The Ediacaran fossils of Charnwood Forest: shining new light on a major biological revolution

Charlotte G. Kenchington, Simon J. Harris, Philip B. Vixseboxse, Chris Pickup, Philip R. Wilby

Department of Earth Sciences, Memorial University of Newfoundland, Prince Philip Drive, St John’s A1B 3X5, Canada. Present address: Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, UK. cgk27@cam.ac.uk

British Geological Survey, Environmental Science Centre, Nicker Hill, Keyworth, Nottingham NG12 5GG, UK. simhar@bgs.ac.uk prwi@bgs.ac.uk

School of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol BS8 1RJ, UK. pv17454@my.bristol.ac.uk

School of Arts & Humanities, Nottingham Trent University, Mary Anne Evans Building, Clifton Campus, Nottingham NG11 8NS, UK. enquiries@hrispickupconservation.co.uk

Corresponding author: prwi@bgs.ac.uk

Keywords

Ediacaran; Charnwood Forest; Reflectance Transformation Imaging; Avalon Assemblage

Abstract
Charnwood Forest (UK) hosts some of the oldest and best-preserved macrofossils known from the Ediacaran. It is the counterpoint to the more widely studied fossil sites of south-eastern Newfoundland (Canada), which include the recently-designated UNESCO World Heritage Site of Mistaken Point. Discoveries made in Charnwood Forest since 2008 have the potential to revolutionise our understanding of the evolution of complex macroscopic life and the subsequent development of ‘modern’ (i.e. Phanerozoic) ecosystems. The sites in Charnwood include the holotypes for several iconic Ediacaran taxa, and both the oldest and potentially youngest representatives of the deep-water Avalon Assemblage. These communities provide a unique opportunity to test models of community ecology, biological endemism and environmental sensitivity and adaptability in the Ediacaran. Here, we review the geology of Charnwood Forest and the palaeobiology of its biotas, and we summarise recent scientific advances in the context of our developing understanding of early macroscopic life. We review the application of Reflectance Transformation Imaging to these ancient communities, and signpost exciting new directions for research in Charnwood Forest, almost 170 years after the fossils were first brought to light.

1.0 Introduction

Charnwood Forest comprises a small (ca. 170 km²) tract of picturesque, craggy, upland heath and pasture to the northwest of Leicester (UK), and reaches a maximum altitude of 278 m at Bardon Hill. It is an area recognised for its long history of geological study (see Ambrose et al., 2007), and is a strategically-important source of aggregate for southern Britain (McGrath, 2006), being the closest source of outcropping ‘hard’ rock to London and the site of Europe’s largest granite quarry (Mountsorrel). However, Charnwood Forest is
best known for hosting a globally-significant assemblage of Ediacaran (terminal Precambrian, 635-541 Ma) fossils. These have played a pivotal role in developing current understanding of the biological revolution that immediately preceded, and perhaps paved the way for, the appearance of the 'modern', metazoan-dominated, biosphere.

The late Ediacaran Period (~571—541 Ma) preserves some of the oldest evidence of large, complex, multicellular life, and records their growing influence over a world that had, for the previous 3 billion years, been almost exclusively occupied by microscopic organisms (see Butterfield, 2007, 2011; Brocks et al., 2017). Molecular evidence points to an origin for animals around 100 Ma earlier (see Cunningham et al., 2016), but it is only in the Ediacaran that body fossils of candidate macroscopic animals appear in abundance (Narbonne and Gehling, 2003). Significant increases in the complexity of marine ecosystems were an inevitable consequence of the evolution of animals, and a range of familiar biological innovations made their first appearance at the same time, including biomineralization (i.e. hard skeletons), macropredation, grazing and burrowing (Hofmann and Mountjoy, 2001; Hua et al., 2003; Seilacher et al., 2005; Bambach et al., 2007; Gehling et al., 2014; Wood et al., 2017). The latter, in particular, fundamentally transformed the nature of benthic substrates, and permanently altered the global cycling of elements (de Goeij et al., 2013; Reinhard et al., 2017). Intriguingly, this all took place in the face of dramatic shifts in the composition of the atmosphere and the oceans, evidenced by the largest known negative carbon stable isotope excursion (Fike et al., 2006; Halverson et al., 2005), though the timing and direction (i.e. cause or consequence) of these shifts is debated (e.g. Grotzinger et al., 2011; MacDonald et al., 2013; Wang et al., 2016). The Ediacaran was also a time of considerable perturbation to redox conditions, with atmospheric oxygen conditions thought
to have risen to anywhere between 0.1 — 10% PAL by 800Ma (e.g. Lyons et al., 2014, Cole et al., 2016, Zhang et al., 2016). This increase has been inferred to have led to oxygenation of the deep oceans, and has been implicated in the rise of animals (e.g. Zhang et al., 2016, though see Lenton et al., 2014).

Most Ediacaran macro-organisms were entirely soft-bodied and are preserved as simple casts and moulds, many of which are thought to be reliant on pyrite mineralisation (Gehling, 1999; Liu, 2016; though see Tarhan et al., 2016). This preservation style limits the level (and type) of palaeobiological information that their fossils can provide, and has frustrated attempts to phylogenetically place them. In particular, the absence of convincing internal anatomy has proved a major challenge to understanding them. Nevertheless, there is growing consensus that a diverse range of groups is present, including extinct clades and stem-line representatives of extant phyla (Erwin et al., 2011). Approximately 40 major fossil occurrences are currently known from around the globe, and these have been grouped into three global assemblages – the Avalon, the White Sea, and the Nama – according to their age, palaeogeographic position and taxonomic composition, though the control of facies and taphonomy in defining the assemblages remains contentious (Waggoner, 2003; see also Yuan et al., 2011; Boag et al., 2016). The Avalon Assemblage is the oldest (ca. 571-560 Ma) and offers particular potential for elucidating the assembly and dynamics of Earth’s nascent macroscopic communities, as well as for calibrating key evolutionary relationships (e.g. see Erwin et al., 2011). It is dominated by frondose forms (rangeomorphs and arboreomorphs) and is principally known from two, broadly coeval, biotas (Noble et al., 2015): those in Charnwood Forest (UK) and those on the Avalon and Bonavista peninsulas in Newfoundland (Canada) (reviewed in Liu et al., 2015). These closely post-date (within <9.5 million years)
the short-lived Gaskiers Glaciation (Pu et al., 2016) and occupied deep-water settings on the peri-Gondwanan Avalonian island arc system (Wood et al., 2003). The fossils in Newfoundland have received considerable attention recently because of their high taxonomic diversity and the number of surfaces on which they are preserved (see Hofmann et al., 2008; Liu et al., 2012, 2015; Mitchell et al., 2015). However, there is renewed interest in the Charnwood Forest localities because of the alternative, but complimentary, view of life in the Ediacaran that they offer. The Charnwood Forest localities host some taxa not known from other Ediacaran successions, with many new forms awaiting formal description. Additionally, some of the taxa with counterparts in Newfoundland are preserved with higher fidelity in Charnwood Forest (e.g. Primocandelabrum, Kenchington and Wilby, 2017).

Charnwood Forest was the first location in the world where Ediacaran macrofossils were documented (see Howe et al., 2012); was the first place where their Precambrian age was confirmed (Ford, 1958); and is the type locality for several iconic organisms (Ford, 1958; Boynton and Ford, 1995). These include Charnia masoni (Plate 1A) and Charniodiscus concentricus (Plate 1B), studies of which fundamentally influenced understanding of Ediacaran fronds (e.g. Jenkins 1985; Antcliffe and Brasier, 2008; Laflamme and Narbonne, 2008) and helped develop a taxonomic framework for them (Brasier et al., 2012). Nevertheless, nearly every aspect of the biology of Ediacaran fronds (e.g. their internal anatomy, feeding, reproduction, etc) continues to be contentious and they (and every other member of the biota) remain deeply enigmatic organisms (see review in Liu et al., 2015; also Liu et al., 2016, Dufour and McIlroy, 2017; Kenchington and Wilby, 2017). Recent major initiatives to laser scan and to mould and cast entire bedding-plane surfaces in Charnwood Forest and Newfoundland, as well as to apply novel techniques such as Reflectance
Transformation Imaging (see 5.0), have revolutionised their study and promise to provide critical new insights into their biology and ecology. These data are the focus of ongoing investigations into the growth and development of fronds, their reproduction and dispersal, and the structure and function of their host communities (e.g. Kenchington and Wilby, 2016; Mitchell et al., 2016; Dunn et al., 2017; Mitchell and Butterfield, 2018). Here, we summarise the most important recent advances in understanding the Charnwood fossils and their global perspective, and briefly anticipate likely future productive research directions.

Note

Many of the fossiliferous surfaces in Charnwood Forest lie on publically-accessible land and are frequented by teaching parties. Others lie on private land and require the landowner’s permission to visit. They are all recognised as being of international, national, or regional importance (i.e. they are GCR or RIGS sites), protected by SSSI legislation, and a strict no-hammering/collecting policy applies. Permission to conduct research activities should be sought from Natural England. Moulds and casts of the most important surfaces and fossils are held at the British Geological Survey (Keyworth), and some of the best examples are on public display in New Walk Museum and Art Gallery (Leicester) and in The Lapworth Museum of Geology (Birmingham).

2.0 Geological setting

The Ediacaran strata of Charnwood Forest occupy the core of a faulted, mesoscale, anticline (Figure 1 A) which has been partially exhumed from beneath a thin cover of Triassic
sediments (Watts, 1947). To the west the strata are confined by a major reverse fault (the Thringstone Fault), and to the south and east they are concealed beneath Early Cambrian strata (Brand Group). The anticline formed during a localised pre-Acadian phase of deformation and epizone-grade metamorphism (Carney et al., 2008), which imposed a complex pattern of cleavage across the inlier (Evans, 1963); an additional phase of deformation, of unknown age, is suggested by the local presence of a weaker, intersecting cleavage.

The Ediacaran strata have a total exposed thickness of ca. 3.2 km, and a further ca. 0.5 km of presumed Ediacaran-aged strata is known at depth. The latter overlies at least 0.3 km of dacite lavas (Pharaoh and Evans, 1987), but the basement to the succession is unknown. The Ediacaran rocks collectively comprise the Charnian Supergroup (Moseley and Ford, 1985; Carney, 1999), which is subdivided into the Blackbrook Group and succeeding Maplewell Group (Figure 1B). The succession is dominated by well-stratified volcaniclastic sediments but, in the northwest of the inlier (see Figure 1A), includes major bodies of andesite and dacite (the Whitwick and Bardon volcanic complexes). These are thought to be the remnants of the magmatic centres from which the bulk of the volcaniclastic sediments were derived (Pharaoh et al., 1987; Carney, 2000), and they are fringed by a thick (up to 1 km) apron of bouldery volcanic breccias and lapilli tuffs (the Charnwood Lodge Volcanic Formation). The Blackbrook Group consists of two formations: the Ives Head Formation, dominated by normally-graded, metre-scale, fine- to medium-grained sandstones, and the overlying Blackbrook Reservoir Formation, mainly comprised of planar-laminated siltstones and mudstones (Moseley and Ford, 1989; Carney, 1999). The Blackbrook Group is separated from the succeeding Maplewell Group by the Benscliffe Breccia Member, a unit of poorly
stratified lithic lapilli tuffs and andesitic breccias which forms a distinctive marker horizon (up to 100 m thick) around much of the inlier. The Maplewell Group is subdivided into two formations: the Beacon Hill Formation, dominated by highly siliceous, decimetre-scale, tabular beds of planar-laminated mudstone and siltstone, and the overlying Bradgate Formation, comprised of similar (but notably less siliceous) facies, interbedded with subordinate, but locally thick, sandstones (see 2.1). The boundary between these two formations coincides with the base of a series of closely-spaced, coarse-grained sandstones containing abundant clasts and contorted rafts of mudstone and siltstone, broadly equating to the prominent Sliding Stone Slump Breccia Member. Locally, the Bradgate Formation is overlain by the Hanging Rocks Formation. This constitutes the uppermost division of the Charnian Supergroup, and consists of up to 20 m of fine- to medium-grained conglomerates and interbedded sandstones, overlain by up to 50 m of red and purple, tuffaceous mudstones and greywacke sandstones (McIlroy et al., 1998).

The overall succession is dominated by gravity-flow deposits, including turbidites, slump-breccias and debris-flows (Moseley and Ford, 1989). It was laid down in a fore- or back-arc basin setting (Le Bas, 1984; Pharaoh et al., 1987), probably at considerable depth based on the complete absence of shallow-water sedimentary structures in the succession, and on the bathymetry of analogous modern island arcs (cf. Trofimovs et al., 2006): this is the basis on which a photosynthetic mode of life has been rejected for the fossil communities. The Hanging Rocks Formation is distinct in that it contains rounded clasts of lithologies that are not known in Charnwood Forest, in addition to familiar epiclastic and pyroclastic components (see Noble et al., 2015). This has been taken to indicate a change in the sedimentary regime during the waning stages of volcanism, perhaps signalling an
amalgamation of the Charnian arc with other arcs and marginal basins during the formation of the Avalonian Superterrane (Gibbons, 1990). Two suites of diorites intrude the Charnian Supergroup, and represent the last phase of magmatism. The North Charnwood Diorites are confined to the Blackbrook Reservoir and Beacon Hill formations, where they form sub-vertical sheets, whereas the younger South Charnwood Diorites form more substantial, broadly concordant, bodies in the upper part of the Bradgate Formation.

2.1 Sedimentology of the Bradgate Formation

Ediacaran fossils are conspicuously more abundant in the succession above the Sliding Stone Slump Breccia Member (i.e. within the Bradgate Formation) than below it. This relationship has been taken to be a primary biotic signal, with the biotas above and below being assigned to the so-called Mercian and Lubcloud assemblages, respectively (Wilby et al., 2011). However, it may alternatively reflect a fundamental change in taphonomy at this level, with the finer-grained and more volcanic-rich sediment that characterises the succession above the Sliding Stone Slump Breccia Member (see 2.0) simply prompting higher fidelity preservation. Whichever the case, the sedimentology of the Bradgate Formation is consequently of particular interest. Its dominant lithology (see Figure 2) comprises decimetre- to metre-scale beds of grey to blue-green, sharp-based siltstone (Plate 2G) interbedded with variably abundant porcellaneous horizons (typically < 20 mm thick; Plate 2B) and laminated, often normally-graded, very fine- to fine-grained tabular sandstone beds (typically < 30 mm thick; Plate 2F). Finely-laminated hemipelagite caps some beds, but it rarely exceeds more than a few tens of millimetres thickness. Some of the siltstones are graded or have a distinctive ‘wispy’ lamination (Plate 2A, C) which broadly
resembles structures documented in mud turbidites (Rebesco et al., 2014), though the lack of clear evidence of traction precludes definitive assignment. The porcellaneous horizons weather white, pale green or pink, are mudstone-grade, and have sharp bases and sharp or gradational tops. Internally, they are laminated or convolute-laminated. They are interpreted as devitrified, primary ash-fall tuffs (Moseley and Ford, 1989; Carney, 1999), likely including examples deposited from the nepheloid plume part of pyroclastic flows, as well as from vertically-settling ash-clouds. Crystal tuffs (Plate 2E) increase in abundance and thickness with increasing proximity to the Whitwick and Bardon volcanic complexes (Moseley and Ford, 1989; Carney, 1999).

Decimetre- to decametre-scale, normally-graded, coarse- to fine-grained sandstone event beds are prominent features, especially at certain levels (see Figure 2). Their bases are invariably sharp, may be gravelly, and are locally erosional and/or loaded, but they lack evidence of extensive scouring or fluting; their upper portions are typically composed of planar- or cross-laminated siltstone. These represent gravity-flows of various magnitude, some formed of reworked volcanic rock (i.e. epiclastic), and others remobilised from un lithified pyroclastic material or formed by primary pyroclastic flows entering the water column (i.e. volcaniclastic, cf. Fisher and Schmincke, 1984). Also present are massive, centimetre- to metre-scale, mudstone to very fine-grained sandstone beds with matrix-supported clasts of deformed, laminated mudstone and subordinate crystals and lithic fragments (Plate 2D). These resemble the thicker slump deposits that define several of the formation boundaries (see 2.0), and were formed by subaqueous debris-flows or by the in situ disruption of partially lithified sediment, perhaps as a result of seismic-induced dewatering (Sutherland et al., 1994). Perhaps significantly, the two most fossiliferous
horizons in the Charnian Supergroup – the ‘Bed B’ and ‘Memorial Crags’ surfaces of Wilby et al. (2011) – lie immediately above prominent (and unusually thick) event beds (see Figure 1B and 2). Such high diversity and high abundance Avalon biotas have been taken to indicate mature (i.e. late-stage) communities (Clapham et al., 2003), and may only have been able to develop in those areas where the potential for deleterious influxes of sediment (cf. Wilby et al., 2015) had been extinguished or curtailed by an earlier mass wasting of the source area(s).

3.0 Age of the Charnian Supergroup

Considerable uncertainty surrounds the rise and demise of the global Ediacaran biota (Narbonne and Gehling, 2003; Laflamme et al., 2013; Darroch et al., 2015; Pu et al., 2016; Smith et al., 2017); the timing of key biological innovations and their connection with coeval changes in the Earth’s chemical and physical environment (e.g. Canfield et al., 2007; Sperling et al., 2015); and the relative importance of biological turnover, palaeoenvironmental setting, taphonomic processes and biogeography in defining the three global assemblages (Waggoner, 2003; Grazhdankin, 2004; Narbonne, 2005; Meert and Lieberman, 2008; Gehling and Droser, 2013; Laflamme et al., 2013; Boag et al., 2016; Droser et al., 2017).

Much of this uncertainty is a consequence of there being insufficient adequately-well dated fossiliferous successions, with the Mistaken Point and Charnian successions being important exceptions (Noble et al., 2015; Pu et al., 2016). The Charnian Supergroup has high precision U-Pb (zircon) ages constraining many of its key stratigraphic horizons (see Figure 1B).

Unfortunately, none are available for the Blackbrook Group, which hosts the lowest known fossiliferous horizon (the Lubcloud surface) near its exposed base: it is merely constrained to
between ca. 611 Ma and 569.1 ± 0.9 Ma. Hence, the succession does not currently contribute to understanding of the appearance of Ediacaran biotas which, at least in SE Newfoundland, occurs less than 9.5 million years after the Gaskiers Glaciation, dated at ca. 580.9-579.9 Ma (Narbonne and Gehling, 2003; Pu et al., 2016). However, given that the Lubcloud surface lies >0.6 km stratigraphically below the horizon dated at 569.1 ± 0.9 Ma, there remains the theoretical possibility that it (uniquely) records a pre-Gaskiers biota. If true, this would have significant ramifications for our understanding of the origin and antiquity of large body size and complex bauplans.

The overlying Maplewell Group, which hosts the most diverse fossil biotas, is constrained to between 569.1 ± 0.9 Ma and ca. 557 Ma. This overlaps with the succession in Newfoundland (Liu et al., 2012), and permitted reliable correlation between the biotas for the first time (Noble et al., 2015). It also extends the known upper ranges of several taxa in the Avalon Assemblage (e.g. C. masoni, Bradgatia linfordensis, Primocandelabrum sp.), suggesting that Ediacaran community structures were comparatively stable over a prolonged period, at least in these deep-water environments. Probable partial temporal overlap with the shallower-water biotas of the White Sea Assemblage (Martin et al., 2000; Grazhdankin, 2004), including those of the Welsh Borderlands and Wales (Cope, 2000; Compston et al., 2002; Liu, 2011), supports the primacy of palaeoenvironment in controlling the taxonomic composition of Ediacaran biotas (Grazhdankin, 2004; Wilby et al., 2011; Gehling and Droser, 2013).

4.0 Biota
The Ediacaran biotas of Charnwood Forest are overwhelmingly dominated by two enigmatic groups of frondose organisms (Plate 1 and 3) – the rangeomorphs (Narbonne, 2004; Erwin et al., 2011) and the arboreomorphs (Xiao and Laflamme, 2009; included in the frondomorphs of Grazhdankin 2014) – neither of which can be confidently placed within any extant (or Phanerozoic) clade. They each consist of an architecturally complex frond that was attached to the substrate, either directly (in the case of reclining and creeping forms), or via a connecting stalk and a buried globular holdfast (in the case of erect forms).

Rangeomorphs adopted a wide range of gross morphologies (e.g. leaf-shaped, bush-shaped, spindle-shaped) and had a distinctive pseudo-fractal branching architecture (Narbonne, 2004) that is generally considered to have been optimised as an exchange surface, perhaps for the osmotic uptake of dissolved organic carbon from the water column (Laflamme et al., 2009; Hoyal Cuthill and Conway Morris, 2014, 2017; though see Dufour and McIlroy, 2017). Arboreomorphs, by contrast, only occur as leaf-shaped forms, though their branching morphology varies between taxa (Laflamme et al., 2004); while recent studies suggest that they may be a monophyletic group (Dececchi et al., 2017), many aspects of their biology and systematics await detailed study. Representatives of both groups would have towered more than half a metre above the substrate (e.g. see Boynton and Ford, 1995), although most fossil specimens are only a few tens of centimetres long (Clapham and Narbonne, 2002).

Other groups are conspicuously scarce in Charnwood Forest and are poorly studied (Wilby et al., 2011), but may well prove to be amongst the most scientifically important in the succession. These include a short (typically <10 cm), gladius-shaped organism with simple transverse bars (Plate 3A), which broadly resembles Hadryniscala from Newfoundland (Hofmann et al., 2008); a hemispherical organism with bifurcating radial ribs (Plate 3C); and
various rather nebulous forms (see 4.3) collectively referred to as ‘ivesheadiomorphs’ (see Liu et al., 2011).

Until recently, fossils were generally thought to have been limited to only a few surfaces in Charnwood, and to have been rather low in taxonomic diversity. However, following a systematic programme of silicone rubber moulding by the British Geological Survey (Plate 4), and prospecting by amateur palaeontologists, they are now know to be preserved on several dozen surfaces and to include communities that rival any in the world in terms of fossil density and diversity (Wilby et al., 2011). The most important fossiliferous surface currently known in Charnwood Forest is the ‘Bed B’ of Wilby et al. (2011): it is the most studied surface, is exposed over an area of ca. 100 m², preserves ca. 900 fossils, and hosts at least 16 different species (Wilby et al., 2011). Other important fossiliferous surfaces include Memorial Crags, which hosts especially large specimens of C. masoni and the type specimens of the bush-like rangeomorph Bradgatia linfordensis (Boynton and Ford, 1995; Wilby et al., 2015), and Aron A, which lies immediately above the Sliding Stones Slump Breccia (i.e. in a similar stratigraphic position to the Memorial Crags surface). The latter preserves a vast number of superimposed holdfast discs (Plate 2H), a relationship that is interpreted to record prolonged (though perhaps interrupted) colonisation of the substrate (cf. Wilby et al., 2015). Most of the fossiliferous surfaces have a subtle pustular and wrinkled surface texture which is taken to indicate that they supported surficial microbial mats (see Callow and Brasier, 2009; Laflamme et al., 2012b). These may have played an important ecological role (e.g. Dufour and McIlroy, 2017), helped anchor the organisms to the substrate, and been critical to the process of fossilization (Kenchington and Wilby, 2017).
Many of the species on Bed B are new and are not known from other Ediacaran localities (Wilby et al., 2011, see also Kenchington and Wilby, 2017), suggesting that Avalon biotas may have had a high degree of endemism, perhaps controlled by differences in their palaeogeographical setting (i.e. back-arc or ocean-facing) and/or their position on the submarine slope. Certainly, there is growing evidence to suggest that the composition of Ediacaran biotas was strongly influenced by depositional environment (Grazhdankin, 2004; Gehling and Droser, 2013). Detailed analysis of Bed B has provided compelling evidence for the role of minor disturbance events (e.g. blanketing by a thin layer of sediment) in shaping their structure, just as they affect the size-frequency distribution of modern populations of benthic organisms (Wilby et al., 2015). An environmental difference, such as substrate character or suspended sediment concentration, would seem the most likely explanation for the conspicuous absence in Charnwood Forest of the reclining rangeomorph Fractofusus, despite its super-abundance on many surfaces in Newfoundland (see Gehling and Narbonne, 2007; Liu et al., 2012; Mitchell et al., 2015), and of other reclining or low-lying forms known from Newfoundland, such as Pectinifrons and Hapsidophyllas (see Bamforth and Narbonne, 2009). Instead, the Charnwood communities are dominated by erect fronds and, compared to many of the surfaces in Newfoundland, they have an abundance of taxa with naked stems (e.g. the informally-named ‘dumbbell’ rangeomorph, Plate 3B) and host diverse multifoliate taxa (namely Primocandelabrum, the ‘dumbbell’, and Bradgatia). The erect forms may have been less susceptible to fouling by benthic plumes of sediment or, being held higher in the water column and exposed to faster currents, better able to shed any settled particles (Kenchington, 2015). Conceivably, this could even have been a driver
for the evolution of the first stems, though stems have more generally been linked to vertical competition for resources (Clapham and Narbonne, 2002; Laflamme et al., 2012a; Ghisalberti et al., 2014).

Nevertheless, several taxa in Charnwood Forest are shared with Newfoundland, providing strong support to the notion that at least some taxa were able to disperse widely via waterborne propagules (Darroch et al., 2013, Mitchell et al., 2015). This is most obviously the case for *C. masoni* (Plate 1A, D), which has a cosmopolitan distribution (both geographically and temporally), but also includes the bush-shaped *B. linfordensis* (Plate 3D), and perhaps *Vinlandia*, which we tentatively report from Charnwood for the first time (Plate 3E). *Primocandelabrum* was until recently only reported from Newfoundland (Hofmann et al., 2008), but it is now also known in Charnwood Forest (Plate 3F and 5F) and may in fact be the commonest rangeomorph present in the region (see Kenchington and Wilby, 2017). The arboreomorphs are comparatively poorly studied in Charnwood and Newfoundland, so their level of commonality is unclear. *Charniodiscus longus* and *C. arborea* are present in both regions, but two of the most distinctive species of *Charniodiscus* in Newfoundland – *C. procerus* and *C. spinosus* (Laflamme et al., 2004) – remain unknown from Charnwood (Plate 1B-C, E-G).

4.2 A sense of community

The great majority of fossils on Bed B are closely co-aligned and are preserved still anchored to the substrate by their holdfasts (Wilby et al., 2011); the small number that have been uprooted or imported (i.e. are allochthonous) are very obviously misaligned and are often
folded, enrolled or distorted beyond recognition. This suggests that the majority of the community was killed *in situ* by a single event (though see 4.3 and Wilby *et al.*, 2015), and that the surface captures an essentially unbiased (i.e. census) record of the original living community. Hence, the surface provides a crucial opportunity to examine the biometrics and population structure of individual taxa in much the same way as for living organisms, potentially providing insights into fundamental aspects of their biology as varied as their ontogeny, mortality, recruitment, metabolic efficiency, and dimorphism. *C. masoni*, for example, was revealed to have two (or perhaps three) key stages in its life history: an initial planktonic dispersal phase, and a benthic phase of isometric growth, characterised by the insertion and subsequent expansion of new primary branches (Wilby *et al.*, 2015). The *C. masoni* population on Bed B, in combination with specimens from Newfoundland, have recently been used to demonstrate that rangeomorphs had a non-deviant form, with the overall shape maintained across the preserved ontogenetic series (Dunn *et al.*, 2017).

Growth trends documented in *C. masoni* suggest that settlement and adoption of this adult life habit took place when the organisms had 4 primary branches (Wilby *et al.*, 2015). Interestingly, at least some of the very largest *C. masoni* specimens (>45 cm long) show a switch to a subsequent expansion-dominated phase of growth, characterised by the inflation of existing branches and a cessation (or very substantial reduction) of the insertion of new ones. The cause of this transition is unclear, but it could conceivably signal maturity, or be a response to improved environmental conditions; whichever, comparable growth programmes are seen in certain modern invertebrates (Wilby *et al.*, 2015).

As well as being preserved *in situ*, many of the fossils preserve exceptionally-fine morphological details (see Plate 1F), despite being very low epirelief (Kenchington and
Wilby, 2014). Previously unknown anatomical features are apparent in several otherwise familiar taxa, promising to improve understanding of their biology, and more thorough treatments of previously poorly characterised genera have been possible. For example, Kenchington and Wilby (2017) were able to significantly augment the original diagnosis for *Primocandelabrum* (Hofmann et al., 2008) because some of the new specimens from Charnwood preserve the frond’s fine branching structure (Plate 5F). Indeed, the specimens are sufficiently well-preserved to have allowed opposing taxonomic schemes for the rangeomorphs to be tested (using multivariate statistical analyses), and the level of intra-specific variability within taxa to be assessed (Kenchington and Wilby, 2017). The latter was shown to be moderately high, providing potential insights into ontogeny, morphological plasticity and ecophenotypic variation within the group.

4.3 Pizza discs and bubble mats

Many of the fossiliferous surfaces in Charnwood Forest host abundant circular or sub-circular features (up to ca. 0.3 m diameter) with variably well-defined margins and a pustular-, polygonal- or ridged internal structure (Plate 5): they comprise 10% of the fossils on Bed B. Initially assigned to discrete species (Boynton and Ford, 1995), these features are now collectively referred to as ‘ivesheadiomorphs’ (Liu et al., 2011), though their origin(s) are debated. In Newfoundland, these structures were originally termed ‘pizza discs’, ‘lobate discs’ and ‘bubble mats’, based on their gross morphological appearances (Narbonne et al., 2001). Liu et al. (2011) interpreted them as the decayed (‘effaced’) remnants of organisms that had died prior to the event which killed the associated, definitively frondose, organisms on the surface. However, Laflamme et al. (2012b) considered them to simply be microbial
colonies, while Wilby et al. (2011) suggested that at least some could be attributed to soft-
sediment disruption associated with the collapse of buried organisms. Most recently, 
Matthews et al. (2017) have suggested that similar features could be generated by modern 
weathering and erosion. If ivesheadiomorphs are produced by abiological means, then one 
might expect any population of them to have an approximately normal size distribution – 
such analyses might prove a useful way of testing the abiological versus biological genesis of 
each type of ivesheadiomorph.

Resolving the true nature(s) of ivesheadiomorphs has become an urgent priority because of 
the need to know how they should be treated in ongoing analyses of community structure: 
either as part of the living system, as separate, or as a potential source of nutrients for other 
taxa on the surface (see Mitchell and Butterfield, 2018). Additionally, since the oldest 
fossiliferous surface in Charnwood Forest (the Lubcloud surface) is comprised entirely of 
ivesheadiomorphs, their nature has a direct bearing on the temporal range of the biota as 
whole. Provisional work suggests that the observed variation in their morphology may 
actually reflect different modes of generation. Examples displaying regular internal structure 
(e.g. those formerly referred to as Blackbrookia, Boynton and Ford, 1995; Plate 5B) are most 
convincingly interpreted as poorly preserved fronds (cf. Liu et al., 2011), though not 
necessarily as a result of decay. We note that sediment preserving the biota on the Lucloud 
surface is very obviously coarser than that capturing any of the higher biotas, and the 
resolution of preservation is correspondingly lower. Examples displaying a polygonal 
internal structure (Plate 5C) imply a component of shrinkage and/or collapse, conceivably as 
a result of fluid escape from beneath the surficial mat, or of decay of the mat itself.

Examples resulting from the uneven collapse of a buried 3D frond are difficult to definitively
prove based on only epirelief impressions. However, possible candidates are provided where a distinctive holdfast and stalk terminate at an appropriately-sized area of pustular relief (Plate 5F), though careful examination is required to eliminate the possibility that the frond is merely poorly preserved (cf. Liu et al., 2011) or was disrupted by having come to rest on an existing ivesheadiomorph. Finally, we recognise examples that might fall into the ivesheadiomorph spectrum which are clearly a consequence of fronds having been felled vertically (i.e. concertinaed), rather than horizontally (the norm). These typically display a splayed or radiating array of structures (Plate 5E), corresponding to the lowest branching order(s), and may flatten more normally preserved fronds.

Several features of ivesheadiomorphs remain to be adequately explained. In particular, some form conspicuously high, positive epirelief impressions, whereas most fossils on the surfaces are preserved as low, negative epirelief impressions. Liu et al. (2011) sought to explain this in terms of preferential trapping and binding of sediment by extracellular-polysaccharides produced by microbes covering a decaying carcass, but this does not fully account for the deflection of sedimentary laminae upwards into the domes of the ivesheadiomorphs, as seen in cross-sections. Instead, these characteristics might reasonably be explained by the build-up of gases from a decaying carcass beneath a microbial mat, and the gases’ uneven displacement during subsequent burial. Ivesheadiomorphs are also largely restricted to the Avalon Assemblage, suggesting a strong depositional, taphonomic, or ecological control on their occurrence. These might include differences in: 1) the geochemical or physical character of the substrate, 2) the microbial community present, or 3) the frequency and scale of sedimentation events.
5.0 A change of view

Ediacaran macrofossils are notoriously difficult to work with, in part because most are very low relief and details are only revealed with low-angle lighting (though see Hoyal Cuthill and Conway Morris, 2017; Sharp et al., 2017). Casts of them are generally too large and unwieldy to be easily examined under a binocular microscope (e.g. see Plate 4B-C), meaning that they are often studied in a darkened room with a mobile light source. 3D laser scanning offers a potential alternative (e.g. Brasier and Antcliffe, 2009), particularly for mapping in situ bedding-plane assemblages (Mitchell et al., 2016), but the technique requires specialist equipment (both hardware and software) and may not always match the resolution achieved by traditional photography. Reflectance Transformation Imaging (RTI) is a composite digital imaging technique that marries many of the key benefits of laser scanning and photography (Duffy, 2013), and is comparatively simple to undertake. This makes it a highly practical alternative, and it is now routinely applied to the fossils from Charnwood Forest. The technique allows the user to interactively and seamlessly change the angle and direction of a virtual light source on a static image (Hammer et al., 2002; Anon, 2013), thereby optimising the view of any feature in the frame. In addition to the lighting, it is also possible to change a variety of other parameters, such as the level of specular reflection and colour saturation, as well as to zoom to areas of interest. The RTI files can be built (from a series of photographs) and viewed in open source software (http://culturalheritageimaging.org/What_We_Offer/Downloads/View/), and they include the option for recording the parameters which best highlight particular anatomical features (Anon, 2013). Hence, they are an excellent tool for interpreting the fossils and are ideally suited as supplements to systematic descriptions.
Because RTI images allow the lighting to be varied very precisely (and by graduations of <1°) it is possible to resolve very subtle morphological features. This is amply illustrated with the holotype of *Charniodiscus concentricus* (Plate 1B). This taxon is known from a single frond in Charnwood Forest (Ford, 1958), whose complex morphology has been the subject of prolonged debate. Early workers considered it to have two opposing rows of branches extending off its central axis (Jenkins and Gehling, 1978), whereas subsequent workers interpreted it to have three or more rows (Dzik, 2002), each with elements of both its upper and lower surface supposedly preserved in a complex composite impression (Brasier and Antcliffe, 2009, Fig. 12). This taphonomic style is not observed in any other fronds from the surface, nor do any of the other ca. 70 arboreomorphs present exhibit more than two rows of branches. Hence, Wilby et al. (2011) considered the specimen to comprise two superimposed fronds, as more obviously apparent in other examples on the surface (Plate 1C, G), though no second holdfast is apparent. The merits of each of these interpretations is easily tested with the RTI (DOI: 10.5285/8f256217-09f1-4807-8357-648f558f3187): in particular, the topographically higher position of the central-left part of the fossil, and the impact of cleavage on the fossil’s morphology, are very apparent.

### 6.0 Looking forward

New fossiliferous surfaces continue to be discovered in Charnwood Forest, and at least half a dozen new species – including intriguing non-frondose forms – await formal description. The Charnwood Forest fossil surfaces therefore hold the potential to give insight into the understudied non-rangeomorph components of the Avalon Assemblage, and also to test palaeobiological hypotheses based on the Newfoundland sites. The *in situ* nature of the
communities makes them a priority target for community structure analysis, with the intention of interrogating the ‘rules’ that governed these earliest, comparatively simple, macroscopic ecosystems. For example, competition and reproductive biology identified in Newfoundland communities (Mitchell et al. 2015) could be tested to determine if there were local geographical/environmental influences on these fundamental biological processes.

There are several specific questions that the Charnwood Forest biotas will play a crucial role in answering. Modern benthic organisms are sensitive to substrate composition (e.g. Smit et al., 2008). While no identifiable signal of local substrate variability has been detected in the communities (Mitchell et al., 2015), the influence of broader-scale variability on community composition (i.e. between different sites or regions) has not been examined. Plausibly, differences in the relative abundance of reactive volcanic material compared to inert epiclastic debris in the substrate could influence not just taxonomic composition, but also organism density, growth rate and maximum size, and these differences could be used to test theories of chemosynthesis (cf. Dufour and McIlroy, 2017).

Charnwood Forest has a notably high abundance of out-size (>45 cm tall) fronds, both in terms of the number of bedding planes on which they occur and their frequency within individual populations (see Wilby et al, 2011, 2015). We don’t yet fully know what this signals or how the fronds benefited from growing to such a large size (Wilby et al., 2015), but a combined analysis of the sedimentological and community structure would allow potential causes to be investigated, such as maturity, resource abundance, frequency of disturbance, and degree of competition.
The exquisite preservation of the specimens on Bed B and the Memorial Crags surface, coupled with the comparatively large population sizes present, makes them ideal for examining intraspecific variation (cf. Kenchington and Wilby, 2017), developmental programmes and ontogeny (cf. Wilby et al., 2015). These will provide control on modelling work that seeks to understand the growth of rangeomorphs and the evolution of large body size (Hoyal Cuthill and Conway Morris, 2014, 2017) which, in turn, may provide insights into their ecology and phylogeny. Further, the preservational pathway(s) in Charnwood Forest may be different to those operating in the classic Newfoundland localities (Liu, 2016; Kenchington and Wilby, 2014). Understanding these differences may help to elucidate the biological composition of these organisms and contribute to arguments relating to a taphonomic cause for the extinction of the Ediacaran biota (cf. Darroch et al., 2015).

The stratigraphically highest fossil surfaces in Charnwood Forest host some of the youngest known communities of the Avalon Assemblage (Noble et al., 2015). Consequently, they provide key constraints on questions of biostratigraphy, the influence of age versus environment on community composition (cf. Boag et al., 2016), and on the timing of appearance of non-rangeomorph phyla in the Ediacaran. Additionally, depending on the duration of the basal Cambrian unconformity (Fig. 1), Charnwood Forest provides a rare opportunity to elucidate the nature of the Precambrian-Cambrian transition in a deep-water setting, and thus provide a crucial complimentary record to the classic, shallower-water, sections of Namibia (e.g. Darroch et al., 2015) and Newfoundland (e.g. Buatois and Mangano, 2016). The Brand Group is thought to be mostly (if not entirely) of Early Cambrian age, based on the presence of *Teichichnus* burrows near its base (Bland and Goldring, 1995), and to be separated from the underlying Maplewell Group by a cryptic unconformity.
Constraining the age of the uppermost division of the Maplewell Group (the Hanging Rocks Formation) is challenged by the paucity of primary datable minerals (Noble et al., 2015) but, if achieved, it could help resolve some of the largest questions in palaeontology – namely, the tempo and diachronicity of the agronomic revolution, the evolution of modern phyla and the cause of the first major extinction on Earth.

Acknowledgements

This work was supported by the Natural Environment Research Council [grant NE/I005927/1 to PRW and CGK], and was facilitated by Natural England, the Mistaken Point Ecological Reserve (Parks and Natural Areas Division, Government of Newfoundland and Labrador) and landowners in Charnwood Forest. Louise Neep, Paul Shepherd, Sue Martin, GeoEd and Alan Weightman are acknowledged for their help with moulding and casting, and Eddie Bailey (Aggregate Industries UK Limited) is especially thanked for granting access to drill core. Ian Longhurst and Simon Ward drafted Figure 1. The authors thank Alex Liu and an anonymous reviewer for their useful comments on an earlier draft of this work.

References


1.1. Cultural Heritage Imaging


**Figure explanations**

**Figure 1**: Geology of Charnwood Forest. A) Simplified bedrock geological map (minus Triassic cover), showing the locations of the most important known fossil surfaces. The Charnian Supergroup comprises the Blackbrook, Maplewell and Brand Groups. B) Simplified stratigraphic log of the exposed Ediacaran-aged succession, showing current U-Pb (zircon) age constraint (after Noble *et al.*, 2015) and the positions of key marker horizons. LC, Lubcloud fossil surface; BB, Benscliffe Breccia Member; SB, Sliding Stones Slump Breccia Member; MC, Memorial Crags fossil surface; Bed B, main fossil surface; HRF, Hanging Rocks Formation. Modified from Carney (1999).

**Figure 2**: Sedimentology of the Bradgate Formation. Lithological log of part of the upper Bradgate Formation, with expanded view of the interval encompassing Bed B. The position of the newly discovered golf course fossil surface is given by GC.

**Plate 1**: Representative rangeomorph and arboreomorph fronds from Bed B, Bradgate Formation. A) *Charnia masoni* holotype (GSM106160). B) *Charniodiscus concentricus* holotype (GSM106161); see also DOI: 10.5285/8f256217-09f1-4807-8357-648f558f3187. C) Arboreomorph, undet., partially overlapped by another (arrowed) smaller specimen (GSM105960). D) Small, potentially immature, *Charnia masoni* specimen (GSM105979). E-F) Arboreomorph, undet., with well-preserved branch divisions highlighted and enlarged in F (GSM106069). G) Three (arrowed) similarly-sized and partially overlapping, conspecific
arboreomorphs (GSM105876). Scale bars = 30 mm. All specimens are casts except C and E-F (moulds), and are housed at the British Geological Survey, Keyworth.

Plate 2: Representative facies of the Bradgate Formation, Charnian Supergroup. A-F)
Polished sections of the Rise Rocks core (SK41SE/192), housed at the British Geological Survey, Keyworth. A) Finely-laminated turbiditic siltstone, sharply overlain by a normally-graded sandstone (43.78-43.83 m). B) Sharp-based, locally graded, porcellaneous horizon, interpreted as a devitrified primary ash-fall tuff (128.50-128.55 m). C) Finely-laminated and ‘wispy’ turbiditic siltstone (158.18-158.23 m). D) Massive sandstone with matrix-supported clasts of laminated mudstone and siltstone, interpreted as a slump deposit (90.0-90.1 m). E) Crystal tuff with multiple, thin, pink ash tuff laminae (49.32-49.37 m). F) Normally-graded, epiclastic sandstone, interpreted as a minor gravity-flow deposit (67.71-67.76 m). G) Planar-bededded siltstones and subordinate thin sandstones, recording multiple turbidite events. H) Superimposed holdfast discs on the Aron A fossil surface, recording prolonged colonisation, perhaps separated by minor influxes of sediment. Scale bars = 10 mm; approximate height of G is 2 m.

Plate 3: Bed B biota, Bradgate Formation. A) Undescribed gladius-shaped organism of uncertain affinity (GSM106083). B) The iconic dumbbell-like taxon with a massive holdfast and complex, artichoke-like frond on top of a long, straight stalk (GSM105875). C) Undescribed hemispherical organism with bifurcating radial ribs (GSM105967). D) Well-preserved Bradgatia linfordensis (GSM105873). E) Frond, tentatively assigned to Vinlandia, a taxon that has not previously been reported from Charnwood Forest (BGS cast 630). F) Newly described Primocandelabrum boyntoni, with frond of typical triangular-outline
Plate 4: Systematic moulding and casting of key fossiliferous surfaces in Charnwood Forest. Following careful cleaning, the surfaces were moulded with silicone rubber by the British Geological Survey and GeoED (A), and then cast with plaster, typically in 1m$^2$ areas (B,C), allowing each surface to be fully reconstructed in the laboratory. Scale bar = 100 mm.

Plate 5: ‘Ivesheadiomorphs’ from the Ives Head and Bradgate formations. A-B and D are casts (Lubcloud surface), whereas C and E-F are moulds (Bed B surface). A) Multiple, sub-circular ivesheadiomorphs (GSM119702). B) *Blackbrookia*-type, displaying some regular internal structure and most plausibly interpreted as a poorly preserved frond (GSM119700). C) Polygonal-type, suggesting generation in association with shrinkage and/or collapse (GSM106094). D) Lobate-type (GSM119699). E) Splayed-type, with ridges originating from a single point and bifurcating near the margins (GSM105969). This pattern is reminiscent of the coarse branching pattern in *Primocandelabrum*, and is plausibly interpreted as a vertically compressed frond; note the sympathetically-oriented and partially overlain *Charnia masoni* (arrowed) frond. F) Two mutually-aligned and morphologically-similar holdfasts and stalks, one with a well preserved *Primocandelabrum boyntoni* frond at its end, and the other terminating in a pustular ivesheadiomorph (GSM105969). Scale bars = 50 mm. All are housed at the British Geological Survey, Keyworth.