

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

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16 **Keywords**

17 Ediacaran; Charnwood Forest; Reflectance Transformation Imaging; Avalon Assemblage

18

19 **Abstract**

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

35

36 **1.0 Introduction**

37 Charnwood Forest comprises a small (ca. 170 km²) tract of picturesque, craggy, upland
38 heath and pasture to the northwest of Leicester (UK), and reaches a maximum altitude of
39 278 m at Bardon Hill. It is an area recognised for its long history of geological study (see
40 Ambrose *et al.*, 2007), and is a strategically-important source of aggregate for southern
41 Britain (McGrath, 2006), being the closest source of outcropping ‘hard’ rock to London and
42 the site of Europe’s largest granite quarry (Mountsorrel). However, Charnwood Forest is

43 best known for hosting a globally-significant assemblage of Ediacaran (terminal
44 Precambrian, 635-541 Ma) fossils. These have played a pivotal role in developing current
45 understanding of the biological revolution that immediately preceded, and perhaps paved
46 the way for, the appearance of the 'modern', metazoan-dominated, biosphere.

47 The late Ediacaran Period (~571—541 Ma) preserves some of the oldest evidence of large,
48 complex, multicellular life, and records their growing influence over a world that had, for
49 the previous 3 billion years, been almost exclusively occupied by microscopic organisms (see
50 Butterfield, 2007, 2011; Brocks *et al.*, 2017). Molecular evidence points to an origin for
51 animals around 100 Ma earlier (see Cunningham *et al.*, 2016), but it is only in the Ediacaran
52 that body fossils of candidate macroscopic animals appear in abundance (Narbonne and
53 Gehling, 2003). Significant increases in the complexity of marine ecosystems were an
54 inevitable consequence of the evolution of animals, and a range of familiar biological
55 innovations made their first appearance at the same time, including biomineralization (i.e.
56 hard skeletons), macropredation, grazing and burrowing (Hofmann and Mountjoy, 2001;
57 Hua *et al.*, 2003; Seilacher *et al.*, 2005; Bambach *et al.*, 2007; Gehling *et al.*, 2014; Wood *et*
58 *al.*, 2017). The latter, in particular, fundamentally transformed the nature of benthic
59 substrates, and permanently altered the global cycling of elements (de Goeij *et al.*, 2013;
60 Reinhard *et al.*, 2017). Intriguingly, this all took place in the face of dramatic shifts in the
61 composition of the atmosphere and the oceans, evidenced by the largest known negative
62 carbon stable isotope excursion (Fike *et al.*, 2006; Halverson *et al.*, 2005), though the timing
63 and direction (i.e. cause or consequence) of these shifts is debated (e.g. Grotzinger *et al.*,
64 2011; MacDonald *et al.*, 2013; Wang *et al.*, 2016). The Ediacaran was also a time of
65 considerable perturbation to redox conditions, with atmospheric oxygen conditions thought

66 to have risen to anywhere between 0.1 — 10% PAL by 800Ma (e.g. Lyons *et al.*, 2014, Cole
67 *et al.*, 2016, Zhang *et al.*, 2016). This increase has been inferred to have led to oxygenation
68 of the deep oceans, and has been implicated in the rise of animals (e.g. Zhang *et al.*, 2016,
69 though see Lenton *et al.*, 2014).

70 Most Ediacaran macro-organisms were entirely soft-bodied and are preserved as simple
71 casts and moulds, many of which are thought to be reliant on pyrite mineralisation (Gehling,
72 1999; Liu, 2016; though see Tarhan *et al.*, 2016). This preservation style limits the level (and
73 type) of palaeobiological information that their fossils can provide, and has frustrated
74 attempts to phylogenetically place them. In particular, the absence of convincing internal
75 anatomy has proved a major challenge to understanding them. Nevertheless, there is
76 growing consensus that a diverse range of groups is present, including extinct clades and
77 stem-line representatives of extant phyla (Erwin *et al.*, 2011). Approximately 40 major fossil
78 occurrences are currently known from around the globe, and these have been grouped into
79 three global assemblages – the Avalon, the White Sea, and the Nama – according to their
80 age, palaeogeographic position and taxonomic composition, though the control of facies
81 and taphonomy in defining the assemblages remains contentious (Waggoner, 2003; see also
82 Yuan *et al.*, 2011; Boag *et al.*, 2016). The Avalon Assemblage is the oldest (ca. 571-560 Ma)
83 and offers particular potential for elucidating the assembly and dynamics of Earth's nascent
84 macroscopic communities, as well as for calibrating key evolutionary relationships (e.g. see
85 Erwin *et al.*, 2011). It is dominated by frondose forms (rangeomorphs and arboreomorphs)
86 and is principally known from two, broadly coeval, biotas (Noble *et al.*, 2015): those in
87 Charnwood Forest (UK) and those on the Avalon and Bonavista peninsulas in Newfoundland
88 (Canada) (reviewed in Liu *et al.*, 2015). These closely post-date (within <9.5 million years)

89 the short-lived Gaskiers Glaciation (Pu *et al.*, 2016) and occupied deep-water settings on the
90 peri-Gondwanan Avalonian island arc system (Wood *et al.*, 2003). The fossils in
91 Newfoundland have received considerable attention recently because of their high
92 taxonomic diversity and the number of surfaces on which they are preserved (see Hofmann
93 *et al.*, 2008; Liu *et al.*, 2012, 2015; Mitchell *et al.*, 2015). However, there is renewed interest
94 in the Charnwood Forest localities because of the alternative, but complimentary, view of
95 life in the Ediacaran that they offer. The Charnwood Forest localities host some taxa not
96 known from other Ediacaran successions, with many new forms awaiting formal description.
97 Additionally, some of the taxa with counterparts in Newfoundland are preserved with
98 higher fidelity in Charnwood Forest (e.g. *Primocandelabrum*, Kenchington and Wilby, 2017).

99 Charnwood Forest was the first location in the world where Ediacaran macrofossils were
100 documented (see Howe *et al.*, 2012); was the first place where their Precambrian age was
101 confirmed (Ford, 1958); and is the type locality for several iconic organisms (Ford, 1958;
102 Boynton and Ford, 1995). These include *Charnia masoni* (Plate 1A) and *Charniodiscus*
103 *concentricus* (Plate 1B), studies of which fundamentally influenced understanding of
104 Ediacaran fronds (e.g. Jenkins 1985; Antcliffe and Brasier, 2008; Laflamme and Narbonne,
105 2008) and helped develop a taxonomic framework for them (Brasier *et al.*, 2012).

106 Nevertheless, nearly every aspect of the biology of Ediacaran fronds (e.g. their internal
107 anatomy, feeding, reproduction, etc) continues to be contentious and they (and every other
108 member of the biota) remain deeply enigmatic organisms (see review in Liu *et al.*, 2015; also
109 Liu *et al.*, 2016, Dufour and McIlroy, 2017; Kenchington and Wilby, 2017). Recent major
110 initiatives to laser scan and to mould and cast entire bedding-plane surfaces in Charnwood
111 Forest and Newfoundland, as well as to apply novel techniques such as Reflectance

112 Transformation Imaging (see 5.0), have revolutionised their study and promise to provide
113 critical new insights into their biology and ecology. These data are the focus of ongoing
114 investigations into the growth and development of fronds, their reproduction and dispersal,
115 and the structure and function of their host communities (e.g. Kenchington and Wilby, 2016;
116 Mitchell *et al.*, 2016; Dunn *et al.*, 2017; Mitchell and Butterfield, 2018). Here, we summarise
117 the most important recent advances in understanding the Charnwood fossils and their
118 global perspective, and briefly anticipate likely future productive research directions.

119

120 *Note*

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

130

131 **2.0 Geological setting**

132 The Ediacaran strata of Charnwood Forest occupy the core of a faulted, mesoscale, anticline
133 (Figure 1 A) which has been partially exhumed from beneath a thin cover of Triassic

134 sediments (Watts, 1947). To the west the strata are confined by a major reverse fault (the
135 Thringstone Fault), and to the south and east they are concealed beneath Early Cambrian
136 strata (Brand Group). The anticline formed during a localised pre-Acadian phase of
137 deformation and epizone-grade metamorphism (Carney *et al.*, 2008), which imposed a
138 complex pattern of cleavage across the inlier (Evans, 1963); an additional phase of
139 deformation, of unknown age, is suggested by the local presence of a weaker, intersecting
140 cleavage.

141 The Ediacaran strata have a total exposed thickness of ca. 3.2 km, and a further ca. 0.5 km of
142 presumed Ediacaran-aged strata is known at depth. The latter overlies at least 0.3 km of
143 dacite lavas (Pharaoh and Evans, 1987), but the basement to the succession is unknown. The
144 Ediacaran rocks collectively comprise the Charnian Supergroup (Moseley and Ford, 1985;
145 Carney, 1999), which is subdivided into the Blackbrook Group and succeeding Maplewell
146 Group (Figure 1B). The succession is dominated by well-stratified volcanoclastic sediments
147 but, in the northwest of the inlier (see Figure 1A), includes major bodies of andesite and
148 dacite (the Whitwick and Bardon volcanic complexes). These are thought to be the
149 remnants of the magmatic centres from which the bulk of the volcanoclastic sediments were
150 derived (Pharaoh *et al.*, 1987; Carney, 2000), and they are fringed by a thick (up to 1 km)
151 apron of bouldery volcanic breccias and lapilli tuffs (the Charnwood Lodge Volcanic
152 Formation). The Blackbrook Group consists of two formations: the Ives Head Formation,
153 dominated by normally-graded, metre-scale, fine- to medium-grained sandstones, and the
154 overlying Blackbrook Reservoir Formation, mainly comprised of planar-laminated siltstones
155 and mudstones (Moseley and Ford, 1989; Carney, 1999). The Blackbrook Group is separated
156 from the succeeding Maplewell Group by the Benscliffe Breccia Member, a unit of poorly

157 stratified lithic lapilli tuffs and andesitic breccias which forms a distinctive marker horizon
158 (up to 100 m thick) around much of the inlier. The Maplewell Group is subdivided into two
159 formations: the Beacon Hill Formation, dominated by highly siliceous, decimetre-scale,
160 tabular beds of planar-laminated mudstone and siltstone, and the overlying Bradgate
161 Formation, comprised of similar (but notably less siliceous) facies, interbedded with
162 subordinate, but locally thick, sandstones (see 2.1). The boundary between these two
163 formations coincides with the base of a series of closely-spaced, coarse-grained sandstones
164 containing abundant clasts and contorted rafts of mudstone and siltstone, broadly equating
165 to the prominent Sliding Stone Slump Breccia Member. Locally, the Bradgate Formation is
166 overlain by the Hanging Rocks Formation. This constitutes the uppermost division of the
167 Charnian Supergroup, and consists of up to 20 m of fine- to medium-grained conglomerates
168 and interbedded sandstones, overlain by up to 50 m of red and purple, tuffaceous
169 mudstones and greywacke sandstones (McIlroy *et al.*, 1998).

170 The overall succession is dominated by gravity-flow deposits, including turbidites, slump-
171 breccias and debris-flows (Moseley and Ford, 1989). It was laid down in a fore- or back-arc
172 basin setting (Le Bas, 1984; Pharaoh *et al.*, 1987), probably at considerable depth based on
173 the complete absence of shallow-water sedimentary structures in the succession, and on
174 the bathymetry of analogous modern island arcs (*cf.* Trofimovs *et al.*, 2006): this is the basis
175 on which a photosynthetic mode of life has been rejected for the fossil communities. The
176 Hanging Rocks Formation is distinct in that it contains rounded clasts of lithologies that are
177 not known in Charnwood Forest, in addition to familiar epiclastic and pyroclastic
178 components (see Noble *et al.*, 2015). This has been taken to indicate a change in the
179 sedimentary regime during the waning stages of volcanism, perhaps signalling an

180 amalgamation of the Charnian arc with other arcs and marginal basins during the formation
181 of the Avalonian Superterrane (Gibbons, 1990). Two suites of diorites intrude the Charnian
182 Supergroup, and represent the last phase of magmatism. The North Charnwood Diorites are
183 confined to the Blackbrook Reservoir and Beacon Hill formations, where they form sub-
184 vertical sheets, whereas the younger South Charnwood Diorites form more substantial,
185 broadly concordant, bodies in the upper part of the Bradgate Formation.

186

187 2.1 Sedimentology of the Bradgate Formation

188 Ediacaran fossils are conspicuously more abundant in the succession above the Sliding Stone
189 Slump Breccia Member (i.e. within the Bradgate Formation) than below it. This relationship
190 has been taken to be a primary biotic signal, with the biotas above and below being
191 assigned to the so-called Mercian and Lubcloud assemblages, respectively (Wilby *et al.*,
192 2011). However, it may alternatively reflect a fundamental change in taphonomy at this
193 level, with the finer-grained and more volcanic-rich sediment that characterises the
194 succession above the Sliding Stone Slump Breccia Member (see 2.0) simply prompting
195 higher fidelity preservation. Whichever the case, the sedimentology of the Bradgate
196 Formation is consequently of particular interest. Its dominant lithology (see Figure 2)
197 comprises decimetre- to metre-scale beds of grey to blue-green, sharp-based siltstone
198 (Plate 2G) interbedded with variably abundant porcellaneous horizons (typically < 20 mm
199 thick; Plate 2B) and laminated, often normally-graded, very fine- to fine-grained tabular
200 sandstone beds (typically < 30 mm thick; Plate 2F). Finely-laminated hemipelagite caps some
201 beds, but it rarely exceeds more than a few tens of millimetres thickness. Some of the
202 siltstones are graded or have a distinctive 'wispy' lamination (Plate 2A, C) which broadly

203 resembles structures documented in mud turbidites (Rebesco *et al.*, 2014), though the lack
204 of clear evidence of traction precludes definitive assignment. The porcellaneous horizons
205 weather white, pale green or pink, are mudstone-grade, and have sharp bases and sharp or
206 gradational tops. Internally, they are laminated or convolute-laminated. They are
207 interpreted as devitrified, primary ash-fall tuffs (Moseley and Ford, 1989; Carney, 1999),
208 likely including examples deposited from the nepheloid plume part of pyroclastic flows, as
209 well as from vertically-settling ash-clouds. Crystal tuffs (Plate 2E) increase in abundance and
210 thickness with increasing proximity to the Whitwick and Bardon volcanic complexes
211 (Moseley and Ford, 1989; Carney, 1999).

212 Decimetre- to decametre-scale, normally-graded, coarse- to fine-grained sandstone event
213 beds are prominent features, especially at certain levels (see Figure 2). Their bases are
214 invariably sharp, may be gravelly, and are locally erosional and/or loaded, but they lack
215 evidence of extensive scouring or fluting; their upper portions are typically composed of
216 planar- or cross-laminated siltstone. These represent gravity-flows of various magnitude,
217 some formed of reworked volcanic rock (i.e. epiclastic), and others remobilised from
218 unlithified pyroclastic material or formed by primary pyroclastic flows entering the water
219 column (i.e. volcanoclastic, cf. Fisher and Schmincke, 1984). Also present are massive,
220 centimetre- to metre-scale, mudstone to very fine-grained sandstone beds with matrix-
221 supported clasts of deformed, laminated mudstone and subordinate crystals and lithic
222 fragments (Plate 2D). These resemble the thicker slump deposits that define several of the
223 formation boundaries (see 2.0), and were formed by subaqueous debris-flows or by the *in*
224 *situ* disruption of partially lithified sediment, perhaps as a result of seismic-induced
225 dewatering (Sutherland *et al.*, 1994). Perhaps significantly, the two most fossiliferous

226 horizons in the Charnian Supergroup – the ‘Bed B’ and ‘Memorial Craggs’ surfaces of Wilby *et*
227 *al.* (2011) – lie immediately above prominent (and unusually thick) event beds (see Figure
228 1B and 2). Such high diversity and high abundance Avalon biotas have been taken to
229 indicate mature (i.e. late-stage) communities (Clapham *et al.*, 2003), and may only have
230 been able to develop in those areas where the potential for deleterious influxes of sediment
231 (cf. Wilby *et al.*, 2015) had been extinguished or curtailed by an earlier mass wasting of the
232 source area(s).

233

234 **3.0 Age of the Charnian Supergroup**

235 Considerable uncertainty surrounds the rise and demise of the global Ediacaran biota
236 (Narbonne and Gehling, 2003; Laflamme *et al.*, 2013; Darroch *et al.*, 2015; Pu *et al.*, 2016;
237 Smith *et al.*, 2017); the timing of key biological innovations and their connection with coeval
238 changes in the Earth’s chemical and physical environment (e.g. Canfield *et al.*, 2007; Sperling
239 *et al.*, 2015); and the relative importance of biological turnover, palaeoenvironmental
240 setting, taphonomic processes and biogeography in defining the three global assemblages
241 (Waggoner, 2003; Grazhdankin, 2004; Narbonne, 2005; Meert and Lieberman, 2008;
242 Gehling and Droser, 2013; Laflamme *et al.*, 2013; Boag *et al.*, 2016; Droser *et al.*, 2017).
243 Much of this uncertainty is a consequence of there being insufficient adequately-well dated
244 fossiliferous successions, with the Mistaken Point and Charnian successions being important
245 exceptions (Noble *et al.*, 2015; Pu *et al.*, 2016). The Charnian Supergroup has high precision
246 U-Pb (zircon) ages constraining many of its key stratigraphic horizons (see Figure 1B).
247 Unfortunately, none are available for the Blackbrook Group, which hosts the lowest known
248 fossiliferous horizon (the Lubcloud surface) near its exposed base: it is merely constrained to

249 between ca. 611 Ma and 569.1 ± 0.9 Ma. Hence, the succession does not currently
250 contribute to understanding of the appearance of Ediacaran biotas which, at least in SE
251 Newfoundland, occurs less than 9.5 million years after the Gaskiers Glaciation, dated at ca.
252 580.9-579.9 Ma (Narbonne and Gehling, 2003; Pu *et al.*, 2016). However, given that the
253 Lubcloud surface lies >0.6 km stratigraphically below the horizon dated at 569.1 ± 0.9 Ma,
254 there remains the theoretical possibility that it (uniquely) records a pre-Gaskiers biota. If
255 true, this would have significant ramifications for our understanding of the origin and
256 antiquity of large body size and complex bauplans.

257 The overlying Maplewell Group, which hosts the most diverse fossil biotas, is constrained to
258 between 569.1 ± 0.9 Ma and ca. 557 Ma. This overlaps with the succession in Newfoundland
259 (Liu *et al.*, 2012), and permitted reliable correlation between the biotas for the first time
260 (Noble *et al.*, 2015). It also extends the known upper ranges of several taxa in the Avalon
261 Assemblage (e.g. *C. masoni*, *Bradgatia linfordensis*, *Primocandelabrum* sp.), suggesting that
262 Ediacaran community structures were comparatively stable over a prolonged period, at
263 least in these deep-water environments. Probable partial temporal overlap with the
264 shallower-water biotas of the White Sea Assemblage (Martin *et al.*, 2000; Grazhdankin,
265 2004), including those of the Welsh Borderlands and Wales (Cope, 2000; Compston *et al.*,
266 2002; Liu, 2011), supports the primacy of palaeoenvironment in controlling the taxonomic
267 composition of Ediacaran biotas (Grazhdankin, 2004; Wilby *et al.*, 2011; Gehling and Droser,
268 2013).

269

270 **4.0 Biota**

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

278 Rangeomorphs adopted a wide range of gross morphologies (e.g. leaf-shaped, bush-shaped,
279 spindle-shaped) and had a distinctive pseudo-fractal branching architecture (Narbonne,
280 2004) that is generally considered to have been optimised as an exchange surface, perhaps
281 for the osmotic uptake of dissolved organic carbon from the water column (Laflamme *et al.*,
282 2009; Hoyal Cuthill and Conway Morris, 2014, 2017; though see Dufour and McIlroy, 2017).

283 Arboreomorphs, by contrast, only occur as leaf-shaped forms, though their branching
284 morphology varies between taxa (Laflamme *et al.*, 2004); while recent studies suggest that
285 they may be a monophyletic group (Dececchi *et al.*, 2017), many aspects of their biology and
286 systematics await detailed study. Representatives of both groups would have towered more
287 than half a metre above the substrate (e.g. see Boynton and Ford, 1995), although most
288 fossil specimens are only a few tens of centimetres long (Clapham and Narbonne, 2002).

289 Other groups are conspicuously scarce in Charnwood Forest and are poorly studied (Wilby
290 *et al.*, 2011), but may well prove to be amongst the most scientifically important in the
291 succession. These include a short (typically <10 cm), gladius-shaped organism with simple
292 transverse bars (Plate 3A), which broadly resembles *Hadryniscala* from Newfoundland
293 (Hofmann *et al.*, 2008); a hemispherical organism with bifurcating radial ribs (Plate 3C); and

294 various rather nebulous forms (see 4.3) collectively referred to as 'ivesheadiomorphs' (see
295 Liu *et al.*, 2011).

296 Until recently, fossils were generally thought to have been limited to only a few surfaces in
297 Charnwood, and to have been rather low in taxonomic diversity. However, following a
298 systematic programme of silicone rubber moulding by the British Geological Survey (Plate
299 4), and prospecting by amateur palaeontologists, they are now known to be preserved on
300 several dozen surfaces and to include communities that rival any in the world in terms of
301 fossil density and diversity (Wilby *et al.*, 2011). The most important fossiliferous surface
302 currently known in Charnwood Forest is the 'Bed B' of Wilby *et al.* (2011): it is the most
303 studied surface, is exposed over an area of ca. 100 m², preserves ca. 900 fossils, and hosts at
304 least 16 different species (Wilby *et al.*, 2011). Other important fossiliferous surfaces include
305 Memorial Crag, which hosts especially large specimens of *C. masoni* and the type
306 specimens of the bush-like rangeomorph *Bradgatia linfordensis* (Boynton and Ford, 1995;
307 Wilby *et al.*, 2015), and Aron A, which lies immediately above the Sliding Stones Slump
308 Breccia (i.e. in a similar stratigraphic position to the Memorial Crag surface). The latter
309 preserves a vast number of superimposed holdfast discs (Plate 2H), a relationship that is
310 interpreted to record prolonged (though perhaps interrupted) colonisation of the substrate
311 (cf. Wilby *et al.*, 2015). Most of the fossiliferous surfaces have a subtle pustular and wrinkled
312 surface texture which is taken to indicate that they supported surficial microbial mats (see
313 Callow and Brasier, 2009; Laflamme *et al.*, 2012b). These may have played an important
314 ecological role (e.g. Dufour and McIlroy, 2017), helped anchor the organisms to the
315 substrate, and been critical to the process of fossilization (Kenchington and Wilby, 2017).

316

317 4.1 Local characters

318 Many of the species on Bed B are new and are not known from other Ediacaran localities
319 (Wilby *et al.*, 2011, see also Kenchington and Wilby, 2017), suggesting that Avalon biotas
320 may have had a high degree of endemism, perhaps controlled by differences in their
321 palaeogeographical setting (i.e. back-arc or ocean-facing) and/or their position on the
322 submarine slope. Certainly, there is growing evidence to suggest that the composition of
323 Ediacaran biotas was strongly influenced by depositional environment (Grazhdankin, 2004;
324 Gehling and Droser, 2013). Detailed analysis of Bed B has provided compelling evidence for
325 the role of minor disturbance events (e.g. blanketing by a thin layer of sediment) in shaping
326 their structure, just as they affect the size-frequency distribution of modern populations of
327 benthic organisms (Wilby *et al.*, 2015). An environmental difference, such as substrate
328 character or suspended sediment concentration, would seem the most likely explanation for
329 the conspicuous absence in Charnwood Forest of the reclining rangeomorph *Fractofusus*,
330 despite its super-abundance on many surfaces in Newfoundland (see Gehling and
331 Narbonne, 2007; Liu *et al.*, 2012; Mitchell *et al.*, 2015), and of other reclining or low-lying
332 forms known from Newfoundland, such as *Pectinifrons* and *Hapsidophyllas* (see Bamforth
333 and Narbonne, 2009). Instead, the Charnwood communities are dominated by erect fronds
334 and, compared to many of the surfaces in Newfoundland, they have an abundance of taxa
335 with naked stems (e.g. the informally-named 'dumbbell' rangeomorph, Plate 3B) and host
336 diverse multifoliate taxa (namely *Primocandelabrum*, the 'dumbbell', and *Bradgatia*). The
337 erect forms may have been less susceptible to fouling by benthic plumes of sediment or,
338 being held higher in the water column and exposed to faster currents, better able to shed
339 any settled particles (Kenchington, 2015). Conceivably, this could even have been a driver

340 for the evolution of the first stems, though stems have more generally been linked to
341 vertical competition for resources (Clapham and Narbonne, 2002; Laflamme *et al.*, 2012a;
342 Ghisalberti *et al.*, 2014).

343 Nevertheless, several taxa in Charnwood Forest are shared with Newfoundland, providing
344 strong support to the notion that at least some taxa were able to disperse widely via
345 waterborne propagules (Darroch *et al.*, 2013, Mitchell *et al.*, 2015). This is most obviously
346 the case for *C. masoni* (Plate 1A, D), which has a cosmopolitan distribution (both
347 geographically and temporally), but also includes the bush-shaped *B. linfordensis* (Plate 3D),
348 and perhaps *Vinlandia*, which we tentatively report from Charnwood for the first time (Plate
349 3E). *Primocandelabrum* was until recently only reported from Newfoundland (Hofmann *et*
350 *al.*, 2008), but it is now also known in Charnwood Forest (Plate 3F and 5F) and may in fact be
351 the commonest rangeomorph present in the region (see Kenchington and Wilby, 2017). The
352 arboreomorphs are comparatively poorly studied in Charnwood and Newfoundland, so their
353 level of commonality is unclear. *Charniodiscus longus* and *C. arborea* are present in both
354 regions, but two of the most distinctive species of *Charniodiscus* in Newfoundland – *C.*
355 *procerus* and *C. spinosus* (Laflamme *et al.*, 2004) – remain unknown from Charnwood (Plate
356 1B-C, E-G).

357

358 4.2 A sense of community

359 The great majority of fossils on Bed B are closely co-aligned and are preserved still anchored
360 to the substrate by their holdfasts (Wilby *et al.*, 2011); the small number that have been
361 uprooted or imported (i.e. are allochthonous) are very obviously misaligned and are often

362 folded, enrolled or distorted beyond recognition. This suggests that the majority of the
363 community was killed *in situ* by a single event (though see 4.3 and Wilby *et al.*, 2015), and
364 that the surface captures an essentially unbiased (i.e. census) record of the original living
365 community. Hence, the surface provides a crucial opportunity to examine the biometrics
366 and population structure of individual taxa in much the same way as for living organisms,
367 potentially providing insights into fundamental aspects of their biology as varied as their
368 ontogeny, mortality, recruitment, metabolic efficiency, and dimorphism. *C. masoni*, for
369 example, was revealed to have two (or perhaps three) key stages in its life history: an initial
370 planktonic dispersal phase, and a benthic phase of isometric growth, characterised by the
371 insertion and subsequent expansion of new primary branches (Wilby *et al.*, 2015). The *C.*
372 *masoni* population on Bed B, in combination with specimens from Newfoundland, have
373 recently been used to demonstrate that rangeomorphs had a non-deviant form, with the
374 overall shape maintained across the preserved ontogenetic series (Dunn *et al.*, 2017).
375 Growth trends documented in *C. masoni* suggest that settlement and adoption of this adult
376 life habit took place when the organisms had 4 primary branches (Wilby *et al.*, 2015).
377 Interestingly, at least some of the very largest *C. masoni* specimens (>45 cm long) show a
378 switch to a subsequent expansion-dominated phase of growth, characterised by the
379 inflation of existing branches and a cessation (or very substantial reduction) of the insertion
380 of new ones. The cause of this transition is unclear, but it could conceivably signal maturity,
381 or be a response to improved environmental conditions; whichever, comparable growth
382 programmes are seen in certain modern invertebrates (Wilby *et al.*, 2015).

383 As well as being preserved *in situ*, many of the fossils preserve exceptionally-fine
384 morphological details (see Plate 1F), despite being very low epirelief (Kenchington and

385 Wilby, 2014). Previously unknown anatomical features are apparent in several otherwise
386 familiar taxa, promising to improve understanding of their biology, and more thorough
387 treatments of previously poorly characterised genera have been possible. For example,
388 Kenchington and Wilby (2017) were able to significantly augment the original diagnosis for
389 *Primocandelabrum* (Hofmann *et al.*, 2008) because some of the new specimens from
390 Charnwood preserve the frond's fine branching structure (Plate 5F). Indeed, the specimens
391 are sufficiently well-preserved to have allowed opposing taxonomic schemes for the
392 rangeomorphs to be tested (using multivariate statistical analyses), and the level of intra-
393 specific variability within taxa to be assessed (Kenchington and Wilby, 2017). The latter was
394 shown to be moderately high, providing potential insights into ontogeny, morphological
395 plasticity and ecophenotypic variation within the group.

396

397 4.3 Pizza discs and bubble mats

398 Many of the fossiliferous surfaces in Charnwood Forest host abundant circular or sub-
399 circular features (up to ca. 0.3 m diameter) with variably well-defined margins and a
400 pustular-, polygonal- or ridged internal structure (Plate 5): they comprise 10% of the fossils
401 on Bed B. Initially assigned to discrete species (Boynton and Ford, 1995), these features are
402 now collectively referred to as 'ivesheadiomorphs' (Liu *et al.*, 2011), though their origin(s)
403 are debated. In Newfoundland, these structures were originally termed 'pizza discs', 'lobate
404 discs' and 'bubble mats', based on their gross morphological appearances (Narbonne *et al.*,
405 2001). Liu *et al.* (2011) interpreted them as the decayed ('effaced') remnants of organisms
406 that had died prior to the event which killed the associated, definitively frondose, organisms
407 on the surface. However, Laflamme *et al.* (2012b) considered them to simply be microbial

408 colonies, while Wilby *et al.* (2011) suggested that at least some could be attributed to soft-
409 sediment disruption associated with the collapse of buried organisms. Most recently,
410 Matthews *et al.* (2017) have suggested that similar features could be generated by modern
411 weathering and erosion. If ivesheadiomorphs are produced by abiological means, then one
412 might expect any population of them to have an approximately normal size distribution –
413 such analyses might prove a useful way of testing the abiological versus biological genesis of
414 each type of ivesheadiomorph.

415 Resolving the true nature(s) of ivesheadiomorphs has become an urgent priority because of
416 the need to know how they should be treated in ongoing analyses of community structure:
417 either as part of the living system, as separate, or as a potential source of nutrients for other
418 taxa on the surface (see Mitchell and Butterfield, 2018). Additionally, since the oldest
419 fossiliferous surface in Charnwood Forest (the Lubcloud surface) is comprised entirely of
420 ivesheadiomorphs, their nature has a direct bearing on the temporal range of the biota as
421 whole. Provisional work suggests that the observed variation in their morphology may
422 actually reflect different modes of generation. Examples displaying regular internal structure
423 (e.g. those formerly referred to as *Blackbrookia*, Boynton and Ford, 1995; Plate 5B) are most
424 convincingly interpreted as poorly preserved fronds (cf. Liu *et al.*, 2011), though not
425 necessarily as a result of decay. We note that sediment preserving the biota on the Lucloud
426 surface is very obviously coarser than that capturing any of the higher biotas, and the
427 resolution of preservation is correspondingly lower. Examples displaying a polygonal
428 internal structure (Plate 5C) imply a component of shrinkage and/or collapse, conceivably as
429 a result of fluid escape from beneath the surficial mat, or of decay of the mat itself.
430 Examples resulting from the uneven collapse of a buried 3D frond are difficult to definitively

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

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

453

454 **5.0 A change of view**

455 Ediacaran macrofossils are notoriously difficult to work with, in part because most are very
456 low relief and details are only revealed with low-angle lighting (though see Hoyal Cuthill and
457 Conway Morris, 2017; Sharp *et al.*, 2017). Casts of them are generally too large and
458 unwieldy to be easily examined under a binocular microscope (e.g. see Plate 4B-C), meaning
459 that they are often studied in a darkened room with a mobile light source. 3D laser scanning
460 offers a potential alternative (e.g. Brasier and Antcliffe, 2009), particularly for mapping *in*
461 *situ* bedding-plane assemblages (Mitchell *et al.*, 2016), but the technique requires specialist
462 equipment (both hardware and software) and may not always match the resolution
463 achieved by traditional photography. Reflectance Transformation Imaging (RTI) is a
464 composite digital imaging technique that marries many of the key benefits of laser scanning
465 and photography (Duffy, 2013), and is comparatively simple to undertake. This makes it a
466 highly practical alternative, and it is now routinely applied to the fossils from Charnwood
467 Forest. The technique allows the user to interactively and seamlessly change the angle and
468 direction of a virtual light source on a static image (Hammer *et al.*, 2002; Anon, 2013),
469 thereby optimising the view of any feature in the frame. In addition to the lighting, it is also
470 possible to change a variety of other parameters, such as the level of specular reflection and
471 colour saturation, as well as to zoom to areas of interest. The RTI files can be built (from a
472 series of photographs) and viewed in open source software
473 (http://culturalheritageimaging.org/What_We_Offer/Downloads/View/), and they include
474 the option for recording the parameters which best highlight particular anatomical features
475 (Anon, 2013). Hence, they are an excellent tool for interpreting the fossils and are ideally
476 suited as supplements to systematic descriptions.

477 Because RTI images allow the lighting to be varied very precisely (and by graduations of $<1^\circ$)
478 it is possible to resolve very subtle morphological features. This is amply illustrated with the
479 holotype of *Charniodiscus concentricus* (Plate 1B). This taxon is known from a single frond in
480 Charnwood Forest (Ford, 1958), whose complex morphology has been the subject of
481 prolonged debate. Early workers considered it to have two opposing rows of branches
482 extending off its central axis (Jenkins and Gehling, 1978), whereas subsequent workers
483 interpreted it to have three or more rows (Dzik, 2002), each with elements of both its upper
484 and lower surface supposedly preserved in a complex composite impression (Brasier and
485 Antcliffe, 2009, Fig. 12). This taphonomic style is not observed in any other fronds from the
486 surface, nor do any of the other ca. 70 arboreomorphs present exhibit more than two rows
487 of branches. Hence, Wilby *et al.* (2011) considered the specimen to comprise two
488 superimposed fronds, as more obviously apparent in other examples on the surface (Plate
489 1C, G), though no second holdfast is apparent. The merits of each of these interpretations is
490 easily tested with the RTI (DOI: 10.5285/8f256217-09f1-4807-8357-648f558f3187): in
491 particular, the topographically higher position of the central-left part of the fossil, and the
492 impact of cleavage on the fossil's morphology, are very apparent.

493

494 **6.0 Looking forward**

495 New fossiliferous surfaces continue to be discovered in Charnwood Forest, and at least half
496 a dozen new species – including intriguing non-frondose forms – await formal description.
497 The Charnwood Forest fossil surfaces therefore hold the potential to give insight into the
498 understudied non-rangeomorph components of the Avalon Assemblage, and also to test
499 palaeobiological hypotheses based on the Newfoundland sites. The *in situ* nature of the

500 communities makes them a priority target for community structure analysis, with the
501 intention of interrogating the 'rules' that governed these earliest, comparatively simple,
502 macroscopic ecosystems. For example, competition and reproductive biology identified in
503 Newfoundland communities (Mitchell *et al.* 2015) could be tested to determine if there
504 were local geographical/environmental influences on these fundamental biological
505 processes.

506 There are several specific questions that the Charnwood Forest biotas will play a crucial role
507 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
508 communities (Mitchell *et al.*, 2015), the influence of broader-scale variability on community
509 composition (i.e. between different sites or regions) has not been examined. Plausibly,
510 differences in the relative abundance of reactive volcanic material compared to inert
511 epiclastic debris in the substrate could influence not just taxonomic composition, but also
512 organism density, growth rate and maximum size, and these differences could be used to
513 test theories of chemosynthesis (cf. Dufour and McIlroy, 2017).

515 Charnwood Forest has a notably high abundance of out-size (>45 cm tall) fronds, both in
516 terms of the number of bedding planes on which they occur and their frequency within
517 individual populations (see Wilby *et al.*, 2011, 2015). We don't yet fully know what this
518 signals or how the fronds benefited from growing to such a large size (Wilby *et al.*, 2015),
519 but a combined analysis of the sedimentological and community structure would allow
520 potential causes to be investigated, such as maturity, resource abundance, frequency of
521 disturbance, and degree of competition.

522 The exquisite preservation of the specimens on Bed B and the Memorial Craggs surface,
523 coupled with the comparatively large population sizes present, makes them ideal for
524 examining intraspecific variation (cf. Kenchington and Wilby, 2017), developmental
525 programmes and ontogeny (cf. Wilby *et al.*, 2015). These will provide control on modelling
526 work that seeks to understand the growth of rangeomorphs and the evolution of large body
527 size (Hoyal Cuthill and Conway Morris, 2014, 2017) which, in turn, may provide insights into
528 their ecology and phylogeny. Further, the preservational pathway(s) in Charnwood Forest
529 may be different to those operating in the classic Newfoundland localities (Liu, 2016;
530 Kenchington and Wilby, 2014). Understanding these differences may help to elucidate the
531 biological composition of these organisms and contribute to arguments relating to a
532 taphonomic cause for the extinction of the Ediacaran biota (cf. Darroch *et al.*, 2015).

533 The stratigraphically highest fossil surfaces in Charnwood Forest host some of the youngest
534 known communities of the Avalon Assemblage (Noble *et al.*, 2015). Consequently, they
535 provide key constraints on questions of biostratigraphy, the influence of age versus
536 environment on community composition (cf. Boag *et al.*, 2016), and on the timing of
537 appearance of non-rangeomorph phyla in the Ediacaran. Additionally, depending on the
538 duration of the basal Cambrian unconformity (Fig. 1), Charnwood Forest provides a rare
539 opportunity to elucidate the nature of the Precambrian-Cambrian transition in a deep-water
540 setting, and thus provide a crucial complimentary record to the classic, shallower-water,
541 sections of Namibia (e.g. Darroch *et al.*, 2015) and Newfoundland (e.g. Buatois and
542 Mangano, 2016). The Brand Group is thought to be mostly (if not entirely) of Early Cambrian
543 age, based on the presence of *Teichichnus* burrows near its base (Bland and Goldring, 1995),
544 and to be separated from the underlying Maplewell Group by a cryptic unconformity

545 (McIlroy *et al.*, 1998). Constraining the age of the uppermost division of the Maplewell
546 Group (the Hanging Rocks Formation) is challenged by the paucity of primary datable
547 minerals (Noble *et al.*, 2015) but, if achieved, it could help resolve some of the largest
548 questions in palaeontology – namely, the tempo and diachronicity of the agronomic
549 revolution, the evolution of modern phyla and the cause of the first major extinction on
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551

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561

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884 **Figure explanations**

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

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

896 **Plate 1:** Representative rangeomorph and arboreomorph fronds from Bed B, Bradgate
897 Formation. A) *Charnia masoni* holotype (GSM106160). B) *Charniodiscus concentricus*
898 holotype (GSM106161); see also DOI: 10.5285/8f256217-09f1-4807-8357-648f558f3187. C)
899 Arboreomorph, undet., partially overlapped by another (arrowed) smaller specimen
900 (GSM105960). D) Small, potentially immature, *Charnia masoni* specimen (GSM105979). E-F)
901 Arboreomorph, undet., with well-preserved branch divisions highlighted and enlarged in F
902 (GSM106069). G) Three (arrowed) similarly-sized and partially overlapping, conspecific

903 arboreomorphs (GSM105876). Scale bars = 30 mm. All specimens are casts except C and E-F
904 (moulds), and are housed at the British Geological Survey, Keyworth.

905 **Plate 2:** Representative facies of the Bradgate Formation, Charnian Supergroup. A-F)

906 Polished sections of the Rise Rocks core (SK41SE/192), housed at the British Geological

907 Survey, Keyworth. A) Finely-laminated turbiditic siltstone, sharply overlain by a normally-

908 graded sandstone (43.78-43.83 m). B) Sharp-based, locally graded, porcellaneous horizon,

909 interpreted as a devitrified primary ash-fall tuff (128.50-128.55 m). C) Finely-laminated and

910 'wispy' turbiditic siltstone (158.18-158.23 m). D) Massive sandstone with matrix-supported

911 clasts of laminated mudstone and siltstone, interpreted as a slump deposit (90.0-90.1 m). E)

912 Crystal tuff with multiple, thin, pink ash tuff laminae (49.32-49.37 m). F) Normally-graded,

913 epiclastic sandstone, interpreted as a minor gravity-flow deposit (67.71-67.76 m). G) Planar-

914 bedded siltstones and subordinate thin sandstones, recording multiple turbidite events. H)

915 Superimposed holdfast discs on the Aron A fossil surface, recording prolonged colonisation,

916 perhaps separated by minor influxes of sediment. Scale bars = 10 mm; approximate height

917 of G is 2 m.

918 **Plate 3:** Bed B biota, Bradgate Formation. A) Undescribed gladius-shaped organism of

919 uncertain affinity (GSM106083). B) The iconic dumbbell-like taxon with a massive holdfast

920 and complex, artichoke-like frond on top of a long, straight stalk (GSM105875). C)

921 Undescribed hemispherical organism with bifurcating radial ribs (GSM105967). D) Well-

922 preserved *Bradgatia linfordensis* (GSM105873). E) Frond, tentatively assigned to *Vinlandia*, a

923 taxon that has not previously been reported from Charnwood Forest (BGS cast 630). F)

924 Newly described *Primocandelabrum boyntoni*, with frond of typical triangular-outline

925 (GSM106046). Scale bars = 10 mm for A, C and F; 50 mm for B, D-E. All specimens are casts
926 except C (mould) and are housed at the British Geological Survey, Keyworth.

927 **Plate 4:** Systematic moulding and casting of key fossiliferous surfaces in Charnwood Forest.

928 Following careful cleaning, the surfaces were moulded with silicone rubber by the British
929 Geological Survey and GeoED (A), and then cast with plaster, typically in 1m² areas (B,C),
930 allowing each surface to be fully reconstructed in the laboratory. Scale bar = 100 mm.

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

Figure 1

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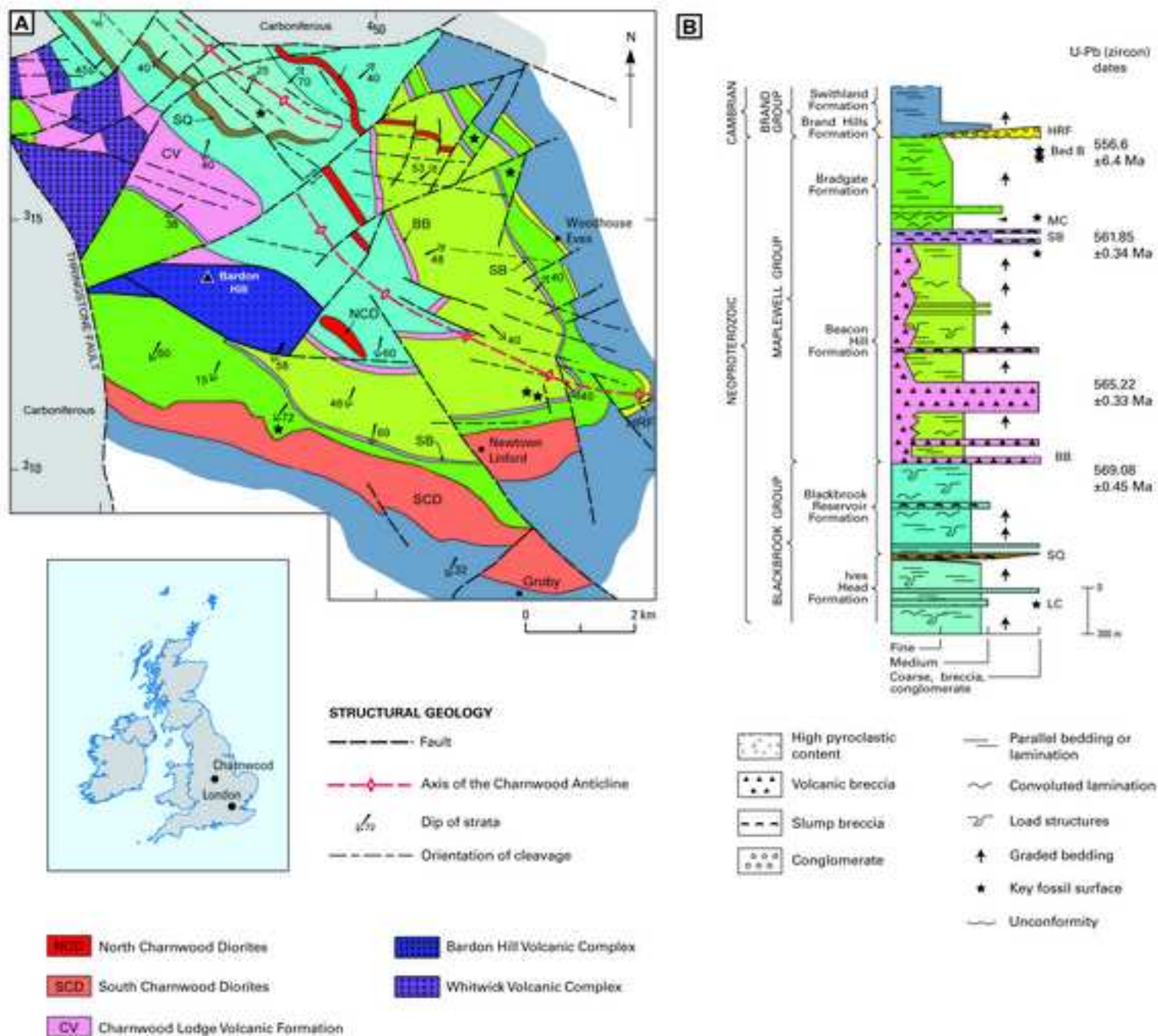
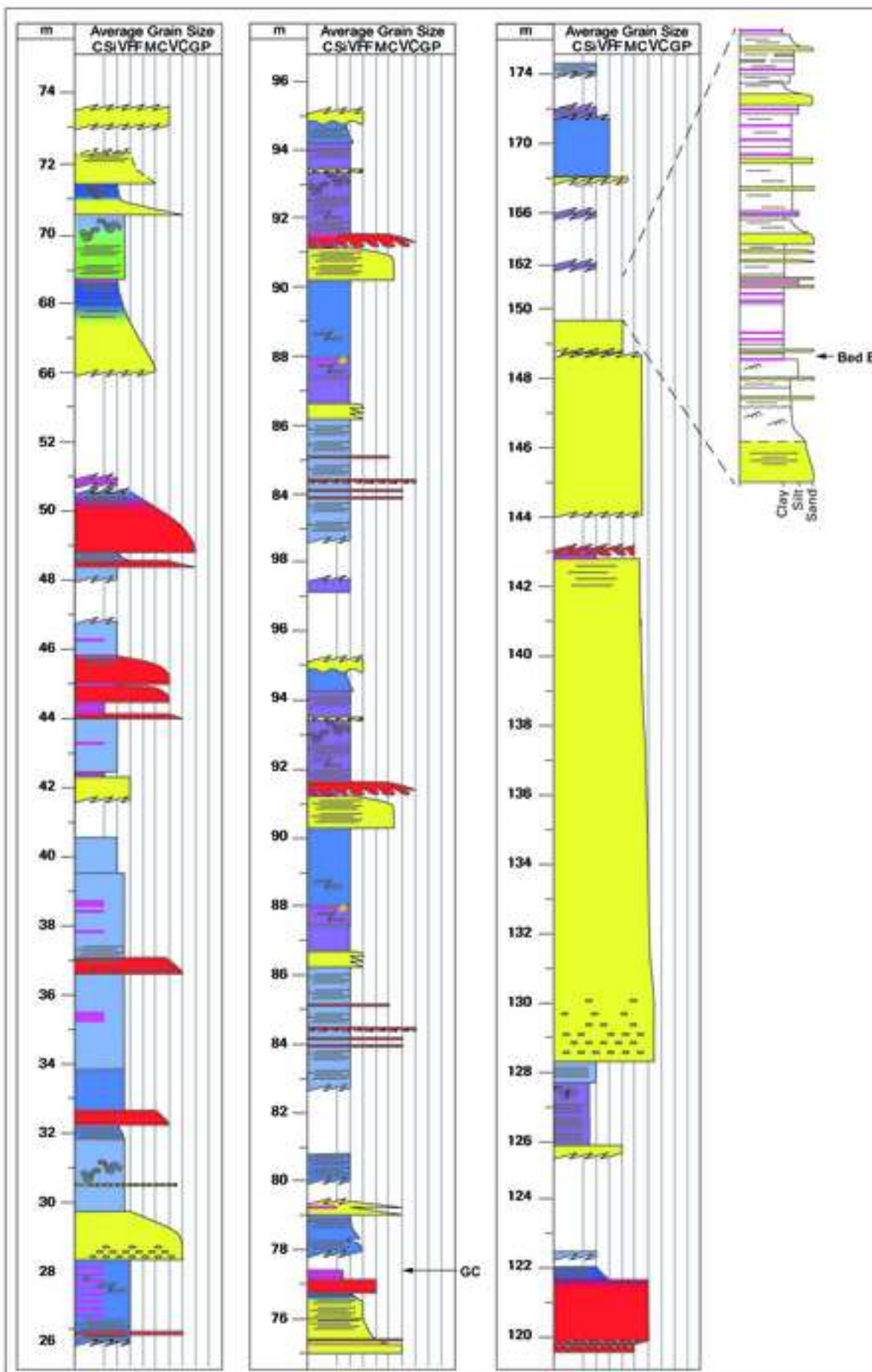


Figure 2

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Key to Figure2

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Lithologies

-  Siliceous, pale-weathering siltstone
-  Siltstone interlaminated with siliceous laminae
-  Siltstone interlaminated with sandstone ribs (<3cm)
-  Siltstone
-  Sandstone with >50% euhedral/angular crystals
-  Lithic sandstone (<50% crystals)
-  Very thinly laminated, siliceous beds

Sedimentological features

-  Lamina of sandstone (>50% crystals)
-  Lamina of sandstone (<50% crystals)
-  Siliceous Lamina
-  Soft-sediment deformation
-  Parallel lamination
-  Syn-sedimentary faulting
-  Lithic granules
-  Pyrite (euhedral)

Contact type

-  Loaded base
-  Missing section, contact unseen
-  Erosional base
-  Sharp contact
-  Contacts unseen
-  Cross-lamination

