 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 utilised waterborne dispersal to become widely
distributed as part of their reproductive strategy (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 they had a considerable, as yet unrecognised, evolutionary
history prior to their first appearance in this study. There are few shallow marine environments
pre-561 Ma (4 of 8 localities present: Lantian Formation, Finnmark, Wonoka Formation and
the Itajaí Basin, and the latter two currently have only one described taxon), or carbonate-
dominated successions (1 of 7 localities is carbonate: Wonoka Formation, while the Nadaleen
Formation is mixed siliciclastic and carbonate lithologies: the rest are all siliciclastic).
Differences in community composition amongst these sites could therefore result from their
recording distinct environments and ecosystems, but it is difficult to make meaningful direct
comparisons when 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 age of the sites. Within the
sub-dendrograms, environment and lithology appear to exert an important control on 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 Kimberellamorpha; although the data are not sufficient to perform chi-squared tests on the individual morphogroups), even after data have been normalised to account for variation in localities/sampling (Supp. Fig. 11). The pattern appears most distinct at the first appearance of Bilateral taxa, between 560–551 Ma (Supp. 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 recognise that our Bilateral grouping is a crude proxy for phylogenetic affinity rather than a direct record of evolutionary relationships, and incorporates some taxa whose bilaterian affinity is contentious (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 an important step in metazoan evolution.

Body composition and tubes

Organic-walled, biomineralising and tubular taxa had a widespread palaeolatitudinal
distribution at the end of the late Ediacaran on both of the palaeocontinental reconstructions
considered (Fig. 5; Supp. Fig. 19). Such a global distribution challenges the notion that
biomineralisation is preferentially restricted to lower palaeolatitudes. This restriction is thought
to exist because modern biomineralisation 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 biomineralising 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 temperatures are suitable, and in cool water conditions if 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 non-uniformitarian possibility
that certain Ediacaran carbonate-bearing successions could have been cool-water settings, until
evidence is found to the contrary.

CaCO$_3$ biomineralising, organic template, agglutinating and soft-bodied tubular taxa are
globally distributed from their first appearance between 560–551 Ma, suggesting that they may
have experienced a rapid global radiation. This result contrasts with that of Waggoner (2003,
fig. 5), who recognised a latitudinal diversity gradient for tubular organisms (n.b. 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 biomineralised calcium carbonate. *Cloudina* is widely distributed, found at 11 of 12 sites recorded to contain biomineralising taxa. Only three low palaeolatitude sites (West USA, Iran and the Dengying Formation) have *Cloudina* as the only biomineralising taxon present, and so even if *Cloudina* specifically is found to have been non-biomineralised, our reported global distribution of biomineralising taxa would remain unchanged. In such a scenario, biomineralising tubular taxa would become less prominent, present in only five of the remaining nine sites.

*Comparison with the SCO01 reconstruction.*

There are three key differences between taxon distributions on 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 ~560 Ma and subsequent decrease ~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). Secondly, the SCO01 distribution of both Bilateral taxa and biomineralisers is global, so no significant difference is found between the low and high palaeolatitude groups. Finally, significant and weakly-significant chi-squared signals are observed for the palaeolatitudinal distributions of soft-bodied taxa and Algal taxa respectively (Supplementary Table 3), likely due to diversity peaks at lower latitudes for algae, biomineralising 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 (~560–551 Ma) arise from differences in the depth of deposition of the available outcrops. Whilst most of the localities plotted on the maps between 580–561 Ma are offshore, and the majority of the younger localities were deposited in shallow settings (Supp. 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 recent discoveries in localities 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 Miaohe 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 Fig. 6a, likely reflecting both different cluster analysis methodology, and a far smaller taxonomic dataset (46 taxa and 13
localities) in that study. The sensitivity of these hierarchical cluster analyses (both within this study and others) to criteria of inclusion (e.g. minimum number of taxa, see Supp. Fig. 23) limits their utility in drawing strong conclusions regarding the similarity of fossil assemblage compositions.

The global distribution of biomineralisers observed in this study contrasts with that of Zakrevskaya (2019), who predicts a tropical distribution of biomineralising organisms by assuming that biomineralisation 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 permitted biomineralising organisms to have been viable across a wider 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 amongst 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 authors (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
biomineralising 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 authors (Boag et al., 2016; Muscente et al., 2019) in suggesting that age, palaeoenvironment, taphonomy and palaeolatitude all likely played a role in shaping the distribution of Ediacaran macrofossil taxa. We consider it likely that age exerts a high-level control on assemblage similarity, and we recognise that at a local to regional scale, palaeoenvironment exhibits a strong relationship with the presence or absence of certain taxa (e.g. Grazhdankin, 2004, Gehling & Droser, 2013; Reid et al., 2020). However, our results indicate that palaeolatitude may also impart organism-specific influences on Ediacaran macrobiota distribution. 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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Figure captions

Figure 1: Precambrian cratons (bold text), and the locations of Ediacaran fossil sites included in this study (italic), plotted on: (a) the modern global map (cratons shaded), and; (b) the Merdith et al. (2021) palaeogeographic reconstruction at 555 Ma.

Figure 2: Distribution of Fossil Types, with each locality presented as a pie chart centred on its palaeo-location (black arrows indicate the palaeo-location for instances where the pie charts have been moved to avoid overlap with neighbouring sites), and each palaeogeographic 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) to 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 rise in taxonomic diversity at low latitudes (yellow line) ~ 560 Ma. However, this increase is coupled with a significant rise in the number of documented fossil localities at low latitudes (green line). Thus, the apparent difference in the magnitude of this ‘radiation’ at high and low latitudes may be a function of increased availability of exposure of that age. Conversely, the dip in generic diversity observed ~550 Ma is coupled with a further increase in the number of available low latitude localities. However, the decline 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-value = 0.093 (Table 1).

Figure 3: Stacked area chart revealing 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 palaeolatitudes, but not at 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 570–561 Ma, with a significant chi-squared result obtained when comparing frondomorph taxa against non-frondomorph taxa at low and high palaeolatitudes (p << 0.001, Table 1).

Figure 4: The 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 palaeo-location where necessary). Pie chart area 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). (b–d) Graphs comparing the distribution of Ediacaran fossil localities for all time (blue) to the distribution of (b) all taxa, (c) Bilateral Type taxa, and (d) Non-bilateral taxa. All Bilateral taxa included in (c) are found between 560–539 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 at high palaeolatitudes, with a weakly-significant chi-squared result when comparing bilateral taxa against non-bilateral taxa at low and high latitudes (p = 0.013, Table 1).

**Figure 5:** The global distribution of biomineralising and tubular Ediacaran taxa. (a) Tubular fossils and all other biomineralising fossils (faint circles), with pie charts of only biomineralising organisms overlain (solid circles), centred over the locality at which they are found at 545 Ma (black arrows indicate the palaeo-location 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 biomineralising organisms between 550–539 Ma. Biomineralising organisms are dominated by tubular taxa, and are often found alongside non-biomineralising tubular organisms. (b–d) Graphs comparing the distribution of Ediacaran fossil sites for all time (blue lines) to the distribution of: (b) CaCO₃ biomineralising 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 biomineralising 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 biomineralising and organic template taxa (b–c) are found between 550–539 Ma. None of the taxonomic groupings in (b–d) show a statistically significant deviation between high and low latitudes.

**Figure 6:** Average linkage dendrograms for localities with >6 Ediacaran macrofossil taxa, including the presence or absence of bilaterian trace fossils: (a) for the whole time interval; and (b–d) 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 dominant fossil-bearing lithology (carbonate or siliciclastic; see Supplementary Information 1 for further information). Height (y-axis) represents taxonomic dissimilarity using the average-linkage method. High cophenetic correlation coefficients of 0.804, 0.994, 0.933, and 0.739 for (a–d), respectively, indicate reliable groupings of the original datapoints. Localities previously recognised 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 (a), and in (d). Some grouping of palaeolatitudes is present within sub-branches in the MER21 reconstruction in (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 (b–d), both environment and palaeolatitude could feasibly explain the clustering within the oldest two time-bins, but there
are no clear relationships between these variables and sub-clusters in (d). Alternative dendrograms with different filters on the number of taxa per locality included can be found in Supp. Fig. 23.
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**Table 1:** Key statistical results for the MER21 reconstruction (results for the SCO01 reconstruction are presented in Supp. Table 3). Significant and weakly-significant p-value results in bold. Significant and weakly-significant p-values for Kruskal-Wallis tests are below 0.05 and between 0.05–0.10, respectively. Significant and weakly-significant p-values for chi-squared tests on Types are corrected to 0.007 and 0.014 using the Bonferroni correction, respectively. Chi-squared tests test whether there is a significant difference between the distributions of the selected taxonomic groups at low and high palaeolatitudes.
Figure 3

(a) Low latitude Types

(b) High latitude Types

Legend
- Algal
- Bilateral
- Erniettomorph
- Frondomorph
- Protist
- Radial
- Tubular
- Miscellaneous
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