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A rich Ediacaran assemblage from eastern Avalonia: Evidence of early widespread diversity in the deep ocean

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Philip R. Wilby, John N. Carney, and Michael P.A. Howe

British Geological Survey, Keyworth, Nottingham NG12 5GG, UK

ABSTRACT

The Avalon assemblage (Ediacaran, late Neoproterozoic) constitutes the oldest evidence of diverse macroscopic life and underpins current understanding of the early evolution of epibenthic communities. However, its overall diversity and provincial variability are poorly constrained and are based largely on biotas preserved in Newfoundland, Canada. We report coeval high-diversity biotas from Charnwood Forest, UK, which share at least 60% of their genera in common with those in Newfoundland. This indicates that substantial taxonomic exchange took place between different regions of Avalonia, probably facilitated by ocean currents, and suggests that a diverse deepwater biota that had a probable biogeochemical impact may already have been widespread at the time. Contrasts in the relative abundance of prostrate versus erect taxa record differential sensitivity to physical environmental parameters (hydrodynamic regime, substrate) and highlight their significance in controlling community structure.

INTRODUCTION

The Ediacaran (late Neoproterozoic) Avalon assemblage (ca. 578.8–560 Ma) preserves the oldest evidence of diverse macroorganisms and is key to elucidating the early radiation of macroscopic life and the assembly of benthic marine communities

(Clapham et al., 2003; Van Kranendonk et al., 2008). However, detailed data are conspicuously localized, and consequently total diversity and provincial variability are poorly constrained. Current understanding is largely based on the classic biotas of Newfoundland, Canada (e.g., Narbonne et al., 2009). These are dominated by rangeomorphs, an eccentric group with a distinctive pseudofractal architecture (Brasier and Antcliffe, 2009) that reached their acme in the Mistaken Point Formation (565 ± 3 Ma). Here they comprise a series of high-diversity census populations, collectively composing the Mistaken Point assemblage, each preserved on top of a fine-grained turbidite beneath a thin volcanic ash (Clapham et al., 2003).

By contrast, the Charnwood Forest (UK) biotas, which occupied comparable deepwater niches in a different part of the peri-Gondwanan Avalonian volcanic arc system (Cocks and Fortey, 2009), are much less well understood. They have yielded the holotypes of several key taxa (e.g., Ford, 1958, Boynton and Ford, 1995) and have formed part of significant phylogenetic studies (see Brasier and Antcliffe, 2009), but they have been considered impoverished and have received comparatively little attention. Most of the previously identified taxa are shared with the Mistaken Point assemblage, but the perceived absence of many of the others has prompted the belief that the Avalon assemblage exhibits high levels of endemism (e.g., Clapham et al., 2004). This has influenced how observed trends in the Ediacara biota as a whole have been interpreted, and the relative significance of temporal, environmental, taphonomic, and biogeographic drivers remains contentious (Waggoner, 2003; Grazhdankin, 2004; Narbonne, 2005).

We report the first high-diversity and abundant **[[SU: vs. abundance?]]** Ediacara biotas from present-day eastern Avalonia. These were revealed by a systematic program of silicone rubber molding in Charnwood Forest that included all of the most important known fossiliferous surfaces (totaling >150 m^2). The biotas overlap those of the Mistaken Point assemblage in terms of their age, depositional setting, and taphonomy. They therefore provide a unique opportunity to determine levels of endemism within the wider Avalon assemblage and the relative importance of paleobiogeography and ecological sensitivity in controlling community composition.

GEOLOGICAL SETTING

The landscape of Charnwood Forest (Leicestershire, UK) includes **[[SU: ok? vs. “forest comprises”]]** a poorly exposed inlier of late Neoproterozoic to early Cambrian rocks (Fig. 1). The late Neoproterozoic strata form the core of a faulted anticline and underwent folding, epizonal metamorphism, and cleavage formation during localized pre-Acadian deformation (Carney et al., 2008). Fine- to medium-grained turbiditic facies dominate; subordinate slumped units and laterally extensive sandstones record downslope mass wasting events and unconfined, high-density turbidites, respectively (Carney, 1999). Thin ashes occur throughout, and coarse-grained pyroclastics constitute a significant proportion of the middle part of the succession. These were sourced from contemporaneous calc-alkaline volcanic centers in the northwest of the inlier and exhibit a geochemical signature consistent with an arc that developed on oceanic or highly attenuated continental crust (Carney, 1999).

Fossils are known on more than 12 bedding planes and compose two assemblages separated by an interval of ~2.2 km. The Lubcloud assemblage is known only from a single surface in the Ives Head Formation, close to the lowest exposed part of the succession. It contains the relatively simple forms *Blackbrookia*, *Ivesheadia*, and

Shepshedia (Boynton and Ford, 1995), and its distinction may be largely taphonomic (see Liu et al., 2011). The younger assemblage, here named the Mercian assemblage, is more diverse and is the focus of this paper. It is recorded at five localities and yielded the holotype of the Ediacaran index species *Charnia masoni* (Ford, 1958). A U-Pb thermal ionization mass spectrometry date of 563 ± 1.9 Ma (data from the British Geological Survey–Natural Environment Research Council Isotope Geoscience Laboratories) **[[SU: ok? *Geology* does not allow "unpublished" citations, except for the authors' unpublished data.]]** has been obtained from between the lowest two fossil levels, but the assemblage's upper age remains poorly constrained (see Compston et al., 2002); it is unconformably overlain by the early Cambrian Brand Group.

MERCIAN ASSEMBLAGE

The Mercian assemblage (Fig. 2; Table 1) is considerably richer than previously recognized: more than 1200 specimens (>95% newly found) and at least 18 taxa (9 new to the assemblage) have been molded, including several undescribed species. The fossils are preserved on top of fine-grained beds as high-fidelity, low-epirelief impressions. None is obviously overlain by a thick ash layer, though disseminated ash constitutes a significant component of the sediment. Pustules, irregular wrinkles, and iron-stained surfaces suggest the widespread presence of biomats (see Callow and Brasier, 2009).

Discoidal fossils dominate (70%) and include a plethora of forms (see Boynton and Ford, 1995). The commonest are simple discs, referable to *Aspidella*, with mean ellipsoidal diameters typically <0.1 m. They occur on all the fossiliferous surfaces and may form monospecific populations (e.g., bed H). Decimeter-scale circular impressions with a lobe and ridge morphology or polygonal ornament, collectively termed ivesheadiomorphs (see Liu et al., 2011), are also common. Also present is *Cyclomedusa davidi*, apparently restricted to surfaces at the Outwoods locality, and rare specimens of the tentaculate holdfast *Hiemalora*, reported here for the first time. **[[SU: correct?]]**

Discoidal fossils are the commonest and longest ranging constituents of the global Ediacara biota, but their status remains controversial (e.g., MacGabhann, 2007). Large specimens, in particular, have been rejected as holdfasts in favor of other explanations (e.g., Hofmann et al., 2008), but examples in the Mercian assemblage as large as 0.35 m mean diameter that are unambiguously attached to fronds (see following) refute this. Many of the attached discs are morphologically distinct, suggesting that isolated holdfasts may hold greater potential as a proxy for frond diversity than hitherto anticipated.

Frondose rangeomorphs constitute most of the remainder of the assemblage (27%) and at least 60% of total diversity. Complete fronds (i.e., with holdfast attached) dominate and most taxa are represented by a range of specimen sizes. *Charnia masoni* (Ford, 1958) is the most abundant frond (Fig. 2A); several new specimens of the globally rare and typically fragmentary large form (*C. grandis* of Boynton and Ford, 1995) are also identified, as well specimens of intermediate size (e.g., see Fig. 4A). These promise to help confirm the likely ontogenetic relationship between these two charnids (see Antcliffe and Brasier, 2008). Of the 70 new *Charniodiscus* specimens located, none exhibit the multifoliate frond that is purportedly present in the type specimen of *C. concentricus* and that has been given considerable phylogenetic weight (Brasier and Antcliffe, 2009). However, examples of closely adjunct, and even overlapping, conspecific fronds are present. At least two other species of *Charniodiscus* are added to the assemblage (Fig. 2B), one of which we tentatively refer to *C. arboreus*.

Bush-shaped rangeomorphs compose nearly half of all the frondose fossils, though only *Bradgatia linfordensis* (Fig. 4A), which is now known to be relatively scarce (3%), had previously been recorded (Boynton and Ford, 1995). At least three additional species are present. Two of the species are allied to *Primocandelabrum* (see Hofmann et al., 2008), though neither bears a *Hiemalora*-like holdfast. In terms of gross morphology, they are distinguished by a sustained disparity in their frond/holdfast proportions through ontogeny (Figs. 2C, 2G). The third species is unique among Ediacara taxa (Fig. 2D): it has a long stem bearing a globular frond with most of the primary branches emanating from a single point, but with some dividing from other branches.

Specimens of uncertain affinity are scarce (3%) and may include taphomorphs or developmental stages of more familiar taxa. They include a diminutive, gladius-like fossil bearing transverse divisions (Fig. 2E), and a hemisphere with a medial ridge and radial bifurcating ribs (Fig. 2H). Rare specimens of *Thectardis* cf. *avalonensis* (Clapham et al., 2004) are also reported here for the first time (Fig. 2F). **[[SU: ok?]]**

COMMUNITY PRESERVATION

The fronds on each bedding plane exhibit a preferred orientation (Figs. 4A, 4B) that is consistent with them having been felled and preserved in situ by the overlying turbidite or ash. Liu et al. (2011) interpreted the ivesheadiomorphs as impressions of organisms that underwent protracted decomposition on the sediment surface prior to burial; consequently, they take each bedding-plane assemblage to constitute a time-averaged record of that biota. We disagree, and interpret each surface as a near census of the standing crop at the time of obrution (cf. Clapham and Narbonne, 2002). We consider the morphology of ivesheadiomorphs to be more consistent with the intrusion of sediment into space created by the decay of buried organisms. These organisms are inferred to have been killed at the same time as the associated aligned specimens, but whereas the fronds of the latter were felled onto the substrate, the fronds (still anchored) of the former were held clear by sediment in the turbid flow or by ash settling beneath them. This interpretation explains a number of ivesheadiomorph peculiarities, notably their high relief and distinctive morphology, and their apparent restriction to turbidite successions.

Separate surfaces preserve markedly different communities (Table 1; Fig. 3). Comparable variation in the Mistaken Point assemblage has been interpreted as recording different stages in an ecological succession (Clapham et al., 2003). Certainly, the occurrence of different populations on closely spaced beds is inconsistent with an evolutionary control. However, the degree of taphonomic overprint is not yet fully resolved and intrinsic differences in the dynamics of the smothering turbidites could have led to the preferential capture of certain taxa (see above). Similarly, the penetrative structural cleavage may introduce a substantial bias. Typically, it is subtle and several orders of rangeomorph branching are visible within fossils, but on bed A, **[[SU: no quote marks needed]]** where it has been accentuated by bedding-plane slip, the only discernable fossils are large discs and fragments of very large *Charnia*.

COMPARISON WITH MISTAKEN POINT ASSEMBLAGE

The largest surface examined in the Mercian assemblage (bed B) has a species richness comparable to the most diverse surface (E surface) in the Mistaken Point assemblage, and its generic composition most closely resembles that of the G surface (cf. Fig. 3 and Clapham et al., 2003, their figure 2). However, total diversity is lower (18 species compared to 20–30; see Clapham et al., 2003), probably due to the smaller sample area. Full taxonomic lists are not yet available for either the Mercian or Mistaken Point assemblages, but our new data show that the former shares at least 60% of its genera in common (*Aspidella*, *Hiemalora*, *Charnia*, *Charniodiscus*, *Bradgatia*), including at least two (*Primocandelabrum*, *Thectardis*) that were previously considered endemic to western Avalonia (Hofmann et al., 2008; Clapham et al., 2004). This indicates that much greater taxonomic exchange took place between these separate locations than previously believed.

Direct morphological evidence of the dispersal strategies utilized by Ediacara organisms is lacking, but they may be inferred from distribution data (e.g., Narbonne et al., 2009). The Charnwood and Newfoundland successions comprise laterally continuous tuffs and tabular event beds (Carney, 1999; Wood et al., 2003), both of which constituted kill mechanisms. Ash falls associated with arc volcanism may blanket vast regions of deepwater substrate (10^5 km^2) and are especially lethal to sessile epibenthos; turbidites typically sterilize smaller areas, but the biotic response may be similar (Hess et al., 2001). Because of the scale of such decimation, recolonization relies on passive planktic immigration from outside areas (e.g., Grassle and Morse-Porteous, 1987). Hence, the repeated recolonization events preserved in the Avalon assemblage, together with the new evidence of abundant shared taxa (see above), strongly support the notion that these organisms were able to disperse widely (Clapham et al., 2003), perhaps passively in ocean currents.

Though the Mistaken Point and Mercian assemblages share many taxa in common, their communities had profoundly different structures: prostrate and creeping **[[SU: no quote marks]]** forms (e.g., *Fractofusus*, *Hapsidophyllas*, *Pectinifrons*) are common in many of the former (Clapham et al., 2003), whereas they are conspicuously absent in the latter; *Bradgatia* may have adopted an intermediate posture (Flude and Narbonne, 2008). Avalonian organisms are thought to have adsorbed dissolved organic carbon directly from the global marine pool (Sperling et al., 2011). Therefore, nutrient availability may have had less impact on community structure than variations in the physical environment. For example, hydrodynamic and depositional regimes vary between deepwater sites (Stow et al., 1996), and locally higher concentrations of particulates immediately above the substrate could have perturbed prostrate taxa by preferentially fouling them. Equally, these taxa may have required different substrate conditions to the erect fronds, which utilized a buried holdfast; they lack a discrete anchor and must have adhered by an alternative means. The comparative rarity of *Thectardis* in Charnwood lends some support to this idea, because it too lacked a holdfast (Clapham et al., 2004). While sediment grain size appears not to have influenced the communities (Clapham et al., 2003), the impact of variations in the nature of the overlying biomats (Callow and Brasier, 2009) remains to be fully elucidated.

CONCLUSIONS

The new Charnwood biotas fill a significant gap in knowledge of the Avalon assemblage and expand the known diversity of the Ediacaran deepwater biotope. Endemism is much less marked than previously reported, suggesting effective communication between separate regions, probably facilitated by ocean currents. Benthic colonization of comparable deepwater environments therefore may have been extensive, and could have played a role in moderating the global carbon cycle. Observed differences between the Charnwood and Mistaken Point assemblages are most consistent with sustained regional differences in hydrodynamic regime or substrate, probably related to wider basin dynamics. They support the growing perception of environmental sensitivity among Ediacara organisms and its primary role in controlling community composition (Grazhdankin, 2004).

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FIGURE CAPTIONS

Figure 1. Lithostratigraphy and location of Charnwood Forest (UK) inlier, including stratigraphic positions of main fossil-bearing horizons.

Figure 2. Mercian assemblage, bed B, North Quarry, Charnwood Forest (UK). All specimens are casts, except B (mold), and are housed at British Geological Survey, Keyworth. A: Immature *Charnia masoni* complete with holdfast (GSM105979). B: *Charniodiscus* sp. (GSM106069). C: Giant *Primocandelabrum* with proportionally large holdfast (GSM105871). D: New multibranched, dumbbell-like taxon (GSM105875). E: New gladius-like frond (GSM106083). F: Largest *Thectardis cf. avalonensis* specimen identified (GSM106054). G: *Primocandelabrum* species with proportionally small holdfast (GSM105969). H: New hemispherical species with bifurcating radial ribs (GSM105967). Scales: A—4.1 cm; B—6.5 cm; C—15.5 cm; D—11.1 cm; E—4.3 cm; F—9 cm; G—11.5 cm; H—1.7 cm.

Figure 3. Lithological log of North Quarry, Charnwood Forest (UK), with compositions of key fossil surfaces; Outwoods (Main) and Bradgate Park (MC—Memorial Crags) **[[SU: correct? If not, what is MC (Mercian?)?]]** included for comparison (boxed). Shaded beds are sandstones; A is ash bed. Data are total fossil counts of surfaces compiled from full molds under low-angle lighting. Taxa are grouped by genera to minimize misidentification and to facilitate comparison with Clapham et al. (2003).

Holdfasts lacking frond are grouped as Discs; indifferently preserved fronds, or those of unknown or undetermined taxonomy, are grouped as Undet. fronds. Rare taxa (individually <1%) are not shown.

Figure 4. Current-aligned fronds, bed B, North Quarry, Charnwood Forest (UK). A: *Charnia masoni*, *Bradgatia linfordensis*, and 2 undetermined (undet.) fronds (arrows) (cast, GSM105873; housed at British Geological Survey, Keyworth). Scale bar = 10 cm. B: Axial azimuths of fronds in 5° bins (n = 99, σ = 24) and mean orientation (65°, n = 28, 2σ = 16.9) of long axes of their ellipsoidal holdfasts. Dotted arrow shows mean frond axial azimuth corrected for structural dip and plunge.

TABLE 1. SUMMARY ATTRIBUTES OF KEY FOSSIL SURFACES, MERCIAN ASSEMBLAGE

Locality	Bed	Area studied (m^2)	Number of fossils	Fossil density (n/m^2)	Taxonomic richness (minimum)	Characterizing taxon
North Quarry	H	12	44	3.6	1	*Aspidella*
	D	4.5	24	5.33	4	-
	B	115	899	7.8	18	*Primocandelabrum*
	A*	40	7	0.17	2	*Charnia grandis*
Outwoods	Main	4	33	7.9	5	*Cyclomedusa*
Bradgate Park	MC	20	203	10.15	7	*Bradgatia*

Note: Taxonomic richness is the combined species and form richness.
*Indicative data only.

[[SU: should define dash used (e.g., no data, not determined); MC should be spelled out; is it Memorial Crags, Mercian, or other?]]