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

2 **revolution**

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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 km$^2$) 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 volcaniclastic 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 volcaniclastic 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. volcaniclastic, 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 Crags' 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 know 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 m$^2$, preserves ca. 900 fossils, and hosts at

304  least 16 different species (Wilby *et al.*, 2011). Other important fossiliferous surfaces include

305  Memorial Crags, 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 Crags 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

**5.0 A change of view**

454

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°)

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*

508    *al.*, 2008). While no identifiable signal of local substrate variability has been detected in the

509    communities (Mitchell *et al*., 2015), the influence of broader-scale variability on community

510    composition (i.e. between different sites or regions) has not been examined. Plausibly,

511    differences in the relative abundance of reactive volcanic material compared to inert

512    epiclastic debris in the substrate could influence not just taxonomic composition, but also

513    organism density, growth rate and maximum size, and these differences could be used to

514    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 Crags 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

550    Earth.

551

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 $1m^2$ 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.

**Figure1**
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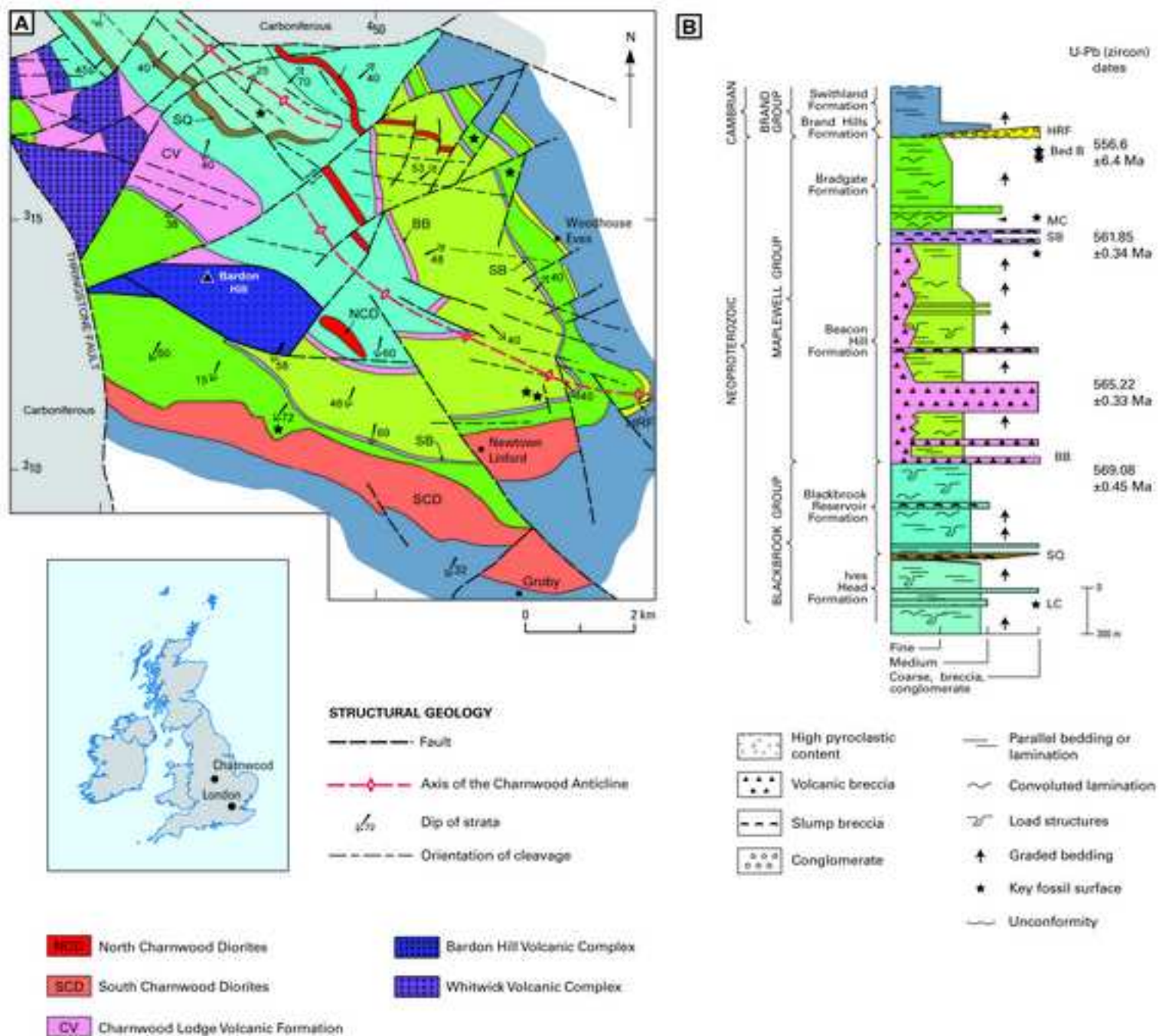
**Figure2**
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Lithologies

- 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

**Plate1**
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