A Chronostratigraphic Framework for the Rise of the Ediacaran Macrobiota: New Constraints from Mistaken Point Ecological Reserve, Newfoundland

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ABSTRACT

The Conception and St. John's Groups of southeastern Newfoundland contain some of the oldest known fossils of the Ediacaran macrobiota. Mistaken Point Ecological Reserve (MPER) UNESCO World Heritage Site is an internationally recognised locality for such fossils, and hosts early evidence for both total-group metazoan body fossils, and metazoan-style locomotion. The MPER sedimentary succession includes ~1500m of fossil-bearing strata containing numerous dateable volcanogenic horizons, and therefore offers a crucial window into the rise and diversification of early animals. Here we present six stratigraphically-coherent radio-isotopic ages derived from zircons from volcanic tuffites of the Conception and St. John's Groups at MPER. The oldest architecturally complex macrofossils, from the upper Drook Formation, have an age of 574.17 ± 0.66 Ma (including tracer calibration and decay constant uncertainties). The youngest rangeomorph fossils from MPER, in the Fermeuse Formation, have a maximum age of 564.13 ± 0.65 Ma. Fossils of the famous 'E' Surface are confirmed to be 565.00 ± 0.64 Ma, while exceptionally preserved specimens on the 'Brasier' Surface in the Briscal Formation are dated at 567.63 ± 0.66 Ma. We use our new ages to construct an age-depth model for the sedimentary succession, constrain sedimentary accumulation rates, and convert stratigraphic fossil ranges into the time domain to facilitate integration with time calibrated data from other successions. Combining this age model with compiled stratigraphic ranges for all named macrofossils within the MPER succession, spanning 76 discrete fossil-bearing horizons, enables recognition and interrogation of potential evolutionary signals. Peak taxonomic diversity is recognised within the Mistaken Point and Trepassey Formations, and uniterminal rangeomorphs with undisplayed branching architecture appear several million years before multiterminal, displayed forms. Together, our combined stratigraphic, palaeontological, and geochronological approach offers a holistic time-calibrated record of evolution during the mid-late Ediacaran Period, and a framework within which to consider other geochemical, environmental, and evolutionary datasets.

Keywords: Ediacaran, Geochronology, Rangeomorph, Evolution, Palaeobiology

1. INTRODUCTION

The Avalon Peninsula of Newfoundland, Canada, has long been recognised as one of the world's leading localities for Ediacaran macrofossils. It hosts a >7.5 km thick late Neoproterozoic volcano-sedimentary succession, with a broadly shallowing-upwards trend encompassing basin, slope, shoreface and fluvial palaeoenvironments (Williams and King, 1979; Gardiner and Hiscott, 1988; Wood et al., 2003; Canfield et al., 2007). Macrofossils of Ediacaran age occur within siliciclastic deposits of the Conception and St. John's Groups, which have been interpreted as deep-marine and slope depositional environments close to a volcanic arc (Wood et al., 2003). The Mistaken Point Ecological Reserve (MPER), located on the southeastern portion of the Avalon Peninsula (Fig. 1), contains some of the most abundant and well-preserved fossil assemblages of Ediacaran taxa in the region (Narbonne in Fedonkin et al., 2007; Liu and Matthews, 2017; Fig. 2). Discovered in the late 1960s (Misra, 1969), this locality has thousands of fossil specimens on bedding planes spanning ~1.5 km of stratigraphic thickness. Fossils are preserved as impressions of external morphology beneath tuffites (Narbonne, 2005; Liu, 2016), which undergo preferential weathering and erosion (Matthews et al., 2017) to reveal the underlying ancient seafloors for scientific study.

Fossils of the Ediacaran macrobiota have received multiple phylogenetic interpretations (summarised Dunn and Liu, 2019), but recent ichnological, palaeontological, developmental and biomarker studies together demonstrate that at least some Ediacaran taxa represent early metazoans (Ivantsov and Malakhovskaya, 2002; Gold et al., 2015; Bobrovskiy et al., 2018; Dunn et al., 2018, 2019; Evans et al., 2019). The Avalonian localities in Newfoundland are considered to be amongst the oldest Ediacaran macrofossil-bearing sites (Boag et al., 2016; Pu et al., 2016), and include body and trace fossils that have been interpreted as evidence for the presence of early metazoans (Liu et al., 2010, 2014, 2015; Menon et al., 2013; Dunn et al., 2018). However, the precise phylogenetic positions of many Newfoundland taxa, and their relationships to one another (Dececchi et al., 2017), remain to be resolved.

Understanding the causes of the emergence, evolution, and extinction of the Ediacaran macrobiota, and the relationship of these events to environmental change, requires the construction of an accurate, highly-resolved chronostratigraphic framework within which biostratigraphic, taphonomic, sedimentological, geochemical, and environmental data can be integrated. This must be achieved region by region, with the ultimate goal being the integration of worldwide geochemical, palaeobiological, and stratigraphic data into a common time domain, facilitating objective comparison and integration (Condon et al., 2015).

Despite the obvious potential of Newfoundland's Ediacaran volcaniclastic successions for geochronological studies, relatively few peer-reviewed dates have been published from these sections (e.g. Pu et al., 2016; Canfield et al., 2020). Similarly, although the extensive succession of fossil-bearing horizons within MPER holds substantial potential for revealing evolutionary patterns within mid-late Ediacaran marine ecosystems, no comprehensive review of the stratigraphic ranges of taxa has previously been published. We here present stratigraphic ranges for all formally described macrofossil taxa throughout the Conception and St. John's Groups in MPER, in addition to six new U-Pb (zircon) chemical abrasion – isotope dilution – thermal ionization mass spectrometry (CA-ID-TIMS) dates from MPER tuffites spanning the majority of the fossil-bearing section. We use these dates to develop and evaluate an age-depth model for the succession, with the aim of facilitating regional and global integration and comparisons. Our ages also permit development of an age model for sediment deposition through the Drook to Fermeuse Formations, and provide temporal constraint for the evolutionary patterns identified in our stratigraphic range charts.

2. SEDIMENTARY CONTEXT OF GEOCHRONOLOGICAL SAMPLES

The radio-isotopic dating in this study is based on analysis of zircons from tuffite horizons within the siliciclastic sedimentary succession. The mechanism by which this tuffaceous material was introduced to the depositional setting is debated, with some workers considering it to have been introduced by turbidite or contourite currents (Benus, 1988). However, others have assumed that tuffaceous material was deposited onto the sea surface by a volcanic event, before settling to the seafloor from suspension (Anderson and Conway-Morris, 1982; Jenkins, 1992;

Wood et al., 2003; Bamforth et al., 2008; Brasier et al., 2011). These competing scenarios have implications both for taphonomy, and for the interpretation of radio-isotopic dates obtained from tuffites.

We analysed tuffite samples from six stratigraphic horizons within MPER for high-precision U-Pb (zircon) radio-isotopic dating (SI1, Fig. S1). The locations and stratigraphic levels of these samples are presented in Figure 1. Stratigraphic levels and distances stated herein are based on new mapping of the MPER succession conducted between 2011 and 2014 (Matthews, 2015).

DRK-10. Sample DRK-10 was collected from the so-called 'Pizza Disc Bed' at Pigeon Cove. This locality lies ~25 m below the top of the Drook Formation, and is notable for its preservation of large lobate 'pizza discs', also known as ivesheadiomorphs (Liu et al., 2011), as well as numerous small frondose fossils (Liu et al., 2012). The fossil-bearing horizon is directly overlain by ~35 cm of green-buff, highly cleaved volcaniclastic sediment (SI1, Fig. S1a). The analysed zircons come from an integrated sample of this ~35 cm-thick tuffite.

A slabbed and polished section through the lower ~25 cm of the tuffite reveals possible convolute bedding and diffuse patches of carbonate, probably of secondary origin, at the base (SI1, Fig. S2). This basal 7.5 cm is darker in colour than the surrounding light green-buff material and consists of normally-graded, fine-grained sandstone to siltstone with extensive chlorite-rich cement. Above this lies a poorly-sorted siltstone with local sand-size clasts, and several laminae with ~25º apparent dip to bedding (i.e. the interpreted palaeo-horizontal plane of section). The bed continues to grade normally into a mudstone at the top. At the very top of the bed (above the analysed sample in SI1, Fig. S2), mm-scale interbeds of the tuffite with the overlying grey siltstone suggest post-depositional reworking of the tuffite.

DRK-1. This sample was collected from the lower Briscal Formation at Daley's Cove, ~50 m above the top of the Drook Formation, within a succession of thin to medium bedded grey sandstones that fine upwards to siltstones (SI1, Fig. S1b). It comprises a discrete ~5 cm thick buff-green, silt-grade tuffite (SI1, Fig. S3), which does not overlie a known fossil-bearing surface. The basal ~1 cm of the sampled horizon is dark grey in colour, and contains shale clasts ~3 mm in diameter and a number of light-grey parallel laminae. This lowest layer grades into ~8 mm of light-buff siltstone dominated by irregularly-shaped "clots", ~1 mm diameter, getting smaller-upwards and composed of authigenic chlorite crystals (interpreted to be replacing unstable volcanic minerals). The remainder of the bed comprises normally-graded, light-buff to green siltstone, with prominent parallel laminae throughout, and some evidence of cross-lamination in the middle of the bed. The sample collected was of the entire ~5 cm thickness of the tuffite.

BRS-1. Sample BRS-1 is from a tuffaceous bed directly overlying the recently described 'Brasier' Surface in the lower Briscal Formation, which yields exceptionally preserved macrofossils including *Fractofusus* and *Charniodiscus* (Liu, 2016; Liu and Matthews, 2017). The sampled bed, lying ~110 m above the base of the Formation, comprises a ~30 cm thick, normally-graded medium sandstone, which is noticeably greener at the base. This buff-green colour commonly indicates the presence of tuffaceous material elsewhere in MPER, and so our sample was preferentially collected from the basal 10 cm of the bed. This bed is the lowest of several thickly-bedded buff-green tuffaceous beds that create a noticeable, metres-thick marker horizon that contrasts with the dark grey deposits of the rest of the local section (SI1, Fig. S1c). It was not possible to collect a sample suitable for slabbing from this bed.

MP-14. This sample is from the tuff that directly overlies the 'E' Surface at Mistaken Point (SI1, Fig. S1d), and lies within the upper Mistaken Point Formation, ~60 m below its boundary with the Trepassey Formation. The sample was collected from above the 'E' Surface 'Yale' outcrop (*sensu* Clapham et al., 2003), and is the same horizon sampled by Pu et al. (2016). The tuffite overlying the fossil surface comprises a ~5 mm thick crystal tuff horizon dominated by feldspar and polycrystalline lithic fragments in a chlorite matrix, overlain by 10 cm of buff, highly cleaved tuffite, grading from medium sand-grade material at the base to mud-grade at the top. There is a marked transition from sand- to silt-grade material 2 cm from the base of the slab (SI1, Fig. S4). The tuffite is capped by ~15 mm of black chlorite and pink carbonate, both of which are interpreted to have been emplaced some time after the deposition of the tuffite. This chlorite-carbonate horizon is only seen above the Mistaken Point 'Yale' and 'Queens' outcrops, and is not observed above other outcrops of the 'E' Surface at Cape Race, Watern Cove, or the Stumps (Matthews et al., 2017). Overlying this enigmatic horizon are 24 cm of normally graded, green to grey siltstone. The basal thin, ~5 mm-thick crystal tuff horizon could not be sampled in volumes necessary for geochronological analysis due to restrictions on collection, so the analysed material comes from the overlying 10 cm-thick tuffite, but below the chlorite-carbonate horizon.

LC-1. This sample is a ~4 cm-thick buff-coloured tuffite from the western edge of Long Cove, and lies directly on top of a fossil surface within the Trepassey Formation informally referred to as the 'Pizzeria' on account of its abundant ivesheadiomorph specimens (formerly "pizza discs") (SI1, Fig. S1e). The recognisable non-ivesheadiomorph taxa at this locality include *Charnia*, *Charniodiscus*, and *Pectinifrons*. The tuffite comprises green to light-grey siltstone, with faint sub-parallel laminae in places (SI1, Fig. S5). Further analysis of internal structure within the tuffite is hampered by weathering and associated iron oxyhydroxide and dendritic manganese mineralisation. The full thickness of this tuffite bed was sampled.

SH-2. SH-2 samples a ~30 cm tuffaceous deposit from within the lower Fermeuse Formation (SI1, Fig. S1f), located adjacent to the well-documented Shingle Head fossil horizon (Clapham et al., 2003). The Shingle Head surface documents the stratigraphically highest published rangeomorph assemblage in the MPER succession. The basal surface of the bed is topographically uneven, which may be associated with the widespread slumping within this part of the succession (Wood et al., 2003). The sampled tuffite unit includes convolute laminae, and is inferred to have acted as the décollement for the overlying slumped beds. As such this tuffite would have been previously deposited upslope.

The basal 8 cm of the tuffite is a fining-upwards sandstone capped by weakly convolute mm-scale laminae of green ash and black mudstone (SI1, Fig. S6). These grade into a ~20 cm thick zone of intense convolute lamination, with recumbently folded sediment. The uppermost 8 cm of the sample is cemented by ferroan calcite (identified by staining with Alizarin Red-S and Potassium Ferricyanide, following Dickson, 1965).

Tuffite Deposition

None of the sampled tuffites have the characteristics of simple water-lain ash fall events. Several of the sampled tuffites exhibit evidence for subaqueous, down-slope deposition, including graded beds with features also found in classical Bouma sequence deposits; ripple cross-lamination; intraclasts; and gradational or interbedded upper boundaries that transition into often finer-grained tuffite-free siliciclastic siltstones and mudstones (Bouma, 1962). The basal coarse-grained crystal tuff unit within the MP-14 sample is here interpreted parsimoniously as a coarser deposit below an upward-fining turbidite. Comparable flow-head deposits of lithic/crystal tuffs with little fine-grained matrix, overlain by normally-graded tuffaceous turbidites, are known from recent ash-rich turbidites, such as those originating from the Minoan eruption of Santorini (Sparks and Wilson, 1983). We therefore propose that at least some of the MPER tuffites were deposited by ash-laden turbidity currents rather than water-lain ash falls. This ashy turbidite model implies a hiatus between initial tuff deposition, its reworking downslope, and its eventual re-deposition. Our interpretation is similar to that made for U-Pb (zircon) dating of similar tuffites in other basins where *a priori* constraints allow for a test of the U-Pb (zircon) dating (e.g. Schmitz and Davydov, 2012). Such studies suggest that any lag between magmatic zircon ages and sedimentation is not significant at the level of interpretation made in this study. Although our dates (and those of most previous studies) do not account for re-sedimentation and erosional mixing (cf. Pu et al., 2016), this need not hinder construction of a MPER age-depth model. Moreover, the bulk rock geochemistry of the MPER tuffites, upon which inferences of tectonic setting have been made (Retallack, 2014, 2016), is called into question by the incorporation into the beds of non-volcaniclastic material during re-sedimentation. Our ashy-turbidite hypothesis infers that the alignment of frondose taxa directly beneath such tuffites may record flow direction of turbidity currents themselves, rather than inter-depositional contour currents as has been suggested previously (e.g. Wood et al., 2003; Flude and Narbonne, 2008).

3. STRATIGRAPHIC RANGE CHART CONSTRUCTION

A total of 22 distinct Ediacaran species have to date been formally reported within MPER (Liu and Matthews, 2017), along with several as-yet unnamed taxa (e.g., ‘ostrich feathers’, Clapham and Narbonne, 2002). Some previously described taxa (e.g. *Aspidella* and *Hiemalora*) have been re-interpreted as the holdfast discs of frondose taxa (Serezhnikova, 2007; Burzynski and Narbonne, 2015), and others such as ivesheadiomorphs are now regarded as taphomorphs (Liu et al., 2011). The combined stratigraphic ranges and temporal distributions of these fossils through the MPER section offer opportunities to identify and critically assess hypothesised evolutionary relationships between Ediacaran macro-organisms (e.g. Brasier and Antcliffe, 2009; Laflamme et al., 2013; Dececchi et al., 2017), and to recognise possible ecological or environmental factors that may have influenced such relationships through time (e.g. Darroch et al., 2013; Mitchell and Kenchington, 2018).

Biostratigraphic ranges can also be used in palaeogeographic reconstruction, and to define regional or global stratigraphic units. The Ediacaran System spans a time interval of over 90 million years, but its formal division is yet to be achieved (Xiao et al., 2016). Determining whether Ediacaran macrofossils are suitable for use in biostratigraphic correlation (possessing distinct stratigraphic ranges, broad geographic ranges, high abundance, and independence from facies) would be an important step towards developing a global Ediacaran stratigraphic framework (e.g. Narbonne et al., 2012; Xiao et al., 2016), but requires detailed records of species occurrence in space and time. Although stratigraphic ranges cannot be taken as accurate indicators of the exact first and last appearances of taxa, owing to the incompleteness of the fossil record (e.g. Jenkins, 1995; Sadler, 2004), they can constrain evolutionary hypotheses by enabling rejection of implausible/unsupported options.

Previous compilations of Avalonian stratigraphic ranges have largely focused on single taxa (typically presented in publications where a taxon is described for the first time; e.g., Gehling and Narbonne, 2007, p. 20), or 'representative' taxa (Brasier and Antcliffe, 2004; Liu et al., 2012). Particularly on the Avalon Peninsula, many fossils have only been described from a handful of well-preserved bedding planes, with other fossiliferous surfaces receiving little attention in the literature. In this study, data regarding the stratigraphic occurrence of individual Ediacaran macrofossil taxa within MPER were collated between 2007 and 2018. Fossils were identified by one of us (AGL) for consistency in taxonomic identification, and the occurrence of taxa was noted on individual studied horizons. Geological mapping and measuring of section (by JJM) throughout MPER enabled construction of a stratigraphic column onto which individual surfaces could be plotted. Where the same surface was found to crop out in multiple locations (e.g. the 'D' and 'E' Surfaces at the Stumps, Watern Cove and Mistaken Point; Matthews et al., 2017), fossil data from each of those locations is thus plotted as coming from a single stratigraphic level.

Taxonomic nomenclature follows previously published systematic descriptions or widely used informal names. Organisms were identified to species level where possible, and data were additionally cross-checked against literature records (see Supplementary Information 2) to ensure that the observations were as complete as possible. Taxa were only included where we are certain that the taxon under consideration is present: possible occurrences of a specific organism, where identification is uncertain due to taphonomic factors, have been omitted from the final figures to facilitate more robust interpretation of patterns in the dataset. Frondose fossils are grouped into the higher-level taxonomic groupings Rangeomorpha and Arboreomorpha (Erwin et al., 2011; Laflamme et al., 2013; though see Grazhdankin, 2014). Within the rangeomorphs, taxa were divided into uniterminal and multiterminal taxa (terminology cf. Dunn et al., 2018). Non-frondose impressions were assigned to discoidal specimens, taphomorphs, or non-frondose taxa/impressions.

The stratigraphic ranges here are not presented as definitive records for individual taxa. They simply summarise the current state of knowledge in the region, and are subject to revision following future discoveries. Despite this caveat, the observed patterns represent a marked advance in published documentation of the stratigraphic ranges of the Ediacaran macrobiota in Newfoundland, and permit formulation of preliminary hypotheses regarding Ediacaran evolutionary patterns and processes, which can be compared to other regional or global records such as those from the Bonavista Peninsula of Newfoundland (e.g. Hofmann et al., 2008), or Charnwood, UK (e.g. Noble et al., 2015).

4. U-Pb GEOCHRONOLOGY ANALYTICAL METHODS

U-Pb dating of zircons from six volcanic tuffs intercalated in the Conception and St. John's Groups in MPER was carried out at the National Environmental Isotope Facility, British Geological Survey, via CA-ID-TIMS analyses. Detailed analytical methods are outlined in Supplementary Information 3, and complete Pb and U isotopic data are presented in

Supplementary Information 4. Age results are illustrated in Figure 3 and reported in SI3, Figure S7. The sample age is calculated based on the weighted mean $^{206}Pb/^{238}U$ date of the youngest population analyses that overlap within 2σ analytical uncertainty, and is reported with its error at 95% confidence level in the ±*X*/*Y*/*Z* Ma format, where *X* is the analytical uncertainty in the absence of all external errors, *Y* includes *X* and the tracer calibration uncertainty, and *Z* includes *Y* and the ^{238}U decay constant uncertainty of Jaffey et al. (1971).

5. U-Pb RESULTS AND AGE INTERPRETATIONS

In this section we outline the U-Pb (zircon) dataset obtained for the six MPER ash samples. As is typical with high-precision U-Pb (zircon) datasets produced by CA-ID-TIMS, there is texture within the data that requires discussion in order to support age interpretations and age assignment. We follow the conventional interpretative approach, assigning ages using the youngest coherent population (e.g. Schmitz and Davydov, 2012), due to the need to be able to reproduce the dates that sample ages are based upon (i.e., significant Pb-loss is not likely to result in reproducible U-Pb dates). Dates older than the 'youngest population' are interpreted to reflect the analyses of xenocrystic material incorporated either prior/during eruption or during final emplacement. Additional complicating factors (i.e., Pb-loss, post-depositional reworking) are discussed below.

DRK-10. Zircon $^{206}Pb/^{238}U$ dates from the DRK-10 tuffite range from 573.36 – 577.38 Ma (n = 9) and the four youngest dates give a weighted mean age of 574.17 ± 0.19/0.24/0.66, with a Mean Square Weighted Deviation (MSWD) of 2.8. The weighted mean $^{207}Pb/^{206}Pb$ date is 573.4 ± 1.9/2.1/5.0 Ma (n = 4, MSWD = 0.32).

DRK-1. Zircon ^{206}Pb/^{238}U dates from tuffite DRK-1 in the basal Briscal Formation range from 571.02 – 580.06 Ma (n = 19), and the 8 youngest dates give a weighted mean age of 571.38 ± 0.16/0.25/0.66 Ma, with an MSWD of 2.0. The weighted mean ^{207}Pb/^{206}Pb date is 573.0 ± 1.6/1.7/4.9 Ma (n = 8/19, MSWD = 2.9).

BRS-1. BRS-1 in the middle Briscal Formation yielded zircon ^{206}Pb/^{238}U dates ranging from 566.33 – 570.63 Ma (n = 8). The youngest date (z3) is excluded due to it being significantly younger than the remaining population of data and is not reproduced. The five youngest analyses, excluding z3, give a weighted mean age of 567.63 ± 0.21/0.26/0.66 Ma, with an MSWD of 2.1. The weighted mean ^{207}Pb/^{206}Pb date is 566.8 ± 2.9/3.1/5.5 Ma (n = 5/8, MSWD = 0.52).

MP-14. Sample MP-14 is interpreted as an ashy turbidite, and the data obtained are interpreted to provide a depositional age. In this study, zircon ^{206}Pb/^{238}U dates from the MP-14 tuffite range from 563.81 – 567.48 Ma (n=11). The youngest age (z16) is interpreted as having undergone post-crystallisation Pb-loss. The four youngest analyses, excluding z16, give a weighted mean age of 565.00 ± 0.16/0.22/0.64 Ma, with an MSWD of 1.2. The weighted mean ^{207}Pb/^{206}Pb date is 567.2 ± 2.5/2.7/5.3 Ma (n = 5/11, MSWD = 0.47).

LC-1. Zircon ^{206}Pb/^{238}U dates from sample LC-1 in the Trepassey Formation range from 564.68 – 567.41 Ma (n = 11). The two youngest dates give a weighted mean age of 564.71± 0.63/0.65/0.88, and their weighted mean ^{207}Pb/^{206}Pb date is 564.9 ± 2.1/2.1/5.0 Ma (n = 2/11, MSWD = 0.69).

SH-2. The SH-2 sample, from the Fermeuse Formation, shows significant signs of slumping and redeposition, and is thus interpreted as an eruptive age providing a maximum age constraint for this level in the section. Zircon ^{206}Pb/^{238}U dates from this sample range from 563.67 – 569.01 Ma (n = 11). The six youngest dates gave a weighted mean age of 564.13 ± 0.20/0.25/0.65, with an MSWD of 1.5. The weighted mean $^{207}Pb/^{206}Pb$ date is 563.6 ± 0.9/1.0/4.7 Ma (n = 6/11, MSWD = 0.96).

All data are compiled in Supplementary Information 4 and interpreted dates are summarised in Table 1.

6. COMPARISON WITH PRIOR DATING OF THE MPER SUCCESSION AND DEVELOPING THE MPER AGE MODEL

The overarching aim of this study was to develop an age-depth model for the MPER succession, in order to provide estimates for the ages of key fossil horizons and age-ranges for fossil assemblages. Our age interpretations for each sample U-Pb dataset are now considered together in a stratigraphic framework to construct an age-depth model. We then compare our age interpretations to previously published radio-isotopic dates from ash layers in the same section.

Our study builds upon a legacy of geochronology investigations on the MPER succession. Following the early work of Benus (1988), Bowring et al. (2003) reported a coherent U-Pb (zircon) data set from ash layers in the top of the Mall Bay Formation; midway through the Gaskiers Formation; in the basal Drook Formation; and a final ash from within the fossiliferous Drook Formation, from above the Pizza Disc surface (Table 2). These unpublished dates were presented in abstract form, and it is not reported whether they are ^{238}U-^{206}Pb or $^{207}Pb/^{206}Pb$ dates. The U/Pb tracer calibration is also unknown. Nevertheless, these samples were used to conclude a short duration (~3.3 Myr) between the termination of the short-lived Gaskiers glaciation and the fossiliferous strata of the Drook Formation (e.g. Narbonne and Gehling, 2003). However it is known that these determinations pre-dated the advent of chemical abrasion for U-Pb ID-TIMS analyses. Subsequently, Pu et al. (2016) published a full U-Pb chemical abrasion ID-TIMS data set for the samples analysed in the Bowring et al. (2003) study, augmented by another Avalon Peninsula date from the 'E' Surface, and ash beds associated with glacial deposits across

Newfoundland. Pu et al. (2016) employed a number of methodological developments made since the Bowring et al (2003) study (e.g., use of zone refined Re with reduced Tl blank, improved UO_2 correction). That study increased the duration of the interval between the base of the Drook Formation and the ash overlying the fossiliferous Pizza Disc Surface from 3.3 to 8.9 Myr (Table 2). However, although the Pu et al. (2016) dates are younger than those in Bowring et al. (2003), the observed differences across the samples are not systematic (see Table 2 and below for further discussion).

This study shares two sampled horizons in common with the Pu et al. (2016) study, but the ages do not agree within the stated analytical uncertainties/laboratory specific calibration uncertainties (Table 2 and SI3 Figures S8 and S9). The first pair of dates we consider are for samples MPMP33.56 (Pu et al., 2016) and MP-14 (this study), which both sample the ash overlying the 'E' Surface. The Pu et al. U-Pb data largely overlap (SI3, Fig. S8), but the weighted mean dates differ by 1.3 ± 0.4 Myr. We note that the MPMP33.56 data are discordant, yielding a weighted mean $^{207}Pb/^{206}Pb$ date of 585.8 ± 8.4 Ma, indicating a component with an 'inherited' composition. This discordance is not observed in our U-Pb data from the same horizon (SI3, Fig. S8). The MPMP33.56 sample's 566.25 ± 0.35 Ma date does not violate the principle of stratigraphic superposition, but the fact that the U-Pb data are discordant leads us to favour the MP-14 date (this study) to constrain the age of the 'E' Surface and the MPER age-depth model.

The second pair of dates (samples DRK-10, this study, and Drook-2, Pu et al., 2016) come from two samples taken from the same horizon above the Pizza Disc surface at Pigeon Cove, based upon sample description and location data. The interpreted $^{206}Pb/^{238}U$ dates differ by 3.3 ± 0.4 Myr (Figure 3 and SI3, Figure S9). Importantly, the 570.94 ± 0.38 Ma date (Pu et al., 2016) is younger than our date of 571.53 ± 0.19 Ma from an ash bed 43 m above the Pizza Disc Surface (DRK-1). Including the 570.94 ± 0.38 Ma age in our age-depth model would require that both our DRK-1 and DRK-10 dates do not reflect deposition, and instead reflect dating of older zircons and/or open system behaviour. Both DRK-1 and DRK-10 ages from this study obey stratigraphic superposition. An alternative is that the Drook-2 (Pu et al., 2016) date is too young, possibly due to post-depositional Pb-loss, although the coherence of the U-Pb data would argue against this. This apparent bias highlights additional sources of uncertainty that require further investigation.

A third point of comparison can be made between the constraint we have for the lower part of the Fermeuse Formation (SH-2, 564.13 +/- 0.20 Ma) and a U-Pb CA-ID-TIMS date of 562.5 +/- 1.1 Ma from an ash bed (N10-SH6B, see Figure 3) that is ~17 m below the SH-2 ash (Canfield et al., 2020). Those authors regard N10-SH6B to be within the Trepassey Formation, however our geological mapping put this locality within the Fermeuse Formation. The slumping associated with SH-2 has led us to consider this as a maximum deposition age. Assuming the N10-SH6B ash is not also slumped it may be a more accurate age estimate for the lower part of the Fermeuse Formation. However the U-Pb data (Canfield et al., 2020) differs from this study and Pu et al. (2016) in a number of ways: (i) it uses a U/Pb tracer without a stated calibration (this study and Pu et al., 2016) use the EARTHTIME U-Pb tracers (Condon et al., 2015); (ii) the individual analyses are based upon multi-grain fractions; (iii) the leaching step lasted 'a few hours'; and (iv) the single dates are considerably less precise (Figure 3). Combined, these points make it difficult to assess the accuracy of this date and whether the difference between the Canfield et al. (2020) depositional age and our maximum age is geological, or reflects bias between the two datasets, or most likely, a combination of both. As such we have not included the N10-SH6B date in our age model, however it is worth noting that our MPER age model does overlap with these data when the 95% confidence interval is considered.

In this study, the age-depth model of the middle-upper Ediacaran in MPER was developed using the Bayesian Markov Chain Monte Carlo model incorporated in Chron.jl by C. Brenhin Keller. Because of potential non-resolved lead loss of analysed zircons, StratMetropolis function was used with inputs of weighted mean $^{206}Pb/^{238}U$ dates. The input data are shown in Figure 3A, and the age-depth model is plotted in Figure 3B (see also Supplementary Information 5). Based upon the discussion above relating to the prior dating, we have based our age-model on dates from this study, with the exception of including the date of 579.88 ± 0.44 Ma (sample NoP-0.9; Pu et al., 2016) that comes from the base of the Drook Formation at 'North Point', St. Mary's Bay, Newfoundland (Fig. 1B) to provide a lower age limit on the base of the Formation. Given this does not come from our measured MPER succession, and we do not know how this basal Drook age constraint projects into our measured section, except that it will either be at the base of our succession, or at a lower level, we use 579.88 ± 0.44 Ma as a maximum age for the lowermost Drook Formation in the MPER measured succession (SI3, Fig. S10). The MP12+5m and CR2 fossil surfaces in the Fermeuse Formation lie in the c.200 m of stratigraphy above the dated section, and so ages for these surfaces within the age model were cautiously ascribed by assuming a constant sedimentation rate through the Formation.

The age-depth model reveals (1) stratigraphic superposition is upheld, and (2) there is an apparent depositional rate change in the middle of the Briscal Formation, separating broadly constant, relatively slow depositional rates in the lower section from more rapid depositional rates in the upper section. The change to more rapid deposition and a greater number of tuffites from the middle of the Briscal Formation onwards is consistent with the Carey and Sigurdsson (1984) model for deposition within a back-arc basin, and could, for example, represent the transition to back-arc spreading and island arc volcanism following the initial rifting and development of an inter-arc basin (Carey and Sigurdsson, 1984).

7. STRATIGRAPHIC RANGES OF EDIACARAN MACROFOSSILS IN MPER

Previous plots of Ediacaran species occurrences against time vary significantly in their scope. They range from treatment of individual taxa in local sections (e.g. Bamforth and Narbonne, 2009), through summaries of distributions within individual regions (e.g., the East European Platform; Grazhdankin, 2014, fig. 6), to discussion of selected iconic taxa on a global scale (e.g. Brasier and Antcliffe, 2004; updated by Xiao and Laflamme, 2009; Narbonne et al., 2012). Global studies (e.g. Laflamme et al., 2013; Grazhdankin, 2014, fig. 7) reveal a broad increase in generic and higher order diversity through the late Ediacaran Avalon and White Sea assemblages (*sensu* Waggoner, 2003), followed by a decline in the Nama assemblage, but fossil occurrences are grouped at a coarse formational scale, and the taxonomic groupings are dictated to varying degrees by the competing influences of taphonomy, depth, environment, age and palaeogeography (Boag et al., 2016). If we are to interpret evolutionary trajectories from Ediacaran macrofossils, link these to geological events and phenomena, or use macrofossils for biostratigraphic correlation, we require finer-scale resolution of biostratigraphic patterns.

Previous work in Newfoundland suffers from either a lack of geochronological constraint (the Catalina Dome; Hofmann et al., 2008), and/or uncertainty surrounding regional correlation. A compilation of MPER and Catalina Dome data presented by Liu et al. (2012, fig. 8) combined fossil occurrences from sites separated by over 200 km, but the published lithostratigraphic correlations on which those correlations were based are now considered by us to be inaccurate (Matthews, 2015). The present MPER study provides a detailed local, time-calibrated dataset with which to assess fine scale, taxon-specific patterns in taxonomic distribution through time. Separating the MPER data from those of the Catalina Dome offers the opportunity to then independently compare the two sections to test observed patterns in the stratigraphic distribution of taxa.

Our data considerably extend the known stratigraphic ranges for *Vinlandia antecedens*, *Fractofusus* species, *Charniodiscus* sp., *Culmofrons*, *Frondophyllas*, *Pectinifrons*, *Primocandelabrum* sp., *Hiemalora* and filamentous impressions in MPER relative to previous studies (Fig. 4). *Hadryniscala avalonica* (Hofmann et al., 2008) is recognised in MPER for the first time. The stratigraphic range of holdfast discs spans the entire range of frondose macrofossil taxa, while the range for *Hiemalora* closely matches that of *Primocandelabrum* specimens, as might be expected given their interpretation as component parts of those frondose organisms (Serezhnikova, 2007; Burzynski and Narbonne, 2015). Ivesheadiomorphs have the longest range of any non-discoidal impression, and are also the oldest impressions seen in MPER.

The oldest non-ivesheadiomorph fossil-bearing surface encountered also contains some of the largest macrofossils in the MPER succession (*Trepassia* at locality DRK3CW), potentially implying an older, as yet unsampled ancestry to these taxa. Uniterminal rangeomorphs with undisplayed first and second order branching architecture (*sensu* Brasier et al., 2012), namely *Charnia*, *Vinlandia*, and *Trepassia*, are the oldest frondose taxa, and these are joined by *Thectardis* and *Charniodiscus* sp. in the Drook Formation (Fig. 4). Multiterminal rangeomorphs, and rangeomorphs with displayed first and second order branches, are not observed until the lower Briscal Formation. When translated to time (Fig. 5), this appearance of new rangeomorph constructions occurs at about 568 Ma, and correlates with a marked increase in the occurrence of fossil-bearing surfaces, and broader taxonomic diversity. Although we recognise that this pattern may result from the smaller number of sampled horizons prior to 568 Ma, the data could be interpreted to point to an extended ~7 Myr interval of gradual diversification of the Rangeomorpha prior to a more rapid radiation in the Briscal Formation. We also note that the turbiditic depositional environments in our study area reflect a mixture of infrequent event-bed deposition and more gradual background sedimentation, but that even the background sedimentation is likely to include breaks in sedimentation of unknown duration (Miall, 2016; Davies and Shillito, 2018). Both the constant sedimentation rates implied by our age model, and the durations represented by each individual ‘snapshot’ of a community preserved on each observed bedding plane, will be affected by the incompleteness of the rock record.

Peak taxonomic diversity is observed in the upper Mistaken Point and lower Trepassey Formations, around 565 Ma (Fig. 5), but this also corresponds to the part of the succession with the most tuffites, and it is therefore entirely possible that this reflects a preservation bias, with increasing numbers of available fossilisation opportunities offering a wider sample of taxonomic diversity.

The sequence of apparent disappearances of taxa through the upper levels of the succession is not considered to be evolutionarily significant, since many of these taxa are known in much younger strata elsewhere (e.g. *Charnia* in Siberia; Grazhdankin et al., 2008). The absence of fossils in the upper St. John’s Group at MPER is thus likely to be a palaeoenvironmental/taphonomic artefact (cf. Narbonne, 2005).

There is considerable variation in the frequency of occurrence of taxa on fossil-bearing bedding planes within MPER. Some taxa (e.g., *Charnia*, *Pectinifrons*, and the various *Charniodiscus* and *Fractofusus* species) are relatively common, whereas others (e.g. *Avalofractus*, *Broccoliforma*, *Plumeropriscum*, and *Primocandelabrum hiemaloranum*) are rare. Taphonomy may play a role in explaining some of these patterns, for example some rare taxa are small, and so are more difficult to identify on poorly preserved surfaces. The rarity of these taxa, both on and between surfaces, is notable and worthy of future investigation. If corroborated at other sites, this observation may imply a tendency towards ecological dominance in certain taxa. As noted at other sites worldwide (e.g. Finnegan et al., 2019), beta diversity can be high amongst Ediacaran bedding plane palaeocommunities, with adjacent surfaces often containing markedly different species diversities and compositions. We note however that there is considerable variability in the areal extent of the studied bedding planes, with some being 100s of m^2 in area, and others limited to small ledges. Where assessment of variation across individual surfaces is possible (Matthews et al., 2017), variation in alpha diversity is moderate. Given that our record essentially compiles random snapshots in time of variably populated ecosystems that have undergone variable degrees of taphonomic filtering, we urge caution in interpreting the stratigraphic ranges we present in isolation as evolutionary trends. Future cross-checking of our results with those from other Avalonian localities (for which we are in the process of compiling palaeontological and geochronological data) will permit testing of apparent patterns. It is worth noting that the observation that uniterminal, undisplayed rangeomorph taxa appear before other forms is consistent with the only currently available compilation of stratigraphic ranges from the Bonavista Peninsula (Hofmann et al., 2008, fig. 4).

8. DISCUSSION

The geochronological ages presented here confirm the Mistaken Point biota as the oldest known assemblage of the Ediacaran macrobiota (spanning at least the interval ~574–564 Ma). Notwithstanding the issue of two different dates for the 'Pizza Disc' surface at the top of the Drook Formation, comparison of our data with those of Pu et al. (2016) suggests that the first *in situ* macrofossils in the MPER succession appear ~5 Myrs after the Gaskiers glaciation. This is a shorter duration than was presented by those authors, but we support their suggestions that macrofossils existed prior to this date (both in MPER and elsewhere in Newfoundland), and that there is no clear link between fossil appearance and a post-Gaskiers oxygenation event (Pu et al., 2016; see also Sperling et al., 2015).

In this paper we attempt to integrate our geochronological data from MPER with data published in other studies (Bowring et al., 2003, Pu et al., 2016 and Canfield et al., 2020). This includes three levels where dates from this study can be compared with previous dates from identical or nearby beds, and we discuss the geological and analytical issues surrounding variance between these ages. Combined, these datasets highlight additional and non-quantified sources of geochronological uncertainty; however our approach of considering these within a stratigraphic framework can aid the development of an age-thickness model.

There is a temporal overlap between the MPER fossil-bearing section and that of Charnwood Forest, U.K. (bracketed to 569–556 Ma; Noble et al., 2015), and some sections in the Central Urals (Maslov et al., 2013), but even the youngest MPER fossils predate macrofossil-bearing strata in Siberia, China, Brazil and Namibia (Grotzinger et al., 1995; Parry et al., 2017; Yang et al., 2017). Detailed studies from the ~558–550 Ma White Sea region of Russia (Martin et al., 2000; Grazhdankin, 2004, 2014), and the as yet undated Ediacara Member of South Australia (Gehling and Droser, 2013; Reid et al., 2018), have demonstrated that facies exert a significant control on the distribution of taxa in those shelf and shallow marine settings, with particular groups of organisms commonly found together in specific palaeoenvironments, while others are excluded. Disentangling evolutionary and palaeoenvironmental controls on the distribution of Ediacaran macrofossils requires temporal integration of the Ediacaran stratigraphic record. On the basis of available evidence, the deep marine MPER succession and its related biota appear to have been older than many other Ediacaran fossil-bearing successions: demonstrably time equivalent shallow marine successions for direct comparison remain to be confirmed.

The new ages importantly provide tighter constraint on the age of horizontal surface traces that have been described from the MPER succession (Liu et al., 2010, 2014). These impressions lie on a surface in the upper Mistaken Point Formation that sits stratigraphically between our MP-14 and LC-1 dated horizons. Our age model predicts that the age of this horizon is ~564.8 Ma, confirming these traces as the oldest known candidate metazoan surface traces in the rock record. The age model also provides a chronostratigraphic framework within which to consider other datasets, such as geochemical trends within the Conception and St John's Groups (e.g., Canfield et al., 2007), can be combined, offering the potential to test hypotheses linking environmental and evolutionary events.

9. CONCLUSIONS

A series of new radio-isotopic dates for the Ediacaran successions of the Mistaken Point Ecological Reserve confirm that the MPER fossils represent the world's oldest examples of the classic Ediacaran macrobiota. Two of the six dated levels have been dated in other studies, and the ages from the two studies differ with respect to the oldest fossiliferous levels. This disagreement requires further investigation. Our new radio-isotopic dates are stratigraphically coherent, and have been used to develop an age-depth model for the succession.

Renewed mapping of the MPER and its surroundings allows for an improved lithostratigraphic record of the succession, and the extension of stratigraphic ranges for several key Ediacaran taxa. This integrated litho- and chrono-stratigraphic framework for south-eastern Newfoundland, enmeshed with palaeontological stratigraphic occurrence data, provides a blueprint for future work to constrain the temporal ranges of many key Neoproterozoic taxa.

Our age-depth model has then been used as a transfer function to propel the fossil ranges from the 'depth domain' into the 'time domain'. As additional Ediacaran successions, both fossiliferous and non-fossiliferous, become similarly temporally calibrated, we hope it will be possible to establish temporal and environmental controls on the distribution of Ediacaran taxa across their entire temporal range. Finally, age models such as this offer opportunities to combine palaeomagnetic, geochemical, microfossil, and other datasets to temporally correlate distantly located global successions, and will prove invaluable for ongoing efforts by the ICS to subdivide the Ediacaran System.

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FIGURES

Figure 1. Map and stratigraphic column for the Mistaken Point Ecological Reserve (MPER). **A:** Map of Newfoundland. **B:** Map of the Avalon Peninsula. **C:** Geological map of the MPER region, with the Reserve highlighted in red. Geological units coloured as in D. Sample localities marked with red stars. **D:** Stratigraphic column for MPER, showing the levels of the sampled horizons.

Figure 2. Representative fossils from surfaces within MPER. **A:** *Trepassia wardae*, bed DRK1T, Drook Fm., Daley's Cove. **B:** *Charnia masoni*, bed MP7, Mistaken Point Fm. **C:** *Charniodiscus procerus*, bed MP7. **D:** *Charniodiscus spinosus*, bed MP N (see Bamforth & Narbonne, 2008). **E:** *Hapsidophyllas flexibilis*, bed 'B' of Landing et al., 1988, Mistaken Point Fm. **F:** *Pectinifrons abyssalis*, bed MP16, Trepassey Fm. Best seen when wet. **G:** Ivesheadiomorphs and frondose taxa on the 'Pizzeria' surface (the surface directly below dated sample LC-1), Long Cove, Trepassey Fm. **H:** *Fractofusus misrai* and holdfast disc, 'D' Surface at the Stumps (see Matthews et al., 2017), Mistaken Point Fm. **I:** *Fractofusus misrai* (the largest specimen we have observed anywhere), bed BR6, Briscal Fm. Scale bars = 50 mm except in C = 10 mm.

Figure 3. A: Ranked ^{206}Pb/^{238}U date plots for the data generated in this study, and two samples also dated as part of the Pu et al (2016) study. **B:** Age-depth model based upon the interpreted ^{206}Pb/^{238}U ages.

Figure 4. Stratigraphic range chart for published Ediacaran macrofossils from Mistaken Point Ecological Reserve, Newfoundland. Each black horizontal bar indicates occurrences of that taxon on a specific bedding plane horizon at a known level within the measured section. Stratigraphic thickness is based on measurements made as part of this study. Fossil occurrence data combine information from the literature (see Supplementary Information 2 for a full list of literature references) with primary observations made by us between 2007–2018.

Figure 5. Chronostratigraphic range chart for published Ediacaran macrofossils from Mistaken Point Ecological Reserve, Newfoundland. Depth to time conversions were performed using the age model in Fig. 3B. Age model uncertainties are not included. Note that multiple surfaces may have been given the same age, and so plot together.