Post-fossilization processes and their implications for understanding Ediacaran macrofossil assemblages

JACK J. MATTHEWS[1,2]*, ALEXANDER G. LIU[3] & DUNCAN MCILROY[1]

[1]*Department of Earth Sciences, Memorial University of Newfoundland, St John's, NL, A1B 3X5, Canada*

[2]*Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW, UK*

[3]*Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, UK*

**Correspondence: jjmatthews@mun.ca*

Abstract: Fossil assemblages from Newfoundland's Avalon Peninsula preserve diverse examples of the enigmatic Ediacaran macrobiota, offering some of the earliest evidence for large and complex multicellular life. These fossils are exposed on extensive coastal bedding planes in extraordinary abundances, permitting palaeoecological studies based on census data from spatially extensive palaeocommunities. Such studies have been used to constrain the reproductive strategy and phylogenetic placement of Ediacaran organisms. Geological mapping and stratigraphic correlation in the Mistaken Point Ecological Reserve reveal that some fossil-bearing surfaces can be tracked over distances of several kilometres. These laterally extensive surfaces reveal that the modern processes by which the sediment overlying a fossil surface is removed may impose important controls on the observed composition of fossil assemblages. Weathering and erosion – along with factors associated with tectonics, metamorphism and discovery – are here grouped as 'post-fossilization processes' and introduce biases that are often not explicitly accounted for in palaeoecological studies. Specifically, post-fossilization processes may differentially influence the preservational fidelity of individual specimens on a given surface and generate features that could be mistaken for original morphological characters. We therefore recommend that post-fossilization processes must be considered when undertaking palaeoecological studies in Ediacaran successions in Newfoundland and, potentially, elsewhere.

Gold Open Access: This article is published under the terms of the CC-BY 3.0 license.

Fossils of large and complex soft-bodied organisms commonly referred to as the Ediacaran macrobiota are found globally in strata of the late Ediacaran Period (580–541 Ma; Fedonkin *et al.* 2007). These organisms, many of which are of uncertain phylogenetic position, have been considered to include some of the earliest animals (e.g. Narbonne *et al.* 2012; Dufour & McIlroy 2016). Some of the oldest Ediacaran macrofossils were discovered in what is now the Mistaken Point Ecological Reserve (MPER), southeastern Newfoundland (Fig. 1) in the late 1960s (Anderson & Misra 1968). The Mistaken Point fossil assemblages, dated to *c.* 580–560 Ma (Van Kranendonk *et al.* 2008), are dominated by a distinctive group of sessile, frondose organisms of enigmatic biological affinity termed the Rangeomorpha (Narbonne 2004). These forms occur in Newfoundland alongside other frondose taxa and a small number of non-frondose forms (reviewed in Liu *et al.* 2015*b*), as well as rare trace and body fossils that may indicate the presence of muscular metazoans (Liu *et al.* 2010, 2014, 2015*a*; Menon *et al.* 2013).

Palaeontological research into the Ediacaran macrobiota has often focused on the most beautiful, finely preserved and complete fossil specimens, which are restricted to a relatively small number of localities worldwide. In Newfoundland, the MPER contains multiple fossil-bearing surfaces with high-quality preservation of thousands of individual organisms. Fossil census data from such bedding planes are increasingly being used to elucidate the population structure (Darroch *et al.* 2013), palaeoecology (Clapham *et al.* 2003) and even palaeobiology (Mitchell *et al.* 2015) of Ediacaran fossil assemblages. These studies are based on the precept that the observed fossil assemblages reflect accurate representations of the original biological communities and are not strongly affected by biases introduced by taphonomic or other secondary processes.

Knowledge of the taphonomic processes and conditions responsible for preserving fossils is

From: Brasier, A. T., McIlroy, D. & McLoughlin, N. (eds) 2017. *Earth System Evolution and Early Life: A Celebration of the Work of Martin Brasier*. Geological Society, London, Special Publications, **448**, 251–269.
First published online March 17, 2017, https://doi.org/10.1144/SP448.20
© 2017 The Author(s). Published by The Geological Society of London.
Publishing disclaimer: www.geolsoc.org.uk/pub_ethics

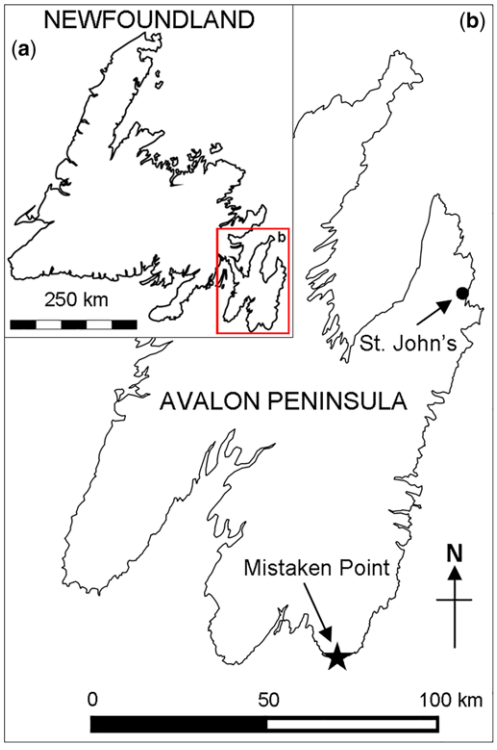

Fig. 1. Maps of (**a**) Newfoundland and (**b**) the Avalon Peninsula showing the location of the Mistaken Point study area.

required to correctly interpret the palaeoecology, morphology and taxonomic affinities of fossil specimens; the original taphonomic processes involved in the preservation of Ediacaran macrofossils are becoming increasingly well understood (e.g. Schiffbauer *et al.* 2014). Fossils in Newfoundland were typically preserved as casts or moulds on the ancient seafloor beneath event beds that are often rich in volcanic material (Narbonne 2005). Bacterial sulphate reduction by micro-organisms immediately following burial led to early diagenetic moulding of the external morphology of both macro-organisms and surrounding microbial mats by iron sulphides (Gehling 1999; Liu 2016). These sulphides combined with microbially produced hydrogen sulphide to form a framboidal pyrite 'death mask' around the soft tissues prior to extensive decay or sediment lithification (Gehling 1999; Liu 2016). This process captured a high-fidelity impression of the external morphology of the organisms (see also Laflamme *et al.* 2011; Darroch *et al.* 2012).

Additional factors that exert influences on Ediacaran fossil assemblages remain less well understood. Notwithstanding the complications arising from the time averaging of Ediacaran fossil communities, and from consideration of the presence of necromass (Liu *et al.* 2011, 2015*b*; Wilby *et al.* 2015), potential biases on the composition of fossil assemblages can be exerted by processes that took place after fossilization and sediment lithification. The implications of these latter processes for the interpretation of Ediacaran fossil assemblages at Mistaken Point are the primary focus of this paper.

The 'E' Surface

One of the best known and most extensively studied fossil horizons in Newfoundland is the Yale outcrop of the 'E' Surface at Mistaken Point (Landing *et al.* 1988, fig. 10; Clapham *et al.* 2003; Figs 1 & 2). This outcrop preserves the fossilized impressions of >4000 organisms, some recording morphological features <0.5 mm in resolution, and its fossils have been the focus of studies into palaeoecology (Clapham *et al.* 2003; Darroch *et al.* 2013, 2015; Liu *et al.* 2015*b*; Mitchell *et al.* 2015), taxonomy (Laflamme *et al.* 2004; Gehling & Narbonne 2007; Flude & Narbonne 2008; Bamforth & Narbonne 2009; Brasier & Antcliffe 2009; Brasier *et al.* 2012) and taphonomy (Seilacher 1992; Liu *et al.* 2011; Liu 2016). The Yale outcrop of the 'E' Surface (Fig. 1) is also the principal locality that tour groups, run by MPER staff, visit to observe the fossil horizons.

The 'E' Surface lies within the siltstone- and mudstone-dominated Mistaken Point Formation, which lies towards the top of the progradational Conception Group. The Mistaken Point Formation is dominated by green, grey and purple normally graded siltstones and mudstones, but characteristically includes thick sandstone turbidites (with normal grading and convolute bedding) and fine- to medium-grained sandstones (e.g. Wood *et al.* 2003). Many bedding planes are overlain by light grey–green tuffs and tuffites that are preferentially cleaved compared with the surrounding beds. These tuffs typically overlie fossil-bearing horizons.

Geology of the Yale outcrop of the 'E' Surface at Mistaken Point

The Yale outcrop of the 'E' Surface (Fig. 2a) lies near the top of the Mistaken Point Formation within a distinctive stratigraphic succession that has been well documented (e.g. Landing *et al.* 1988; figs 10–11). The 'E' Surface lies *c.* 2.5 m above the fossiliferous 'D' Surface, which is overlain by two thick green–grey tuffites, each *c.* 20 cm thick (Fig. 3). Above these tuffites lie a number of silty and sandy turbidites, the most distinctive of which is a *c.* 80 cm thick sandstone bed with parallel

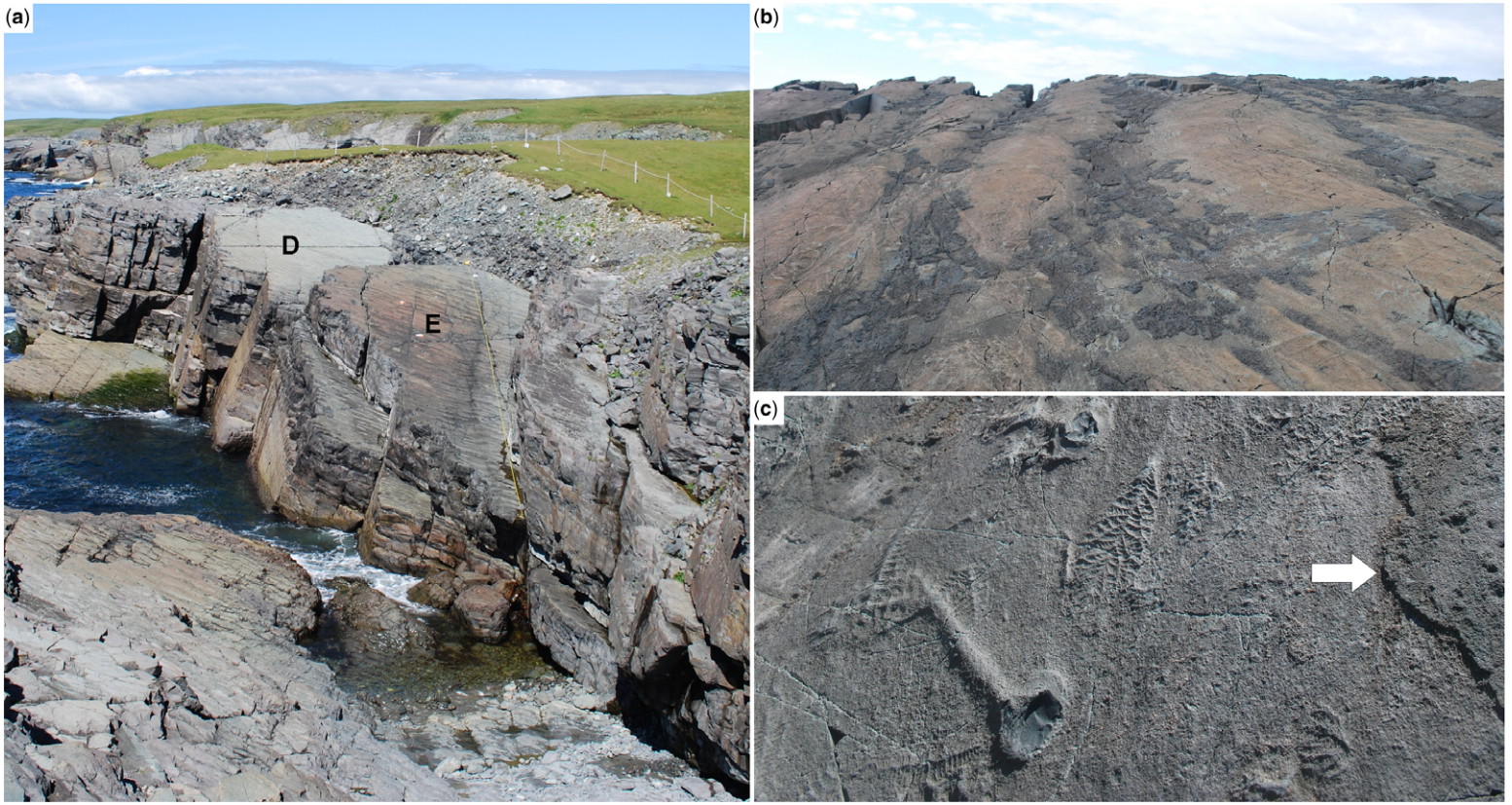

Fig. 2. The Yale outcrop of the 'E' Surface at Mistaken Point. (**a**) Overview of the Mistaken Point Yale locality, looking west. 'E' Surface labelled E and 'D' Surface labelled D. (**b**) Looking up the trough of a tectonic ripple on the Mistaken Point Yale 'E' Surface. Note how the remaining tuff (black) is largely confined to the topographic troughs. (**c**) Example of fossils on the Mistaken Point Yale 'E' Surface outcrop. Note how the exposed surface is almost completely devoid of tuff and those areas where tuff remains still retain a complete covering (white arrow).

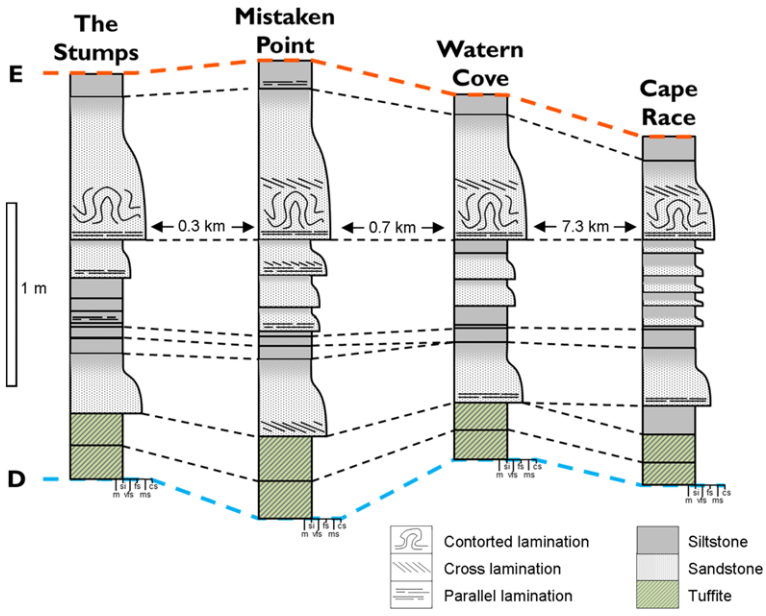

Fig. 3. Detailed sedimentology of the 'D' and 'E' surfaces, Mistaken Point Formation shown as a simplified graphical section from the 'D' to 'E' surfaces at each of the studied outcrops. The Mistaken Point Yale and Queens outcrops are combined due to their close proximity to each other, as are those at Watern Cove East and West. Scale bar = 1 m.

lamination, rare rounded mudstone clasts and patchy carbonate cementation. This sandstone bed fines upwards into a *c.* 30 cm thick zone with contorted bedding that is also carbonate-cemented in places (Fig. 3). The contorted bedding, considered to result from a period of post-depositional dewatering, lies 95 cm below the 'E' Surface (Fig. 3). Above this is a zone of cross-laminated, fine-grained sandstone that grades into a purple siltstone; the entire marker turbidite is topped by a *c.* 2 cm thick mottled olive green layer. Above this marker turbidite, and directly below the fossil horizon, is a *c.* 15 cm thick bed of green laminated coarse siltstone that fines upwards through grey–dark purple siltstone into a purple mudstone and is topped by a *c.* 2 cm thick mottled olive green layer – the substrate on which the organisms preserved on the 'E' Surface resided.

Directly above the 'E' Surface is a *c.* 5 mm thick black crystal tuff that is widely considered to have cast the fossil assemblage (Seilacher 1992). The crystal tuff is overlain by a *c.* 10 cm thick, cleaved, normal graded grey–green tuffite.

The subvertical portions of the contorted bedding within the marker turbidite are preferentially cleaved, probably due to grain sorting during fluid escape. Where the irregularly distributed cleavage within the contorted bed reaches the 'E' Surface, it is observed that it corresponds with undulating troughs on the surfaces (Fig. 2b). These undulations of bedding, colloquially termed 'tectonic ripples', have previously been interpreted by some researchers as asymmetrical wave ripples (Williams & King 1979), but there is no evidence to suggest that these undulations are ripples associated with current or wave action (Wood *et al.* 2003). The black crystal tuff overlying the 'E' Surface is often absent on the crests of the bedding undulations, revealing high-fidelity fossil specimens. By contrast, the troughs of the bedding undulations of the 'E' Surface remain largely covered by crystal tuff, locally prohibiting the direct observation of any underlying fossils (Fig. 2b). Some of the adhered crystal tuff remains at its original *c.* 5 mm thickness and minute amounts of the overlying grey–green tuffite can be observed on top. Where the crystal tuff remains on the 'E' Surface, the outer edges of these patches may be weakly adherent and may be plucked off due to mechanical action to reveal a pristine fossil surface (Fig. 2c).

Newly identified 'E' Surface outcrops

The distinctive stratigraphic succession between the 'D' and 'E' surfaces has allowed the recognition and correlation of these surfaces within the MPER and as far east as Cape Race (Fig. 4). In particular,

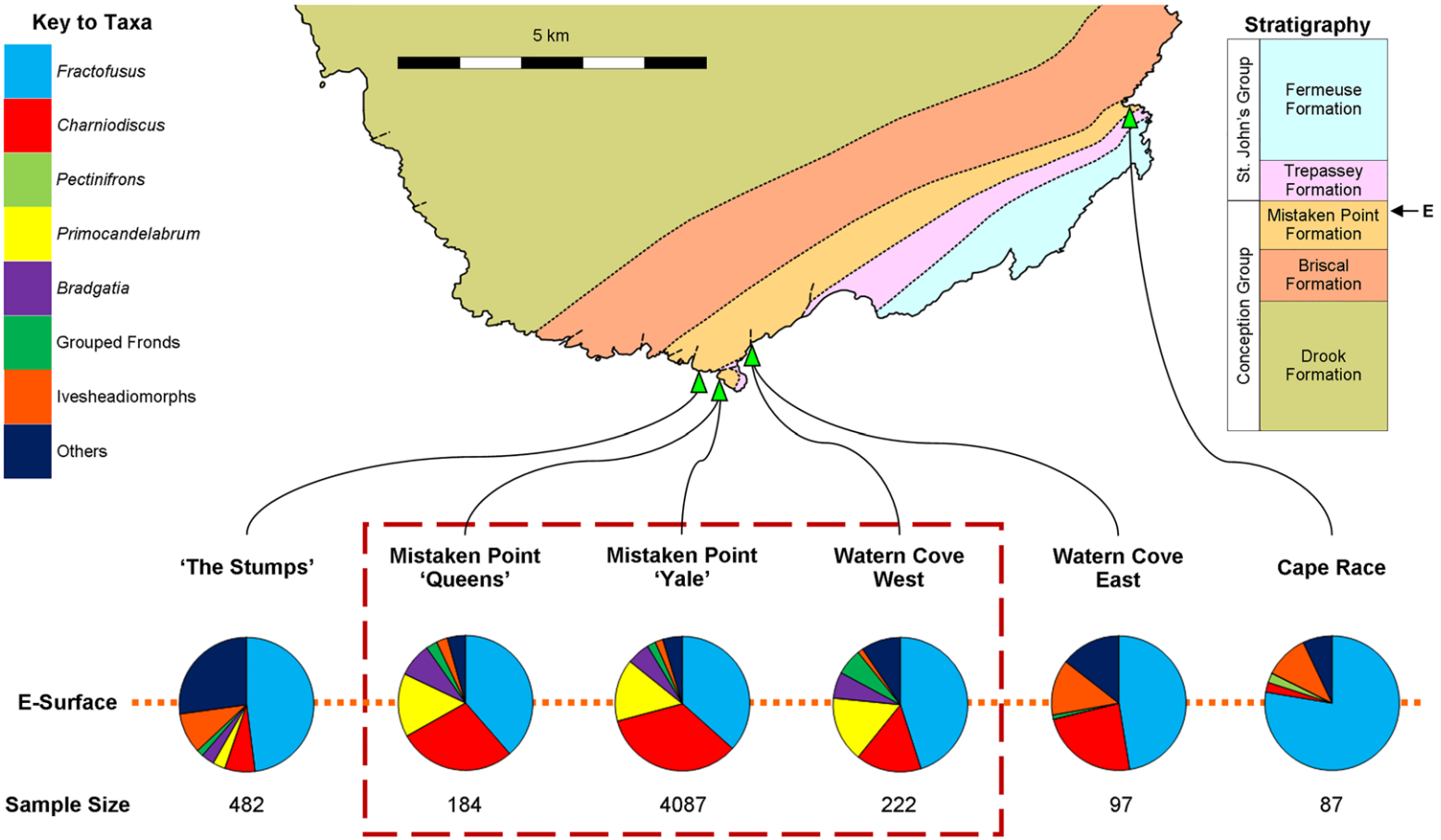

Fig. 4. Comparison of observed fossil assemblages at different outcrops of the 'E' Surface within and around the Mistaken Point Ecological Reserve. Data collected by Clapham *et al.* (2003) are highlighted by the dashed red box. Other data were collected by the authors. Geological map reflects our new understanding of field relationships following recent mapping by one of us (JJM).

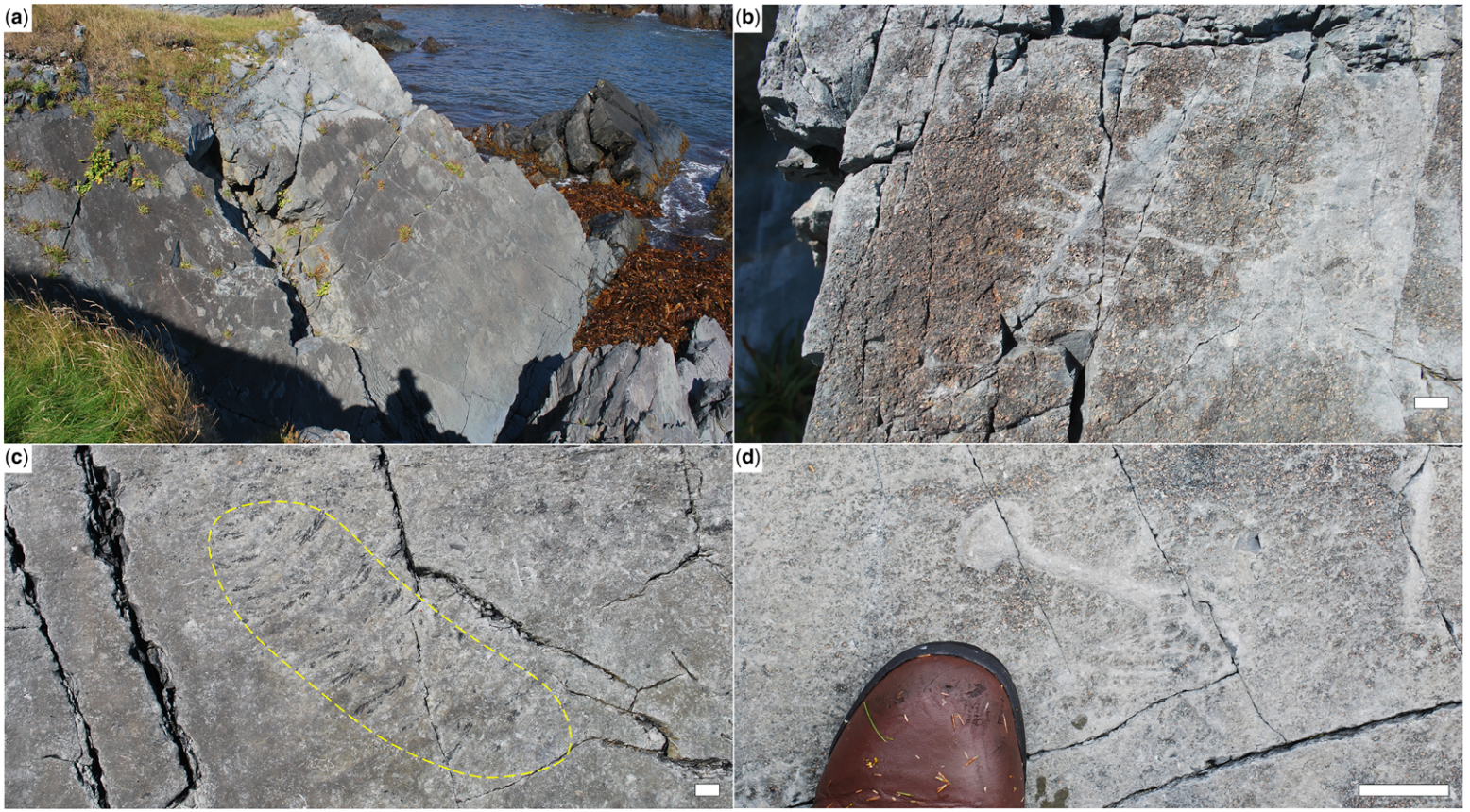

Fig. 5. The 'E' Surface at Watern Cove West. (**a**) Overview of the outcrop, looking sub-parallel to strike into Watern Cove. (**b**) Example of *Fractofusus*, with prominent high epirelief features slightly eroded, while finer negative epirelief elements remain masked by the crystal tuff. Scale bar = 10 mm. (**c**) Another example of *Fractofusus*, near the bottom of the surface. Only those elements preserved in negative epirelief are still visible. The outline of the specimen is highlighted by the dashed yellow line. Scale bar = 10 mm. (**d**) Example of a heavily abraded *Charniodiscus* specimen. Scale bar = 50 mm.

the black 5 mm thick chloritic crystal tuff that overlies the 'E' Surface is highly distinctive in having coarse-grained white and pink feldspar phenocrysts, permitting confident field recognition of the 'E' Surface horizon itself. The 'E' Surface has previously been documented at three localities (Clapham *et al.* 2003), but our own detailed mapping has revealed four additional localities (Fig. 4) spanning a modern geographical extent of almost 9 km.

The three previously described outcrops of the 'E' Surface are as follows.

(1) The Yale outcrop. This is the most studied outcrop of the 'E' Surface, 104 m^2 in total areal extent and located several metres above sea-level on Mistaken Point itself (Fig. 2a).
(2) The Queens outcrop. This outcrop lies downdip of the Yale surface, from which it is separated by a narrow gully, and is therefore closer to sea-level. Most of the 'E' Surface here is only impacted by waves during storm conditions, except for the most southwestern portion located near a small gully, which experiences constant, intense wave action. Most of the tuff overlying the Queens outcrop has been removed by weathering and abrasion.
(3) Watern Cove West. This steeply seawards-dipping outcrop is *c.* 18 m^2 in areal extent (Fig. 5a) and lies 700 m east of Mistaken Point (see Clapham *et al.* 2003). The crystal tuff at this locality is not eroded updip, but at sea-level wave action and the presence of shingle has abraded the surface at its base to the extent that no fossils can be discerned (Fig. 5b–d).

Four 'E' Surface outcrops, recognized here through fine-scale lithostratigraphic correlation, have not to our knowledge been previously described. These are as follows.

(1) Watern Cove East. This 29 m^2 'E' Surface outcrop lies *c.* 60 m east of Watern Cove West and is offset from it by a north–south orientated normal fault with a throw of 1.5 m. The Watern Cove East outcrop is coastline-parallel and largely several metres above sea-level (Fig. 6a); it only experiences significant wave action at its western margin. Most of the 'E' Surface (estimated *c.* 85%) at this locality is still covered in crystal tuff, so much so that the fossils are generally not exposed at all (Fig. 6b).
(2) Laurentian Gulch. A *c.* 3 m^2 highly cleaved and fractured outcrop of the 'E' Surface was found 150 m NW of Mistaken Point, adjacent to a large fault in Laurentian Gulch. Only a few poorly preserved *Fractofusus* were observed at this locality and it is presently deemed of little use for palaeontological study.
(3) The Stumps. This newly described locality is >150 m^2 in area and is located *c.* 330 m NW of the Yale outcrop (Fig. 4). It consists of three outcrops of the 'D' and 'E' surfaces, separated by minor faults with throws of *c.* 2 m. The cleaved fossiliferous 'E' Surface on the seaward-most outcrop is very steeply dipping (*c.* 45°) at the top, with a shallower dip of around 30° at the lowest part of the outcrop. Portions of the outcrop furthest from the sea remain covered by the *c.* 5 mm thick layer of crystal tuff typical of the 'E' Surface. Within the surf zone the 'E' Surface is wave-polished, with variable thicknesses of tuff remaining, and fossil fidelity is generally poor. Strongly positive morphological features have been eroded and those portions of fossils preserved in negative epirelief are generally tuff-filled (Fig. 7). Some high-quality preservation does exist between these end-members.
(4) Cape Race. This is the first documentation of the 'E' Surface beyond the MPER, *c.* 8 km NE of Mistaken Point (Fig. 4). The beds here are very steeply dipping and those in the surf zone are highly abraded. The 'D' and 'E' surfaces are recognizable as notches in the outcrop caused by preferential weathering and erosion of the tuffaceous horizons that overlie the fossiliferous surfaces (Fig. 8a). The 6 m^2 outcrop of the 'E' Surface is rarely >1 m wide and is laterally continuous for *c.* 25 m. The steeply dipping bedding surface receives little direct sunlight and is covered by algae, making photography and the field observation of fossils particularly difficult (Fig. 8b). It is estimated that $>95\%$ of the surface is covered to some extent by the overlying tuff.

We note that the undulation of the surface at the Yale and Queens outcrops (Fig. 2a, b) is barely evident 700 m away at Watern Cove (Fig. 5a) and is absent at Cape Race (Fig. 8a). This is consistent with the undulations at Mistaken Point being a result of localized tectonic processes rather than representing sedimentary features of the 'E' Surface.

Fossil census study

Recognition of multiple outcrops of the 'D' and 'E' surfaces offers a unique opportunity to explore the variation within a fossil assemblage on a single fossilized seafloor over a large (several kilometre) lateral extent. To our knowledge, this is the first time an Ediacaran fossil-bearing surface has been studied over such a distance, potentially allowing the

Fig. 6. Outcrop of the 'E' Surface at Watern Cove East, looking NE. 'E' Surface marked E. Note geologist for scale.

investigation of changes in community composition, sedimentation and ecosystem dynamics on a broad scale. We now compare fossil census data from six outcrop localities of the 'E' Surface and consider the possible controls on the observed variability in community composition.

Our study combines new data from The Stumps, Watern Cove East and Cape Race localities with pre-existing species occurrence data from the Yale, Queens and Watern Cove West localities from a published dataset (Clapham *et al.* 2003; Clapham 2011). We chose to assess the fossil assemblages at the generic level, to minimize the introduction of errors associated with the species identification of poorly preserved specimens, and to maximize compatibility between our work and the pre-existing datasets. Because the previous work was undertaken before the formal description of many of the macrofossil taxa from the Conception Group (cf. Liu *et al.* 2015*b*), use of these datasets requires consideration of how to deal with early informal descriptors (Clapham *et al.* 2003) and their relationship with current formal generic diagnoses (Table 1).

Most of the groupings used in the Clapham datasets are directly applicable to current taxonomic groups. However, consideration of some taxa remains problematic, particularly the '*Charnia* Type A' and '*Charnia* Type B' of Clapham *et al.* (2003). '*Charnia* Type A', as identified in that study, included specimens now assigned to *Charnia masoni* (Ford 1958), *Vinlandia antecedens* (Laflamme *et al.* 2007; Brasier *et al.* 2012) and *Beothukis mistakensis* (Brasier & Antcliffe 2009). '*Charnia* Type B' included *Trepassia* (previously *Charnia*) *wardae* (Narbonne *et al.* 2009) and *Beothukis* (formerly *Culmofrons*) *plumosa* (Laflamme *et al.* 2012; Liu *et al.* 2016). In addition, some *Beothukis plumosa* were considered as '*Charnia* Type A' rather than '*Charnia* Type B' (Clapham *et al.* 2003; Laflamme

Fig. 7. Outcrop of the 'E' Surface at The Stumps, showing an example of the surface close to the high-tide mark. Note the *Charniodiscus* with heavily abraded holdfast disc and stem and its frond barely visible (white arrow) and a *Fractofusus* with high portions exposed through partial abrasion of the tuff, while the finer detail elements remain obscured by the remaining tuff (black arrow). Scale bar = 10 cm.

et al. 2012). Since these taxonomic revisions are difficult to disentangle in the original dataset, *Beothukis*, *Vinlandia*, *Trepassia* and *Charnia* are, for the purposes of this comparative study, combined as 'Grouped Fronds' (Table 1), allowing for the direct comparison of our new data with the data of Clapham *et al.* (2003). We realize that the artificial grouping 'Grouped Fronds' is of limited relevance to taxon-specific palaeoecological studies, but it may prove informative when considering ecological parameters such as tiering at a community scale (cf. Clapham & Narbonne 2002). The only remaining fossil not encompassed by formal genera or the 'Grouped Fronds' is the 'Spoon Frond' (Clapham *et al.* 2003). We consider that this morphotype is most likely to be a *Charniodiscus*, but because this taxon is a rare component (<0.6%) of the total community (Clapham 2011), we do not consider its exclusion to adversely affect our results. A large proportion of the specimens assigned to the 'Dusters' morphogroup of Clapham *et al.* (2003) are now ascribed to the genus *Primocandelabrum*. A small number have instead been assigned to the new taxa *Plumeropriscum* and *Broccoliforma* (Mason & Narbonne 2016). Four specimens of these two taxa were described from the Yale outcrop of the 'E' Surface, comprising <0.01% of the total assemblage. As such, we do not consider direct comparison of data regarding 'dusters' (data from Clapham *et al.* 2003) and '*Primocandelabrum*' (our data) to significantly perturb our results.

These taxonomic discussions led us to organize taxa into the following groupings: *Fractofusus*, *Charniodiscus*, *Pectinifrons*, *Primocandelabrum*, *Bradgatia*, Grouped Fronds, Ivesheadiomorphs, and Others. Datasets for the Yale, Queens and Watern Cove West localities were collected from subsections of the total areal extent, as described by Clapham *et al.* 2003. On Watern Cove East, Cape Race and The Stumps, we recorded census data only from accessible regions on the bedding planes (Table 2). In all cases, fossil identification at new sites was undertaken by one of us (AGL) to reduce inconsistencies associated with differences in opinion between different researchers; each identified fossil was marked with a temporary plasticine marker to ensure it was not counted multiple times.

Spatial variability in 'E' Surface fossil assemblages

The studied area, total number of specimens and fossil densities for each of the studied surfaces are presented in Table 2. Overall fossil abundances and fossil densities (i.e. individual fossils per square metre) were found to be highly variable at the different sites.

Fossil census data for the 'E' Surface at the Queens, Yale, The Stumps, Watern Cove West, Watern Cove East and Cape Race outcrops show that *Fractofusus* is the dominant taxon at all localities, comprising between 36 and 75% of the

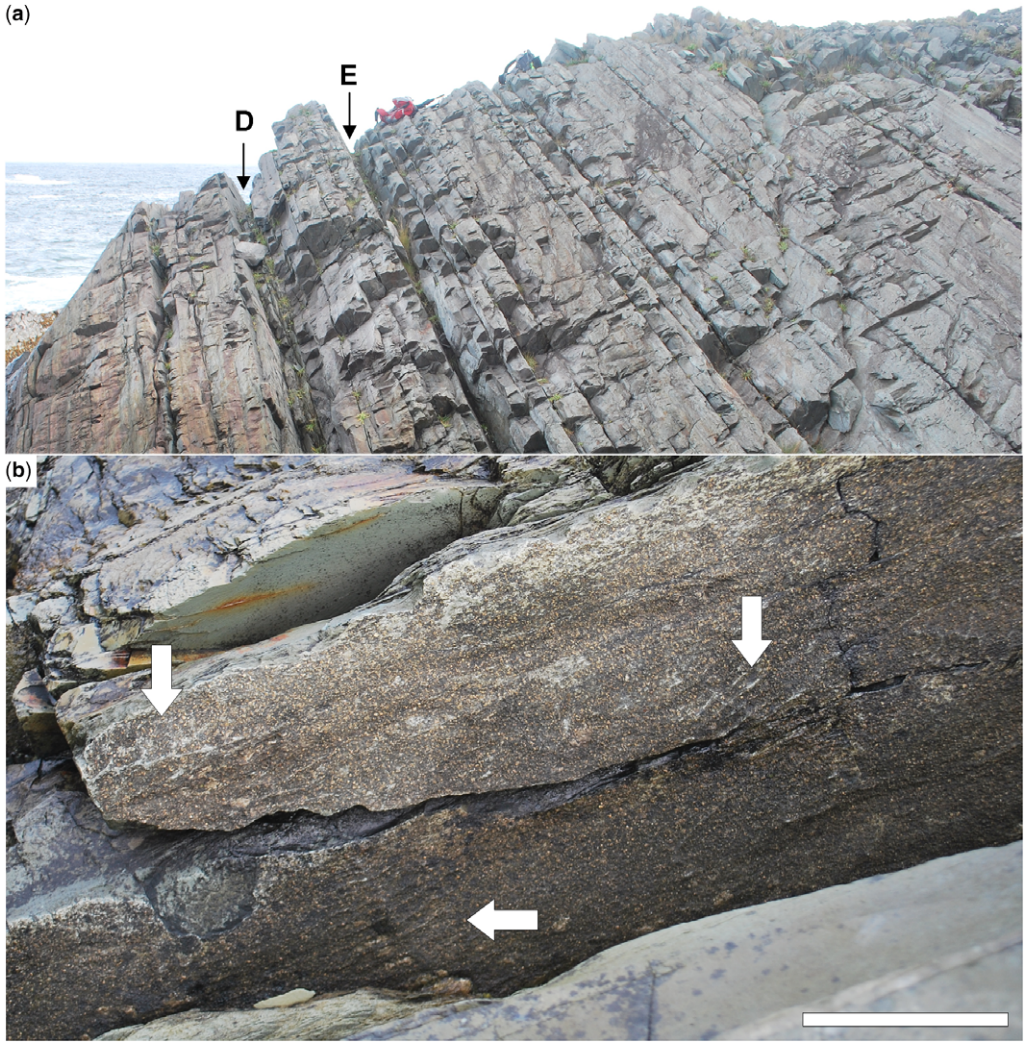

Fig. 8. Outcrop of the 'E' Surface at Cape Race. (**a**) Overview of the locality. 'E' Surface labelled E and 'D' Surface labelled D. Distance between the 'D' and 'E' surfaces is 1.85 m. (**b**) Example of 'E' Surface at Cape Race. Note also *Fractofusus* specimens beginning to be exposed (white arrows), while finer detail elements remain obscured by remaining tuff. Scale bar = 10 cm.

measured populations (Fig. 4). *Charniodiscus* forms a significant portion of the biota at the Yale outcrop, but its relative abundance varies significantly from 2.3 to 34.2% across the studied sites (Fig. 4). *Primocandelabrum* is interestingly only found at the closely spaced Queens, Yale and Watern Cove West localities and comprises between 0 and 15.8% of the studied assemblages (Fig. 4). Ivesheadiomorphs, inferred to be the decayed, microbially colonized and modified remnants of dead Ediacaran organisms, are considered by us to be necromass rather than part of the standing crop (Liu *et al.* 2011, 2015*b*). It is interesting to note that they form a significant component of the fossil assemblage at The Stumps, Watern Cove East and Cape Race, but are a relatively minor component of the biota on the Queens, Yale and Watern Cove West outcrops, constituting between 1.4 and 13.4% of the population. This phenomenon may reflect patchiness in the distribution of the pioneer colonizers of the 'E' Surface, but it requires explanation because there is no obvious reason why there should be spatially uneven rates of mortality (Fig. 4). The Cape Race locality is the only outcrop of the 'E' Surface

Table 1. *Correspondence between previous informal descriptive names (Clapham et al. 2003) and recent taxonomic diagnoses*

Clapham *et al.* (2003) nomenclature	Current nomenclature
Dusters	*Primocandelabrum* (Hofmann *et al.* 2008) and Others (comprising *Broccoliforma* and *Plumeropriscum*; Mason & Narbonne 2016)
Pectinate	*Pectinifrons* (Bamforth *et al.* 2008)
Spindle	*Fractofusus misrai* and *F. andersoni* (Gehling & Narbonne 2007)
Triangle	*Thectardis* (Clapham *et al.* 2004)
Network	*Hapsidophyllas* (Bamforth & Narbonne 2009)
Charniodiscus	*Charniodiscus spinosus* and *C. procerus* (Laflamme *et al.* 2007)
Ivesia	Ivesheadiomorphs (Liu *et al.* 2011)
Charnia Type A	*Charnia*, *Vinlandia*, some *Beothukis* = Grouped Fronds
Charnia Type B	*Trepassia*, most *Beothukis* = Grouped Fronds
Lobate discs	Others
Spoon frond	Others

The ivesheadiomorphs are considered to be the decayed remains of other organisms (Liu *et al.* 2011). Taxonomy of *Beothukis* is detailed in Liu *et al.* (2016), while that of other Grouped Fronds is discussed in Brasier *et al.* (2012).

to contain examples of *Pectinifrons*, which comprise 2.3% of the measured population at that site.

Potential biases in census data from the 'E' Surface

We observed differences in the relative abundance of taxa from outcrop to outcrop (Table 2, Fig. 4). This may partially reflect the original variability within the fossil assemblage – for example, variability in community composition related to depth, nutrient flux, regularity of disturbance, or distance offshore. However, before exploring these possibilities, potential non-biological explanations for this variability should first be considered to ensure that apparent patterns in the dataset are correctly interpreted.

The fossilization processes from biostratinomy through to lithification and diagenesis are familiar to palaeontologists and are routinely included within taphonomy and incorporated into quantitative palaeontological studies (Allison & Bottjer 2011). Some definitions of taphonomy consider tectonic, metamorphic, weathering and erosional processes that may influence the fossil record (e.g. Lawrence 1968; Rolfe & Brett 1969; Valentine 1973; Behrensmeyer & Kidwell 1985), but this is far from the norm and a diverse series of rock-altering processes are often not explicitly discussed. For clarity, the processes associated with metamorphism, tectonics, erosion, weathering and discovery are herein termed post-fossilization processes.

Observational and interpretational biases

There is a noticeable difference between the proportion of the 'E' Surface population recognized as ivesheadiomorphs and *Primocandelabrum* between the older assemblage data (Clapham *et al.* 2003) and the data presented herein (Fig. 4). This may result from a difference in opinion regarding the nature of ivesheadiomorphs, with the most recent suggestion being that they reflect a heterogeneous grouping of the partly decayed remains of a range of taxa (Liu *et al.* 2011). This hypothesis recognizes a continuum between pristinely preserved fossils and the decayed remnants of the same taxa that would be

Table 2. *Summary of the studied surface area, fossil abundance and fossil density for all studied outcrops of the 'E' Surface*

Outcrop	Studied surface area (m^2)	Specimens	Fossil density (fossils/m^2)
The Stumps	36	482	13.2
Mistaken Point Queens	3	184	56.5
Mistaken Point Yale	104	4087	39.0
Watern Cove West	7	222	31.9
Watern Cove East	29	97	3.3
Cape Race	6	87	14.5

recognized by all researchers as ivesheadiomorphs. In the middle ground between these end-members, biases of field practice might influence datasets collected at different times by different researchers. Human bias is less likely to explain the variability in the relative abundance of *Fractofusus* – a genus that is comparatively difficult to misdiagnose due to its highly distinctive zigzag midline and a morphology that tapers at both ends (Gehling & Narbonne 2007). As such, some of the variability in the fossil assemblages cannot simply be due to different historical field practices.

Although researchers may disagree on the taxonomic affinity of any given specimen, there is rarely any disagreement that impressions on the 'E' Surface are indeed fossils. Yet there is considerable variation in the measured fossil density, from 3.3 to 56.5 individuals per square metre across the studied area (Table 2). This variance could represent patchiness in the distribution of organisms on the Ediacaran seafloor, but possible abiogenic explanations also require consideration.

Fossilization bias

Although variations in sedimentology, particularly of the overlying bed, can be marked among different Ediacaran fossil-bearing horizons in Newfoundland (Liu 2016), all of the studied outcrops of the 'E' Surface consistently overlie a mottled silty mudstone and are overlain by a tuff that shows little lateral variation in mineralogy or grain size on the scale of this study. The crystal tuff is inferred to have rapidly smothered the entire seafloor recorded by the various 'E' Surface outcrops (Seilacher 1992). The processes of sedimentation, decay and casting by a microbially induced sulphidic death mask (cf. Gehling 1999) are therefore considered to have been consistent across all outcrops of the 'E' Surface (although note the anomalous absence of an extant mineralized veneer on the 'E' Surface, unlike other surfaces; Liu 2016). On the spatial scale of the collected data, any observed variation in preservational quality or assemblage composition is thus unlikely to reflect variability in biostratinomy or taphonomy between the studied sites.

Biases introduced by ambient conditions and bed aspect

Ediacaran fossils in Newfoundland are usually impressions cast in low positive or negative epirelief and are therefore best studied under low-angle lighting. As the use of artificial lighting is often not practical in the field, the ambient meteorological conditions can significantly affect the observation of fossils. The strike and dip of a bed, the time of day it is studied and the calendar date combine to determine the angle at which sunlight strikes a fossil horizon and affect how, and even if, fossils can be observed. The Laurentian Gulch outcrop, for example, never experiences favourable lighting due to its position in the cliff face and its small spatial extent, and as such it would be unlikely to reveal many fossils even if they were unaffected by mechanical fracturing. By contrast, other localities in the MPER experience good to optimum lighting conditions at different times throughout the day. For example, the Yale outcrop is best viewed in the late afternoon.

The tectonic processes responsible for determining the varying strikes and dips of beds observed today, combined with the time and date a bed is observed, thus influence the likelihood of the discovery of new fossils and fossiliferous surfaces. Necessary regulations governing field activities within the MPER forbid the collection of fossils. This makes the casting of specimens, under permit, a vital field technique because replicas of the surfaces can be studied under controlled lighting conditions in the laboratory. Although we have made every effort to observe our studied outcrops under optimum lighting conditions, variation in weather conditions may feasibly have introduced an observational bias into the dataset because the smallest and lowest relief specimens are less likely to be observed in poor lighting than larger, high-relief specimens.

Erosion and weathering

We can rule out most factors relating to observation, interpretation, and the original taphonomy and fossilization when attempting to determine the controls on observed variability between 'E' Surface fossil assemblages. But before we can interpret these patterns as reflecting the original biology or ecology, we must consider modern weathering and erosion. There were, in general, four states in which 'E' Surface exposures were found.

(1) Covered by the full (*c.* 5 mm) thickness of the crystal tuff of the over-bed. No fossil was exposed.
(2) With little to no overlying tuff present on the surface, resulting in the exposure of all the fossils present.
(3) Exhibiting partial erosion of the crystal tuff, resulting in only high positive epirelief elements of fossils protruding through the remaining tuff. In such instances we could only partially document the original fossil assemblage.
(4) Where the surface has been greatly eroded or worn smooth, such that all the tuff has been removed, and fossils are either of poor quality or absent. Some tuff may remain above fossils preserved in negative epirelief. The fossil assemblage can only be partially documented.

The six outcrops of the 'E' Surface studied herein show a mixture of these states (Fig. 9), with individual localities commonly containing several of these states of exposure on different parts of the outcrop.

These four states resulted from the action of two major mechanisms by which the crystal tuff was weathered and eroded from the 'E' Surface (Fig. 10). First, prominent spalling processes completely removed discrete chips of the *c.* 5 mm thick crystal tuff, which in some cases left a surface with no remaining tuffaceous material to obscure the fossils (Fig. 10f, l–n). Spalling is dominant on outcrops with a low angle of dip close to the ocean, such as the Yale outcrop of the 'E' Surface, where it is evident particularly on the crests of tectonic undulations (e.g. Fig. 2b). The exact mechanism by which the crystal tuff detached from the fossil surface is unclear, but might have included frost action and/or the pressure effects associated with the growth of salt crystals (Wellman & Wilson 1965).

The second process was progressive abrasion of the crystal tuff, which was typically observed at outcrops where the surface was at or near sea-level, such as the Watern Cove West surface (Figs 5, 10f–j). As this process of erosion acts upon the 'E' surface bedding plane, the most positive epirelief features of fossil specimens on the surface begin to be polished away, while the lowest relief – often the most highly detailed – features remain covered in crystal tuff (Fig. 5). Abrasion may be the product of erosion caused by the mechanical action of sediment-bearing waves and surface runoff, rockfalls and scree flows, as well as footwear. Abrasion due to wave action often results in surfaces that exhibit pristine coverings of complete tuff in areas well above sea-level, but progressively more highly abraded areas closer to sea-level (Fig. 5a). Abrasion was the major process that removed the overlying tuff from the studied areas of the 'E' Surface at The Stumps, Watern Cove East and Cape Race outcrops (Figs 6–8). Additional abrasion and erosion may result from the passage of feet on the Yale outcrop and projects are underway to quantify the impact of such anthropogenic activity.

Implications of post-fossilization processes for palaeoecological studies

As weathering and erosional processes differ in the degree to which they expose or erode fossils at different outcrops (and even on individual outcrops), they may bias the observed fossil assemblage compositions and densities (Fig. 10). Where spalling processes are the dominant means by which the 'E' Surface was exposed, the bedding plane and its fossils are either fully concealed by tuff or completely exposed (Fig. 10). On the Yale outcrop, where the majority of the fossil surface was found exposed, statistical analysis of the fossil population suggests that the presence of regions still covered by tuff does not greatly bias the data relating to the abundance and distribution of the fossil assemblage (Mitchell *et al.* 2015). By contrast, where abrasion is active, comparatively small amounts of abrasion of the crystal tuff might be expected to result in a situation where high-relief fossils (e.g. *Charniodiscus*) are over-represented within the observed assemblages (Fig. 10h, k). By contrast, increased abrasion (but not quite to the level of the underlying bed) will increase the proportion of low-relief *Fractofusus* observed in the assemblage (Fig. 10i, k). Progressive abrasion down to and below the underlying bed is expected to result in positive epirelief fossils being completely removed, while fossils preserved in low and negative epirelief (e.g. *Fractofusus*) are predicted to become over-represented with respect to the original population (Fig. 10j, k).

The effects of abrasion are dominant on the 'E' Surface outcrops at The Stumps, Watern Cove West, Watern Cove East and Cape Race (Figs 5–8). Fossil assemblages at those localities, and at outcrops with near-complete thicknesses of tuff with some areas of high abrasion, show a larger proportion of low-relief taxa such as *Fractofusus* than the (spalling-dominated) Yale and Queens outcrops (Fig. 9). These abrasion-dominated localities exhibit fossil assemblages with smaller proportions of taxa preserved in positive epirelief, such as *Charniodiscus*, than are observed at the Yale and Queens outcrops (Fig. 9).

It is important to note that in the abrasion model proposed herein, there is only one point at which the proportion of taxa observed in positive and negative epirelief will be a broadly accurate representation of the 'E' Surface assemblage (Fig. 10k). This is in contrast with the spalling model, which does not impart a significant temporal post-fossilization bias to the composition of the 'E' Surface assemblage, so long as a significant portion of the bedding plane is exposed for study (Fig. 10o). An additional bias is introduced when considering the size of Ediacaran organisms on surfaces prone to abrasion. The size of Ediacaran fossils commonly correlates with the maximum topographic height of their positive epirelief impressions. As such, localities dominated by abrasion processes may reveal individuals of different topographic height only after specific degrees of abrasion, such that certain components of the assemblage may not be recorded depending on how far abrasion has progressed. This effect may potentially impact studies examining the life cycle and reproduction of

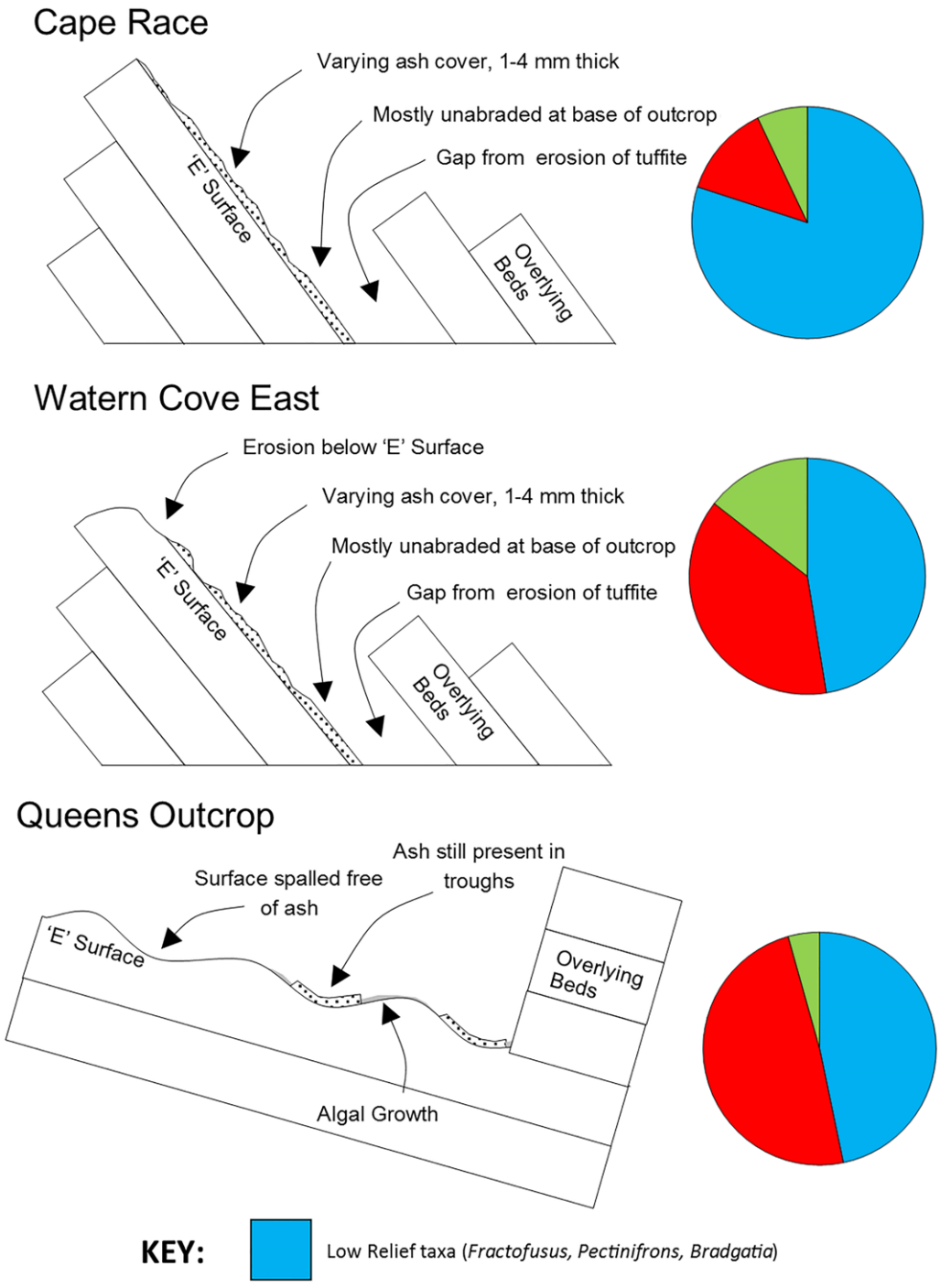

Fig. 9. Simplified representation of each studied outcrop of the 'E' Surface. Diagrams are not to scale, but graphically represent the dip, relative amounts and styles of ash cover, styles of erosion and weathering, and important surrounding features. The pie chart next to each diagram records the composition of the census populations in terms of low- and high-relief taxa. The 'Other' category includes those organisms of unknown or uncertain taxonomic affinity that cannot be confidently included within the other two categories.

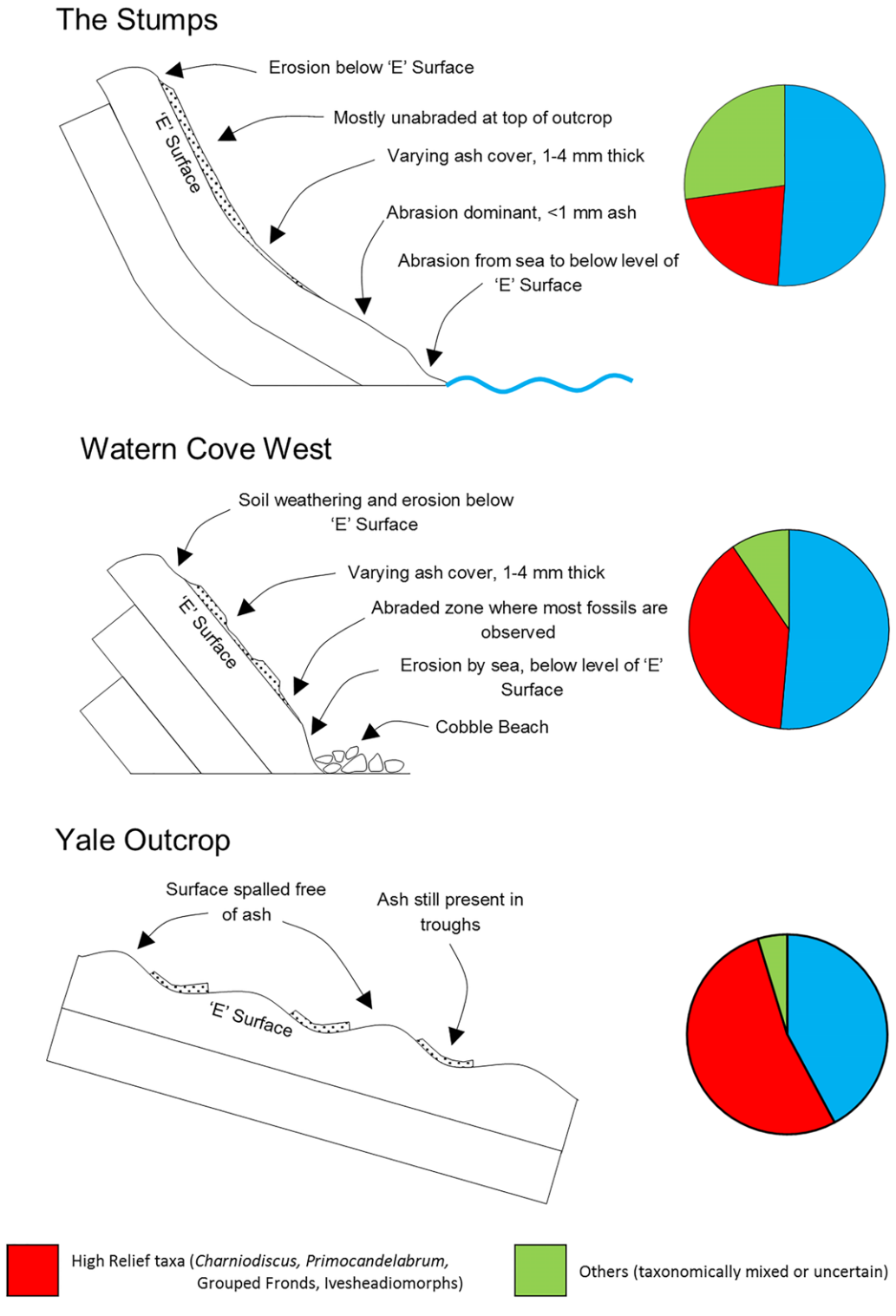

Fig. 9. *Continued.*

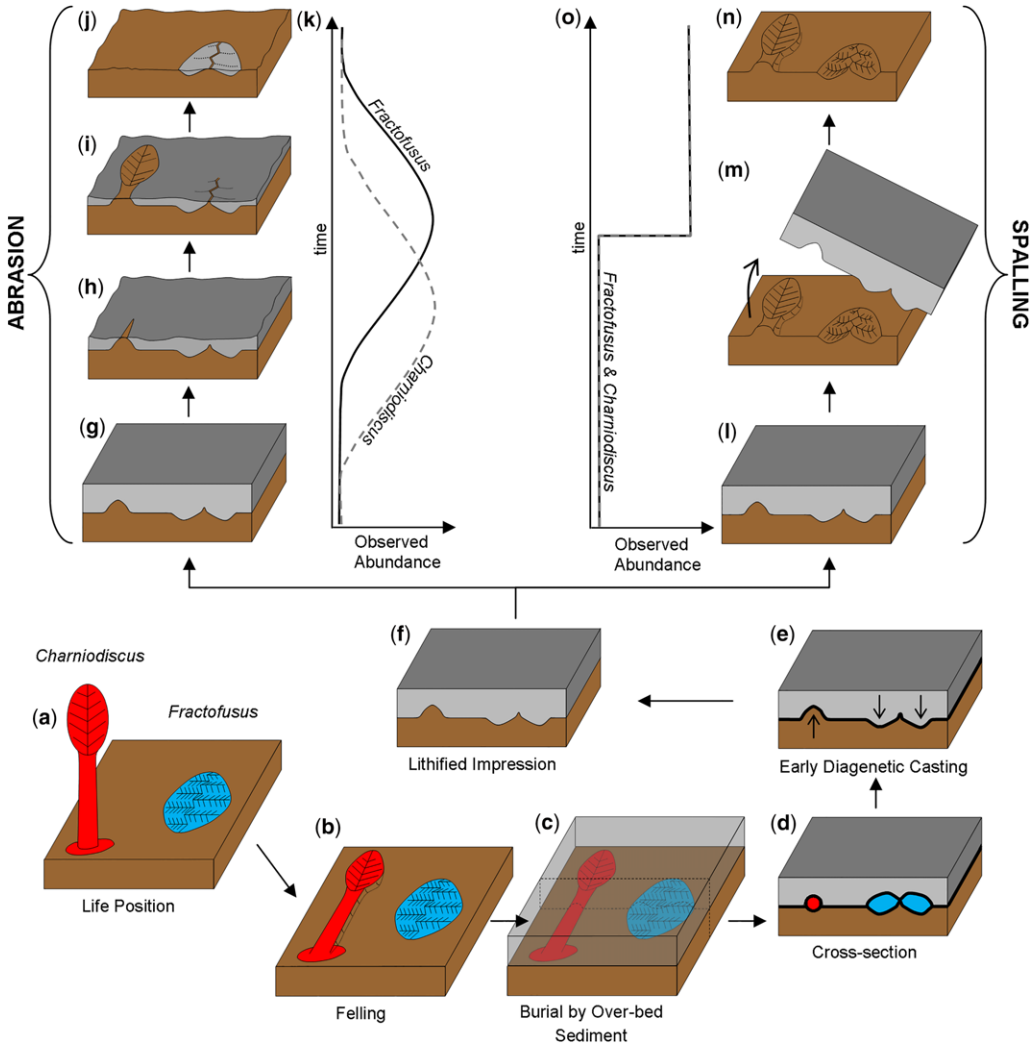

Fig. 10. Block diagram showing the process of preserving a *Charniodiscus* (red) and a *Fractofusus* (blue) specimen and the effects of both abrasion and spalling post-fossilization processes on the observed community. Fossil surface substrate in brown, overlying volcanogenic material in grey. (**a**) Organisms in life position. (**b**) Organisms toppled immediately prior to burial. (**c**) Specimens buried by volcanogenic material, shown as partly transparent. (**d**) Section through (c) showing the organisms pre-decomposition and the formation of a mineralized veneer around all organic matter (cf. Liu 2016). (**e**) Following decomposition, the underlying substrate moves upwards to the meet the cast and preserve the upper surface of *Charniodiscus,* while the overlying ashy layer falls in to meet the cast and preserve the lower surface of *Fractofusus* (*sensu* Gehling 1999). (**f**) Final section through preserved specimens pre-exhumation. (**g, h**) Beginning of abrasion of overlying ashy layer, first partially exposing the positively preserved *Charniodiscus* stem while leaving *Fractofusus* concealed. (**i**) Abrasion continues and, while abrading away the *Charniodiscus*, the central axis of the *Fractofusus* specimen is revealed. (**j**) *Fractofusus* specimen, preserved largely in negative hyporelief, remains visible even when *Charniodiscus* has been abraded away. (**k**) Schematic plot showing the observed potential of each taxon throughout the abrasion process. (**l, m**) Spalling of the overlying ashy layer from the fossil surface. (**n**) Example of fossil surface exposed by spalling process. (**o**) Schematic plot showing the observed potential of each taxa throughout the spalling process.

Ediacaran organisms because fossil organisms of different sizes – which may relate to a different generation within the population – will be differentially represented through the abrasion process. Such studies should collect data from spalling-dominated outcrops where possible.

Fossil census data, specifically the proportions of various taxa comprising the observed populations, have been used to argue for ecological succession within the MPER assemblages (Clapham *et al.* 2003). On the basis of data from multiple surfaces, it has been postulated that the pioneer colonizers of the seafloor surface would be dominated by reclining forms such as *Fractofusus* and that as the community matured it would become progressively more tiered, with taxa such as *Charniodiscus* and *Primocandelabrum* comprising a larger percentage of the population (Clapham *et al.* 2003). If metrics such as the proportion of reclining, low-relief forms like *Fractofusus* and *Pectinifrons* within a documented assemblage are dependent on the extent of post-fossilization processes such as weathering and erosion, as suggested herein, then the extent to which palaeoecology controls the observed assemblage may be questioned. It is noted that although the fossil assemblage at the Yale outcrop is described as being within the middle stages of ecological succession (Clapham *et al.* 2003, Fig. 8), the data collected from the Cape Race outcrop of the same 'E' Surface would best be associated with an early stage of ecological succession. This could reflect original ecological variation, but caution must be exercised when interpreting such signals.

We would advise that future work assessing the palaeoecology of Ediacaran benthic communities: (1) explicitly considers the possible influence of spalling, abrasion and other post-fossilization processes on the collected datasets; (2) restricts, wherever possible, comparisons between populations to surfaces that have undergone similar post-fossilization processes to compare like with like; and (3) restricts, where possible, studies to surfaces that have undergone extensive spalling-dominated weathering, which is most likely to reveal faithful representations of the original biotic community.

Effects of spalling and abrasion on fossil morphology

The manner in which fossils are exposed on a surface by post-fossilization processes may theoretically have significant implications for the morphological characterization of Ediacaran taxa, as it should be anticipated that such effects could be evident at the scale of a single fossil. It is possible that the topography of individual fossils could enhance abrasion – for example, by surface runoff – in localized areas. The observed variability in the quality of fossil specimens on a surface has previously been expressed as a measure of their decay index (Antcliffe *et al.* 2015) and ascribed to differing amounts of microbial decay prior to burial. However, at least some of the observed differences could be explained through differential post-fossilization processes acting on individual specimens. The prospect of such small-scale abrasion emphasizes the importance of studying multiple specimens from numerous bedding planes when discussing variations among individual taxa. Further work to investigate the impact of localized weathering on such studies is required.

Conclusions

The most widely studied Ediacaran fossil horizon in Newfoundland, the Yale outcrop of the 'E' Surface at Mistaken Point, crops out at six other localities in and around the MPER over a distance of several kilometres. Fossil census data from six outcrops of this single horizon reveal a range of fossil abundances, with significant lateral variability in both the proportions of different taxa within the assemblage and the fossil density (Fig. 4). Whereas biological communities may be expected to exhibit ecologically controlled patchiness in their benthic distributions (McIlroy 2007), the observed differences between the six localities are here attributed, at least in part, to differences in the tectonic, weathering and erosion histories of the various outcrops.

The term 'post-fossilization processes' helps to clearly communicate the group of processes that acts on a fossil assemblage after those processes that are normally grouped together under the study of taphonomy (cf. Wilson 1988). This study emphasizes the need for palaeontologists to consider and document the potential biases introduced by tectonics, metamorphism, weathering, erosion and discovery, when analysing and presenting Ediacaran palaeoecological data, and even when considering the presence or absence of perceived characters in individual specimens. It is hoped that by bringing post-fossilization processes to the attention of the wider community, their influence can be identified and accounted for, leading to a more accurate interpretation of Ediacaran palaeobiology.

This research was supported by the Natural Environment Research Council (grant numbers NE/J5000045/1 to JJM and NE/L011409/1 to AGL). Joe Stewart and Tom Hearing are thanked for assistance in gathering field data. Thanks are also extended to Martin Brasier, without whom this research would never have taken place. Reviews from Matthew Clapham and one anonymous reviewer greatly improved the manuscript. The Parks and Natural Areas Division, Department of Environment and Conservation, Government of Newfoundland and Labrador, provided permits to conduct research within the Mistaken Point Ecological Reserve. Access to fossil localities within the Mistaken Point Ecological Reserve for research is by permit only. The fossils around Cape Race are protected by the Paleontological Resource Regulations 67/11 under the Historic Resources Act 1990.

References

Allison, P.A. & Bottjer, D.J. 2011. Taphonomy: bias and process through time. *In*: Allison, P.A. & Bottjer, D.J. (eds) *Taphonomy*. Springer, Dordrecht, 1–17.

Anderson, M.M. & Misra, S.B. 1968. Fossils found in the Pre-Cambrian Conception Group of south-eastern Newfoundland. *Nature*, **220**, 680–681.

Antcliffe, J.B., Hancy, A.D. & Brasier, M.D. 2015. A new ecological model for the *c.* 565 Ma Ediacaran biota of Mistaken Point, Newfoundland. *Precambrian Research*, **268**, 227–242.

Bamforth, E.L. & Narbonne, G.M. 2009. New Ediacaran rangeomorphs from Mistaken Point, Newfoundland, Canada. *Journal of Paleontology*, **83**, 897–913.

Bamforth, E.L., Narbonne, G.M. & Anderson, M.M. 2008. Growth and ecology of a multi-branched Ediacaran rangeomorph from the Mistaken Point assemblage, Newfoundland. *Journal of Paleontology*, **82**, 763–777.

Behrensmeyer, A.K. & Kidwell, S.M. 1985. Taphonomy's contributions to paleobiology. *Paleobiology*, **11**, 105–119.

Brasier, M.D. & Antcliffe, J.B. 2009. Evolutionary relationships within the Avalonian Ediacara biota: new insights from laser analysis. *Journal of the Geological Society, London*, **166**, 363–384, https://doi.org/10.1144/0016-76492008-011

Brasier, M.D., Antcliffe, J.B. & Liu, A.G. 2012. The architecture of Ediacaran fronds. *Palaeontology*, **55**, 1105–1124.

Clapham, M.E. 2011. Ordination methods and the evaluation of Ediacaran communities. *In*: Laflamme, M., Schiffbauer, J.D. & Dornbos, S.Q. (eds) *Quantifying the Evolution of Early Life*. Topics in Geobiology, **36**. Springer, Dordrecht, 3–21.

Clapham, M.E. & Narbonne, G.M. 2002. Ediacaran epifaunal tiering. *Geology*, **30**, 627–630.

Clapham, M.E., Narbonne, G.M. & Gehling, J.G. 2003. Paleoecology of the oldest known animal communities: Ediacaran assemblages at Mistaken Point, Newfoundland. *Paleobiology*, **29**, 527–544.

Clapham, M.E., Narbonne, G.M., Gehling, J.G., Greentree, C. & Anderson, M.M. 2004. *Thectardis avalonensis*: a new Ediacaran fossil from the Mistaken Point biota, Newfoundland. *Journal of Paleontology*, **78**, 1031–1036.

Darroch, S.A.F., Laflamme, M., Schiffbauer, J.D. & Briggs, D.E.G. 2012. Experimental formation of a microbial death mask. *Palaios*, **27**, 293–303.

Darroch, S.A.F., Laflamme, M. & Clapham, M.E. 2013. Population structure of the oldest known macroscopic communities from Mistaken Point, Newfoundland. *Paleobiology*, **39**, 591–608.

Darroch, S.A., Sperling, E.A. *et al.* 2015. Biotic replacement and mass extinction of the Ediacara biota. *Proceedings of the Royal Society B*, **282**, https://doi.org/10.1098/rspb.2015.1003

Dufour, S.C. & McIlroy, D. 2016. Ediacaran pre-placozoan diploblasts in the Avalonian biota: the role of chemosynthesis in the evolution of early animal life. *In*: Brasier, A.T., McIlroy, D. & McLoughlin, N. (eds) *Earth System Evolution and Early Life: A Celebration of the Work of Martin Brasier*. Geological Society, London, Special Publications, **448**. First published online September 15, 2016, https://doi.org/10.1144/SP448.5

Fedonkin, M.A., Gehling, J.G., Grey, K., Narbonne, G.M. & Vickers-Rich, P. 2007. *The Rise of Animals: Evolution and Diversification of the Kingdom Animalia*. John Hopkins University Press, Baltimore.

Flude, L.I. & Narbonne, G.M. 2008. Taphonomy and ontogeny of a multibranched Ediacaran fossil: *Bradgatia* from the Avalon Peninsula of Newfoundland. *Canadian Journal of Earth Sciences*, **45**, 1095–1109.

Ford, T.D. 1958. Precambrian fossils from Charnwood Forest. *Proceedings of the Yorkshire Geological Society*, **31**, 40–57, https://doi.org/10.1144/pygs.31.3.211

Gehling, J.G. 1999. Microbial mats in Terminal Proterozoic siliciclastics: Ediacaran death masks. *Palaios*, **14**, 40–57.

Gehling, J.G. & Narbonne, G.M. 2007. Spindle-shaped Ediacara fossils from the Mistaken Point assemblage, Avalon Zone, Newfoundland. *Canadian Journal of Earth Sciences*, **44**, 367–387.

Hofmann, H.J., O'Brien, S.J. & King, A.E. 2008. Ediacaran biota on the Bonavista Peninsula, Newfoundland, Canada. *Journal of Paleontology*, **82**, 1–36.

Laflamme, M., Narbonne, G.M. & Anderson, M.M. 2004. Morphometric analysis of the Ediacaran frond *Charniodiscus* from the Mistaken Point Formation, Newfoundland. *Journal of Paleontology*, **78**, 827–837.

Laflamme, M., Narbonne, G.M., Greentree, C. & Anderson, M.M. 2007. Morphology and taphonomy of an Ediacaran frond: *Charnia* from the Avalon Peninsula of Newfoundland. *In*: Vickers Rich, P. & Komarower, P. (eds) *The Rise and Fall of the Ediacaran Biota*. Geological Society, London, Special Publications, **286**, 237–257, https://doi.org/10.1144/SP286.17

Laflamme, M., Schiffbauer, J.D., Narbonne, G.M. & Briggs, D.E.G. 2011. Microbial biofilms and the preservation of the Ediacara biota. *Lethaia*, **44**, 203–213.

Laflamme, M., Flude, L.I. & Narbonne, G.M. 2012. Ecological tiering and the evolution of a stem: the oldest stemmed frond from the Ediacaran of Newfoundland, Canada. *Journal of Paleontology*, **86**, 193–200.

Landing, E., Narbonne, G.M., Myrow, P.M., Benus, A.P. & Anderson, M.M. 1988. Faunas and depositional environments of the Upper Precambrian through Lower Cambrian, Southeastern Newfoundland. *In*: Landing, E., Narbonne, G.M. & Myrow, P.M. (eds) *Trace Fossils Small Shelly Fossils and the Precambrian–Cambrian Boundary*. New York State Museum Bulletin, **462**, 59–71.

Lawrence, D.R. 1968. Taphonomy and information losses in fossil communities. *Geological Society of America Bulletin*, **79**, 1315–1330.

Liu, A.G. 2016. Frambiodal pyrite shroud confirms the 'death mask' model for moldic preservation of Ediacaran soft-bodied organisms. *Palaios*, **31**, 259–274.

Liu, A.G., McIlroy, D. & Brasier, M.D. 2010. First evidence for locomotion in the Ediacara biota from the 565 Ma Mistaken Point Formation, Newfoundland. *Geology*, **38**, 123–126.

Liu, A.G., McIlroy, D., Antcliffe, J.B. & Brasier, M.D. 2011. Effaced preservation in the Ediacara

biota and its implications for the early macrofossil record. *Palaeontology*, **54**, 607–630.

Liu, A.G., Matthews, J.J., Menon, L.R., McIlroy, D. & Brasier, M.D. 2014. *Haootia quadriformis* n. gen., n. sp., interpreted as a muscular cnidarian impression from the Late Ediacaran period (approx. 560 Ma). *Proceedings of the Royal Society B: Biological Sciences*, **281**, https://doi.org/10.1098/rspb.2014.1202

Liu, A.G., Matthews, J.J., Menon, L.R., McIlroy, D. & Brasier, M.D. 2015*a*. The arrangement of possible muscle fibres in the Ediacaran taxon *Haootia quadriformis*. *Proceedings of the Royal Society B: Biological Sciences*, **282**, https://doi.org/10.1098/rspb.2014.2949

Liu, A.G., Kenchington, C.G. & Mitchell, E.G. 2015*b*. Remarkable insights into the paleoecology of the Avalonian Ediacaran macrobiota. *Gondwana Research*, **27**, 1355–1380.

Liu, A.G., Matthews, J.J. & McIlroy, D. 2016. The *Beothukis/Culmofrons* problem and its bearing on Ediacaran macrofossil taxonomy: evidence from an exceptional new fossil locality. *Palaeontology*, **59**, 45–58.

McIlroy, D. 2007. Lateral variability in shallow marine ichnofabrics: implications for the ichnofabric analysis method. *Journal of the Geological Society, London*, **164**, 359–369, https://doi.org/10.1144/0016-764920005-101

Mason, S. & Narbonne, G. 2016. Two new Ediacaran small fronds from Mistaken Point, Newfoundland. *Journal of Paleontology*, **90**, 183–194.

Menon, L.R., McIlroy, D. & Brasier, M.D. 2013. Evidence for Cnidaria-like behavior in ca. 560 Ma Ediacaran *Aspidella*. *Geology*, **41**, 895–898.

Mitchell, E.G., Kenchington, C.G., Liu, A.G., Matthews, J.J. & Butterfield, N.J. 2015. Reconstructing the reproductive mode of an Ediacaran macro-organism. *Nature*, **524**, 343–346.

Narbonne, G.M. 2004. Modular construction in the Ediacaran biota. *Science*, **305**, 1141–1144.

Narbonne, G.M. 2005. The Ediacaran biota: Neoproterozoic origin of animals and their ecosystems. *Annual Review of Earth and Planetary Sciences*, **33**, 421–442.

Narbonne, G.M., Laflamme, M., Greentree, C. & Trusler, P. 2009. Reconstructing a lost world: Ediacaran rangeomorphs from Spaniard's Bay, Newfoundland. *Journal of Paleontology*, **83**, 503–523.

Narbonne, G.M., Xiao, S. & Shields, G.A. 2012. The Ediacaran Period. *In*: Gradstein, F.M., Ogg, J.G., Schmitz, M.D. & Ogg, G. (eds) *The Geologic Time Scale*. Elsevier, Amsterdam, 413–435.

Rolfe, W.D.I. & Brett, D.W. 1969. Fossilization processes. *In*: Eglinton, G. & Murphy, M.T.J. (eds) *Organic Geochemistry*. Springer, Berlin, 213–244.

Schiffbauer, J.D., Xiao, S. *et al.* 2014. A unifying model for Neoproterozoic-Palaeozoic exceptional fossil preservation through pyritization and carbonaceous compression. *Nature Communications*, **5**, https://doi.org/10.1038/ncomms6754

Seilacher, A. 1992. Vendobionta and Psammocorallia – lost constructions of Precambrian evolution. *Journal of the Geological Society, London*, **149**, 607–613, https://doi.org/10.1144/gsjgs.149.4.0607

Valentine, J.W. 1973. *Evolutionary Paleoecology of the Marine Biosphere*. Prentice-Hall, New York.

Van Kranendonk, M.J., Gehling, J.G. & Shields, G.A. 2008. Precambrian. *In*: Ogg, J.G., Ogg, G. & Gradstein, F.M. (eds) *The Concise Geologic Time Scale*. Cambridge University Press, Cambridge, 23–36.

Wellman, H.W. & Wilson, A.T. 1965. Salt weathering, a neglected geological erosive agent in coastal and arid environments. *Nature*, **205**, 1097–1098.

Wilby, P.R., Kenchington, C.G. & Wilby, R.L. 2015. Role of low intensity environmental disturbance in structuring the earliest (Ediacaran) macrobenthic tiered communities. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **434**, 14–27.

Williams, H. & King, A.F. 1979. *Trepassey Map Area, Newfoundland*. Geological Survey of Canada, Energy, Mines, and Resources Canada, St. John's, Newfoundland.

Wilson, M.V.H. 1988. Taphonomic processes: information loss and information gain. *Geoscience Canada*, **15**, 131–148.

Wood, D.A., Dalrymple, R.W., Narbonne, G.M., Gehling, J.G. & Clapham, M.E. 2003. Paleoenvironmental analysis of the late Neoproterozoic Mistaken Point and Trepassey formations, southeastern Newfoundland. *Canadian Journal of Earth Sciences*, **40**, 1375–1391.