



GR focus review

Remarkable insights into the paleoecology of the Avalonian Ediacaran macrobiota



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ABSTRACT

Ediacaran macrofossils from the Avalon Terrane (primarily eastern Newfoundland and the central UK) record some of the earliest large and complex multicellular organisms on Earth. Perhaps the greatest unknown regarding these fossils is their relevance to the early evolutionary history of the Kingdom Animalia. In recent years, new data and discoveries have revealed insights into Ediacaran paleobiology, taxonomic relationships, paleoecology and taphonomy, significantly refining our understanding of Avalonian ecosystems. Here, we summarise recent observational and quantitative studies, and their bearing on the current understanding of Avalonian benthic marine ecosystems. A review of existing knowledge of the biological composition of Avalonian marine assemblages demonstrates that they record densely-populated ecosystems inhabited by a diverse range of organisms, likely representing multiple biological Kingdoms. Appreciation of this diversity, and of the complexities it introduces to paleoecological studies, is vital when considering the relationship between macroevolution and contemporaneous climatic, tectonic and geochemical events. We then summarise current understanding of Avalonian paleoecology. Studies into locomotion, reproduction, feeding strategies, and community structure and succession reveal that these ecosystems were considerably different to Phanerozoic settings. Furthermore, we suggest that Avalonian ecosystems witnessed the appearance of novel nutrient sources, offering new opportunities and niches for benthic organisms. The suggestion that the numerically dominant rangeomorphs were osmotrophic is reviewed and appraised in light of geochemical, morphological, and biological information. Finally, the use of modern ecological metrics in the study of Ediacaran fossil assemblages is assessed. Concerns regarding the interpretation of paleoecological data are outlined in light of current taphonomic and sedimentological understanding, and these cast doubt on previous suggestions that the Avalonian assemblages were largely composed of metazoans. Nevertheless, we emphasise that if treated with necessary caution, paleoecological data can play a significant role in assisting efforts to determine the biological affinities of late Ediacaran macroscopic organisms.

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1. Avalonia and the Ediacaran Period

The appearance and radiation of animals was a monumental event in the history of life. Following around three billion years of evolution of exclusively microscopic life, the arrival of animals contributed to major changes in ecosystem structure (Seilacher and Pfluger, 1994; Bambach et al., 2007), redox conditions in marine substrates (e.g. Callow and Brasier, 2009a; Shields-Zhou and Och, 2011), nutrient cycling (Brasier, 1992; de Goeij et al., 2013), and global ocean chemistry (Canfield and Farquhar, 2009; Butterfield, 2011; Lenton et al., 2014). Paleontological interest in the initial evolution and diversification of metazoans focuses on the Neoproterozoic Era. Molecular clock studies (e.g. Peterson et al., 2008; Erwin et al., 2011), as well as Cryogenian biomarkers (Love et al., 2009) and putative body fossils (Maloof et al., 2010; Brain et al., 2012), have all been suggested to support a pre-Ediacaran origin of animals (though see Antcliffe, 2013; Antcliffe et al., 2014). The oldest abundant and diverse macroscopic fossils are of middle Ediacaran age. These are centimetre-scale impressions from the Lantian Formation of China (Yuan et al., 2011, 2013), and are generally considered to be algal remains. Although a handful of specimens within that biota remain of uncertain affinity (with some even suggested to be cnidarian; Van Iten et al., 2013), the Lantian assemblage has not yet been widely considered as a potential cradle for the origin of major metazoan clades.

The accurate identification of animals within Ediacaran strata is of critical importance for studies of metazoan evolution. Not only can such fossils refine evolutionary histories and reveal hitherto unimagined biological attributes, they may also provide important calibration points for molecular clocks investigating the tempo and mode of metazoan evolution across the Neoproterozoic–Cambrian transition (e.g. Peterson et al., 2008; Erwin et al., 2011; Lee et al., 2013). The late Ediacaran Period records assorted macroscopic, soft-bodied organisms whose biological affinities have long provoked debate: enigmatic fossils often referred to as the “Ediacara biota” (e.g. Narbonne, 2005). These fossils, found globally in sedimentary successions ~580–541 Ma (Fedonkin et al., 2007), have long been considered to record the impressions of early animals, including bilaterians (e.g. Glaessner, 1984; Budd and Jensen, 2000). However, unlike the Cambrian Period, which possesses body-fossil evidence for two thirds of modern animal phyla (Erwin et al., 2011) alongside abundant locomotory traces and evidence for bioturbation (Seilacher et al., 2005; Mángano and Buatois, 2014), only a handful of proposed Ediacaran metazoan body fossils or ichnofossils have passed rigorous scientific scrutiny (e.g. Jensen et al., 2006; Fedonkin et al., 2007; Budd, 2008).

The appearance of widespread macroscopic fossil assemblages in the late Neoproterozoic broadly coincides with a period of considerable global tectonic (Smith, 2009; Evans, 2013), climatic (Hoffman et al., 1998; Li et al., 2013), and geochemical upheaval (e.g. Halverson et al.,

2005; Halverson and Hurtgen, 2007; Shields-Zhou and Och, 2011; Lyons et al., 2014). There have been many suggested links between these extrinsic events and biological evolution (e.g. Logan et al., 1995; Runnegar, 2000; Butterfield, 2009b; Canfield and Farquhar, 2009; Sperling et al., 2013; Lenton et al., 2014; McKenzie et al., 2014), and efforts to unite them into a coherent narrative continue (e.g. Knoll and Sperling, 2014). However, it is clear that an accurate understanding of Ediacaran macrofossil taxa—particularly their biological affinity and ecology—is fundamental to elucidation of the evolution of morphological complexity, and investigation of the interplay between ecosystems and organisms during extraordinary environmental perturbations.

Ediacaran macrofossils were first discovered in the mid-19th Century (Salter, 1856; Billings, 1872; Howe et al., 2012), but were not accepted to be pre-Cambrian in age until the mid-1900s (Gürich, 1930; Kalberg, 1940; Sprigg, 1947; Sokolov, 1952; Ford, 1958). The Ediacaran System was only formally ratified in 2004 (Knoll et al., 2004), and discussions regarding the division of this 90 million-year interval of Earth history are just beginning (Narbonne et al., 2012b). Despite this relatively short history of study, late Ediacaran macrofossils have been reported from over 50 localities worldwide, with more than 100 genera described (Fedonkin et al., 2007). Attempts to assess the numerous conflicting interpretations for the phylogenetic placement of Ediacaran taxa (summarised in Narbonne et al., 2012b) are hindered by a paucity of preserved original organic tissue, a broad spectrum of preservational styles (see Section 1.3), and morphologically-unusual body plans. Further confusion has been introduced by the often ambiguous usage of the terms “Ediacara biota” or “Ediacaran biota”, which have variously been used to group fossils on taphonomic, taxonomic, geographical, morphological, and/or phylogenetic grounds (MacGabhann, 2014). Often, the “Ediacara biota” has referred solely to organisms from the Ediacara locality of South Australia, but it is also commonly used to discuss similar modular forms preserved as casts and moulds within late Ediacaran siliciclastic sediments worldwide. However, to focus solely on those taxa is to neglect other late Ediacaran organisms such as those from the Miaohé (Xiao et al., 2002), Lantian (Yuan et al., 2011) and Gaojiashan (Zhang et al., 1992) biotas, which are themselves important components of Ediacaran marine ecosystems, and are often preserved in taphonomic styles other than as siliciclastic casts or moulds. We support calls for clarification of the terminology used to discuss Ediacaran fossils (cf. MacGabhann, 2014). Despite these obstacles, new insights into Ediacaran macrofossils are being made at a remarkable rate, with recent studies discussing aspects of their growth (e.g. Laflamme et al., 2004; Antcliffe and Brasier, 2008; Cai et al., 2014), metabolism (e.g. Laflamme et al., 2009), geographic distribution (Laflamme et al., 2013), reproduction (Liu et al., 2012; Darroch et al., 2013), taphonomy (e.g. Tarhan et al., 2010; Laflamme et al., 2011b; Pacheco et al., 2011), life habit (e.g. Droser et al., 2014) and macroecology (e.g. Grazhdankin, 2004; Gehling and

Droser, 2013). However, fundamental questions remain to be resolved, for example the causes and consequences of the seemingly sudden evolution of macro-organisms in the middle to late Ediacaran (Narbonne and Gehling, 2003; Yuan et al., 2011), and the apparent disappearance of most Ediacaran taxa ~541 Ma (Laflamme et al., 2013).

This review outlines recent major advances in the study of the earliest macroscopic Ediacaran benthic communities preserved as siliciclastic moulds and casts: those of the Avalon Terrane. We describe the current state of understanding regarding the biological components of Ediacaran Avalonian ecosystems, and summarise prescient paleoecological studies, considering their influence on interpretations of late Ediacaran paleobiology. Finally, we consider the biases that may affect paleoecological data, and their impact on our interpretation of paleoecological information.

1.1. The Avalon Terrane

Late Ediacaran fossils from sites in the central United Kingdom and eastern Newfoundland, Canada (Fig. 1), currently represent some of the oldest evidence for macroscopic soft-bodied organisms. During the Ediacaran Period, these sites lay offshore from the microcontinent of Avalonia (Murphy and Nance, 1989), at a latitude of between 40 and 60°S, close to the West African and Amazonian cratons (Li et al., 2008; Pisarevsky et al., 2008).

Strata of the late Ediacaran Conception Group in eastern Newfoundland and the Charnian Supergroup in the U.K. both exhibit several-kilometre-thick sedimentary successions of largely turbiditic facies with no indication of shallow-water sedimentary structures (Carney, 1999; Wood et al., 2003; Narbonne, 2005; Ichaso et al., 2007; Liu et al., 2010a; Mason et al., 2013), and are widely interpreted to record deep-marine depositional environments. Appreciable influence from contour currents is inferred from macrofossil alignments and thin hemipelagites capping the turbidites (Wood et al., 2003), and there is also evidence for seismites and tsunamites in some units (Mason et al., 2013). In the absence of positive sedimentological or geochemical evidence to demonstrate a deep (i.e. sub-photic) setting, terrestrial sedimentation regimes have been suggested for the Newfoundland strata, both in fossil-bearing (Retallack, 2010, 2014b) and non-fossil-bearing units (Retallack, 2013). However, as with similar claims for the terrestrial nature of Australian (see Retallack, 2012) and even Chinese (Retallack, 2014a) Ediacaran sites, the sedimentological and geochemical observations upon which these terrestrial hypotheses are based have not been

convincingly demonstrated to be unique to paleosols. They contradict abundant data collected during decades of detailed sedimentological and geological research by numerous international authors (e.g. Misra, 1971; Benus, 1988; Conway Morris, 1989; Myrow, 1995; Narbonne et al., 2001; Wood et al., 2003; Grazhdankin, 2004; Narbonne, 2005; O'Brien and King, 2005; Ichaso et al., 2007; Grazhdankin et al., 2008; Hofmann et al., 2008; Grazhdankin et al., 2009; Liu et al., 2010a, 2012; Gehling and Droser, 2013; Macdonald et al., 2013; Mason et al., 2013; as discussed in Liu et al., 2010b; Callow et al., 2012; Antcliffe and Hancy, 2013; Xiao et al., 2013; Z. Chen et al., 2014). As such, we reject the identification of paleosols in the Conception Group and Charnian Supergroup, and concur with the overwhelming body of evidence and opinion that they are marine, turbiditic sequences deposited below storm-wave-base on the edge of a volcanic island arc complex (cf. Carney, 1999; Landing, 2004; Mason et al., 2013). Shallow-marine to fluvial deposits have been convincingly demonstrated from higher in the sections in the Avalon region, and include terrestrial beds (e.g. the Signal Hill Group of Newfoundland or the Longmyndian Supergroup in Shropshire; Williams and King, 1979; Pauley, 1991; Sala Toledo, 2004). However, these units yield only a depauperate assemblage of microbial fabrics and “pit and mound” structures (e.g. McIlroy et al., 2005), with no Ediacara-type macrobiota. This observation is further evidence against the suggestion that Ediacaran macro-organisms resided on land.

Newly discovered fossil assemblages of the informally-named June beds at Sekwi Brook, NW Canada, are similar in biotic composition, age, and depositional environment to those of the Conception and St. John's Groups (Macdonald et al., 2013; Narbonne et al., 2014). Although these assemblages could feasibly be considered part of the Avalon biota from a biological perspective (Narbonne et al., 2014; sensu Waggoner, 2003; see Section 1.4), we focus this review on the paleobiology of sites paleogeographically located on the margins of the microcontinent of Avalonia (Fig. 1).

1.2. Geochemical context for Avalonian paleoecology

The Neoproterozoic Era witnessed extraordinary changes in atmospheric and ocean chemistry, which may have significantly impacted evolutionary progress at this time. Atmospheric oxygen levels are thought to have risen from between 1–10% PAL at ~800 Ma to levels closer to modern by the latest Ediacaran (Lyons et al., 2014). This rise

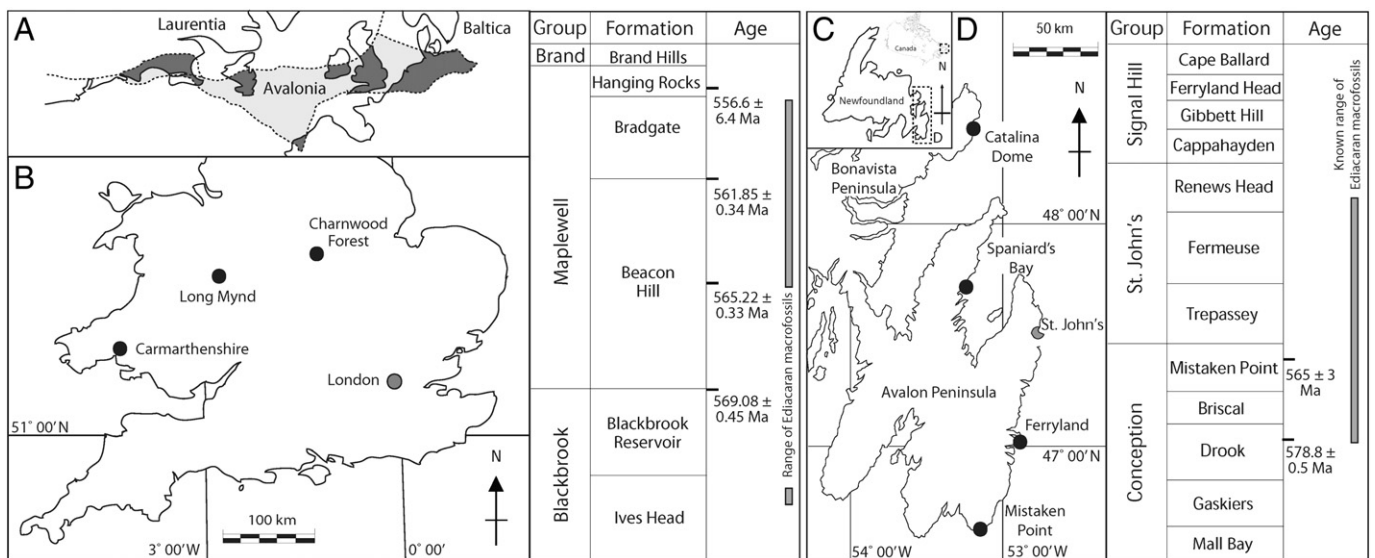


Fig. 1. Geological context for Avalonian Ediacaran macrofossil localities. A: Map showing the current distribution of areas that formed part of the Avalon Terrane in the Ediacaran Period (highlighted, after Cocks et al., 1997). B: Map of England and Wales, showing the major Ediacaran fossil localities (black circles), accompanied by schematic stratigraphic column for the Charnwood Forest sections. Date and fossil distributions after Noble et al. (in press). C: Location map of Newfoundland, eastern Canada. D: The Avalon and Bonavista Peninsulas and their major Ediacaran macrofossil localities (black circles), accompanied by a representative stratigraphic column (not to scale). Dates from Benus (1988), and Van Kranendonk et al. (2008) (latter after Bowring et al., 2003). Unfortunately none of the geochronological dates from Newfoundland are published with isochrons.

is inferred to have triggered the oxidation of the deep oceans (e.g. Fike et al., 2006; Canfield et al., 2007; McFadden et al., 2008; Scott et al., 2008; though see Lenton et al., 2014), broadly coincident with a shift from ferruginous to oxic deep-marine conditions, and large fluctuations in global carbon isotopic ratios (summarised in Halverson et al., 2009; Shields-Zhou and Och, 2011). Since there is currently no direct way to measure oxygen levels in the ancient oceans, interpretations of oceanic oxygen concentrations are reliant on data from redox geochemistry, in particular iron speciation and trace element techniques.

Existing geochemical studies suggest that chemical conditions within the oceans during the late Ediacaran were not uniform across the globe. In several areas, basin transects through early- and middle-Ediacaran successions reveal oxic surface waters in some basins underlain by a euxinic wedge on the continental shelf, with ferruginous (anoxic) conditions in the deep oceans (cf. Li et al., 2010). Some workers consider marine chemistry to have changed following the Gaskiers glaciation (~583–582 Ma; dates from Van Kranendonk et al., 2008 after Bowring et al., 2003), with iron speciation data from Newfoundland suggesting a switch from ferruginous to oxic deep-marine conditions coincident with the termination of the glacial event (Canfield et al., 2007). Perhaps importantly, this shift immediately precedes the local first appearance of Ediacaran macrofossils (Narbonne and Gehling, 2003). However, studies elsewhere indicate that the perceived change in redox conditions was not globally contemporaneous. Analysis of framboidal pyrite within the Doushantuo Formation of China suggests fluctuations in redox conditions within the deep oceans throughout much of the Ediacaran (Wang et al., 2012). Data from Russian shallow-marine sediments suggest the ferruginous to oxic shift occurred in the late Cryogenian (Johnston et al., 2012). In contrast, data from sites in NW Canada suggest a significantly pre-Gaskiers (early Ediacaran) shift to oxic conditions in the Mackenzie Mountains (Macdonald et al., 2013) but no distinguishable shift in the Wernecke Mountains (Johnston et al., 2013). There are three possible explanations for this temporal and facies-related variation: oxidation of the deep oceans was diachronous and/or progressed intermittently (cf. Narbonne et al., 2012b); oxidation followed different trajectories in different basins; or our interpretation of geochemical data requires refinement. Until our temporal resolution of the oxidation event/s improves, we cannot fully assess the inferred causal relationship (cf. Cloud, 1968; Y. Shen et al., 2008) between the evolution of the Ediacaran macrobiota and the rise of oceanic oxygen levels.

The recognition that modern sponges can survive at very low oxygen levels (e.g. Mills et al., 2014; though it has not yet been demonstrated that they can complete their entire life cycle under such conditions) suggests that the initial evolution of animals may have taken place at lower oxygen levels than are generally assumed necessary. Indeed, some authors consider that animals may themselves have been responsible for the oxygenation of the deep oceans (Lenton et al., 2014). Suggestions that redox stability, achieved in shallow-marine Russian sections at ~560 Ma, may have been more important for supporting animal evolution than a rise in oxygen above a threshold level (Johnston et al., 2012) are intriguing, but require testing via comparison with geochemical and paleontological data from additional localities.

Other important aspects of ocean chemistry are also considered to have been significantly different in the Ediacaran Period. The ferruginous conditions hypothesised for many deep Ediacaran basins, coupled with high C_{org}/S_{py} ratios, pyrite enriched in ^{34}S , and low carbonate associated sulphate (CAS) concentrations, have been taken to imply that sulphate concentrations in the deep oceans were likely to have been lower than in the Phanerozoic (e.g. Halverson and Hurtgen, 2007; Canfield et al., 2008; Ries et al., 2009). Another important consideration is the global dissolved organic carbon (DOC) concentration, since DOC is a major source of nutrients in the modern oceans. Estimating the size of the late Ediacaran DOC pool is therefore highly relevant when considering the possible feeding strategies of Ediacaran macro-organisms (Section 2.2). Whilst total organic carbon (TOC) measured in Newfoundland (Canfield et al., 2007) is extremely low, these low levels may not accurately reflect

original values. The Neoproterozoic units of the Avalon Peninsula underwent Cambrian prehnite–pumpellyite-grade metamorphism (Papezik, 1974), corresponding to the anchizone metamorphic facies (200–300 °C) of Merriman and Frey (2009). The Conception Group would therefore have reached the top of the dry gas or over-mature hydrocarbon zone. Laumontization of tuffs on the nearby Bonavista Peninsula (Fig. 1), suggested to indicate negligible metamorphism (Retallack, 2014b), is inconclusive due to the wide range of conditions under which this mineral can form (e.g. Coombs et al., 1959; Boles and Coombs, 1977; Arkai et al., 2007). In the absence of observed structural caps, any methane produced would likely have been driven off upon subsequent exhumation, resulting in TOC measurements that represent, at best, minimum estimates of original carbon concentrations. Furthermore, facies-related variability in the location and abundance of organic matter (OM) mean that bulk rock measurements (as collected in the Canfield et al., 2007 study) may not accurately reflect carbon (or indeed sulphur or iron) concentrations during the intervals in which the organisms were alive (typically represented by relatively thin hemipelagites). Therefore, since we cannot exclude the possibility that a diagenetic and/or metamorphic overprint has significantly altered measureable carbon concentrations in Avalonia, we must be cautious in interpreting local or global chemical conditions from such sections.

Clearly, the latest Neoproterozoic oceans were considerably different to those of the Phanerozoic, with lower oxygen and sulphate concentrations in the deep oceans. DOC levels remain to be resolved. Under such conditions, interpreting the biology of Ediacaran macro-organisms requires consideration of not only extant organisms and their capacity to survive in comparable environments, but also of how ocean chemistry may have influenced Ediacaran ecosystems, environments, and biological activity.

1.3. Taphonomy

Global Ediacaran fossil assemblages exhibit a wide variety of taphonomic styles, each offering a distinct perspective on the original biological communities (reviewed in Kenchington and Wilby, 2014). Fossils can be preserved by siliciclastic ‘cast and mould’ preservation (Narbonne, 2005), within carbonates (Grazhdankin et al., 2008; Z. Chen et al., 2014), as carbonaceous compressions in mudstones (Grazhdankin et al., 2008; Zhu et al., 2008; Xiao et al., 2013; Wang et al., 2014), as pyrite replacements (e.g. Steiner and Reitner, 2001) and, in the case of microfossils, via phosphatisation and aluminosilicate mineralization (e.g. Xiao et al., 1998; Callow and Brasier, 2009b). Considerable work has been done to elucidate the mechanisms involved in Ediacaran soft tissue preservation (e.g. Gehling, 1999; Mapstone and McIlroy, 2006), including several experimental studies (Norris, 1989; Bruton, 1991; Laflamme et al., 2011b; Liu, 2011b; Darroch et al., 2012). However, certain aspects of these taphonomic processes, particularly the formation of framboidal pyrite (e.g. Rickard, 2012), remain to be fully resolved.

In Newfoundland, fossils are typically preserved on fine-grained siliciclastic hemipelagite (mud, silt) substrates, beneath either volcanic ash deposits (Conception-type preservation of Narbonne, 2005), or sandstones (more commonly in shallower settings at the top of the sequence; Fermeuse-type preservation of Narbonne, 2005). Gehling recognised the widespread occurrence of microbial mats in terminal Proterozoic sections, and suggested that early diagenetic mineralization of organic material following microbially-induced iron sulphide precipitation, coupled with sealing of the sediment by further mat growth on the seafloor above, played a significant role in the preservation of Ediacaran soft tissues (Gehling, 1999; Droser et al., 2006). This taphonomic model is corroborated by geochemical evidence for the close association of biofilms with Avalonian macrofossils (Laflamme et al., 2011b), by petrological evidence tracking the mineralogical evolution from pyrite to haematite in Australia (Mapstone and McIlroy, 2006), and by experimental studies that reveal the generation of iron sulphides around carcasses decayed on (cyano)bacterial mats (Darroch et al., 2012). The role

of authigenic clays in Ediacaran preservation is also recognised to be important in some instances (Mapstone and McLroy, 2006; Cai et al., 2012; Darroch et al., 2012). These clays are suggested to stabilise organic impressions either in conjunction with pyrite (Mapstone and McLroy, 2006; Laflamme et al., 2011b) or in its absence (e.g. under conditions that did not favour pyrite formation; Cai et al., 2012). A combination of diagenetic pyrite formation and clay mineral production likely explains the preservation of Avalonian macrofossil impressions (e.g. Laflamme et al., 2011b).

Certain parts of organisms that were positioned within the sediment during life (e.g. holdfast discs) have a greatly increased preservation potential relative to surficial remains (e.g. fronds). This taphonomic bias can artificially inflate the number of such impressions relative to those of other organisms (Droser et al., 2006). Examination of the taphonomy of individual bedding planes reveals further useful paleobiological insights. For example, the unusually deep topographic relief of fossil impressions on the remarkable Spaniard's Bay fossil surface (famous for its '3-D' preservation of rangeomorphs; Narbonne, 2004), results from scouring of the sediment surrounding the organisms by a high-velocity current (Brasier et al., 2013a). Consequently, several features previously interpreted as biogenic may have abiological origins. One such feature is the 'bubble train', originally interpreted to result from the decay of rolled-up microbial mats (Laflamme et al., 2011a), but alternatively suggested to be a sedimentary load-cast structure (Brasier et al., 2013a). Possessing a detailed understanding of the taphonomic and sedimentological context of individual bedding planes is key to recognising true morphological features and taphonomic biases, ultimately enabling constraint of biological hypotheses (discussed further in Section 3.2.1.1).

1.4. Avalonian organisms and their affinities

Marine life diversified extensively during the Neoproterozoic, and a wide range of biological groups existed by the start of the Ediacaran Period. These included multiple microscopic prokaryotes and eukaryotes (Schopf and Barghorn, 1969; Porter and Knoll, 2000; Knoll et al., 2006; Butterfield, 2009a; Bosak et al., 2011b, 2012; Cohen et al., 2011), acritarchs (e.g. Grey et al., 2011), a wide range of simple macroscopic discoidal specimens (e.g. Grazhdankin et al., 2012; Liu et al., 2013a), and putative metazoans (Malooof et al., 2010). The lower and middle Ediacaran Period yields the predominantly macro-algal Lantian biota (e.g. Yuan et al., 2011, 2013), microfossils of the Doushantuo Formation previously interpreted as embryos (see discussion in Xiao et al., 1998; Hultgren et al., 2011; L. Chen et al., 2014), multiple acritarchs (e.g. Moczydlowska, 2005; Willman et al., 2006; Xiao et al., 2014), and putative trace fossils of bilaterian metazoans (Pecoits et al., 2012, although see the discussion in Gaucher et al., 2013; Pecoits et al., 2013). These discoveries demonstrate the considerable evolutionary innovations taking place throughout the entire Neoproterozoic, and remind us that soft-bodied macro-organisms (themselves considerably diverse) were not the sole inhabitants of late Ediacaran marine ecosystems.

To evaluate the differences between different global biotic communities, late Ediacaran macrofossil taxa known at the time were subjected to Parsimony Analysis of Endemism (PAE), which found them to cluster into three broadly-supported biotic assemblages (Waggoner, 2003). These assemblages—the Avalon, White Sea and Nama—have been widely cited (e.g. B. Shen et al., 2008), but it has remained difficult to untangle the competing contributions of temporal, paleoenvironmental, taphonomic, latitudinal, ecological and evolutionary influences on their composition (cf. Waggoner, 2003). Recent discoveries of new fossil localities (e.g. Liu et al., 2013a; Narbonne et al., 2014; Warren et al., 2014), alongside more complete stratigraphic and geographical sampling for geochronology, and improvements in stratigraphic understanding, have revealed temporal overlaps between the three assemblages, which have been interpreted by some to reflect large-scale macroevolutionary events (Grazhdankin, 2014). Meanwhile, facies,

paleolatitude, taphonomic and tectonic processes have been shown to exert significant controls on the occurrence of specific taxa within individual assemblages (e.g. Grazhdankin, 2004; Grazhdankin et al., 2008; Gehling and Droser, 2013; Laflamme et al., 2013). This implies that there is interplay between biotic assemblage compositions and both biological and abiological processes, at a variety of scales.

The Avalon biotic assemblage is largely composed of fossils from sites in the central UK and eastern Newfoundland (Waggoner, 2003), although the Olenek Uplift of Siberia and Sekwi Brook in NW Canada also host typically Avalonian taxa (Grazhdankin et al., 2008; Narbonne et al., 2014). The Lubcloud and Mercian Assemblages of Charnwood (cf. Wilby et al., 2011) and the Conception and St. John's Groups of Newfoundland, share taxonomic, sedimentological and geochronological similarities (e.g. Benus, 1988; Carney, 1999; Wood et al., 2003; Wilby et al., 2011; Noble et al., in press), and close paleogeographic proximity on the edge of the Avalonian microcontinent (Murphy et al., 1999; Fig. 1). Avalonian fossils are considerably older (~580–557 Ma; Van Kranendonk et al., 2008; Noble et al., in press) than those observed at other classic Ediacaran sites such as the White Sea or the Flinders Ranges (which are dated at ~555 Ma; Martin et al., 2000).

Avalonian macrofossils form a reasonably diverse assemblage of soft-bodied taxa, and range from a few millimetres (Liu et al., 2012) to almost 2 m (Narbonne and Gehling, 2003) in maximum dimension. They have been prominent in the debate surrounding the broader phylogenetic interpretation of Ediacaran macro-organisms. To distinguish between the various conflicting biological affinities previously proposed for these organisms, existing hypotheses must be critically assessed, and tested using information gleaned from multiple approaches, permitting rejection of implausible hypotheses. Classification of Ediacaran macrofossil genera into higher-order clades (e.g. Durham, 1978; Glaessner, 1979; Sepkoski, 1992) may assist this endeavour, but few previous attempts have gained wide acceptance within the scientific literature. Recent efforts to formulate higher-order groupings (Xiao and Laflamme, 2009; Erwin et al., 2011; Laflamme et al., 2013; Grazhdankin, 2014) offer promise, but require testing via phylogenetic and ontogenetic approaches. These recent higher-order groupings also do not consider several significant components of the late Ediacaran macroscopic biota, such as tubular body fossils, or biomineralizing organisms.

If paleoecological studies are to usefully inform us about ancient ecosystems, they need to incorporate an accurate knowledge of community composition, with full appreciation of the present limits to our scientific understanding. With this in mind, we here review the organisms found within late Ediacaran Avalonian deep-marine settings. To date, 30 macrofossil species have been formally described from Avalonian deep-marine paleoenvironments, belonging to 23 genera (Table 1). It is only in the last decade that serious efforts have been made to systematically classify and describe the common Ediacaran taxa of Newfoundland (largely by the group headed by Guy Narbonne at Queens University, Ontario). Additionally, a casting project led by the British Geological Survey has significantly increased the number of specimens known from Charnwood Forest (Wilby et al., 2011). Despite these advances, a surprisingly small number of exceptionally preserved Ediacaran fossil localities (see Fig. 1) are responsible for a disproportionately high volume of the information we possess about these organisms.

1.4.1. Rangeomorphs

The majority of Avalonian macrofossils, both numerically and taxonomically, are termed rangeomorphs (Narbonne, 2004). Rangeomorph taxa possess one or many leaf-like structures, termed fronds, often arranged around a stem and/or holdfast (cf. Brasier et al., 2012). The rangeomorph clade is united by the construction of constituent taxa by self-similar branching elements, and possession of a glide plane of symmetry (Fig. 2; Narbonne, 2004; Narbonne et al., 2009; Brasier et al., 2012; Hoyal Cuthill and Conway Morris, 2014). Twelve rangeomorph genera have been formally described from Avalonia (Table 1), with ten of them being monospecific.

Table 1
Body fossil taxa described to date from Newfoundland, and their suggested assignment to higher order groups (latter largely after Laflamme et al., 2013). # Taxa referred to as frondomorphs by Grazhdankin (2014).

Genus	Species	Key publications	Group
<i>Avalofractus</i>	<i>abaculus</i>	Narbonne et al. (2009)	Rangeomorphs
<i>Beothukis</i>	<i>mistakensis</i>	Brasier and Antcliffe (2009)	Rangeomorphs
<i>Bradgatia</i>	<i>linfordensis</i>	Boynton and Ford (1995), Flude and Narbonne (2008)	Rangeomorphs
<i>Charnia</i>	<i>masoni</i>	Ford (1958)	Rangeomorphs
<i>Culmofrons</i>	<i>plumosa</i>	Laflamme et al. (2012)	Rangeomorphs
<i>Fractofusus</i>	<i>andersoni</i>	Gehling and Narbonne (2007)	Rangeomorphs
<i>Fractofusus</i>	<i>misrai</i>	Gehling and Narbonne (2007)	Rangeomorphs
<i>Fronndophyllas</i>	<i>grandis</i>	Bamforth and Narbonne (2009)	Rangeomorphs
<i>Hapsidophyllas</i>	<i>flexibilis</i>	Bamforth and Narbonne (2009)	Rangeomorphs
<i>Pectinifrons</i>	<i>abyssalis</i>	Bamforth et al. (2008)	Rangeomorphs
<i>Primocandelabrum</i>	<i>hiemalorum</i>	Hofmann et al. (2008)	Rangeomorphs
<i>Primocandelabrum</i>	sp.	Hofmann et al. (2008)	Rangeomorphs
<i>Trepassia</i>	<i>wardae</i>	Narbonne and Gehling (2003), Narbonne et al. (2009)	Rangeomorphs
<i>Vinlandia</i>	<i>antededens</i>	Laflamme et al. (2007), Brasier et al. (2012)	Rangeomorphs
<i>Parviscopa</i>	<i>bonavistensis</i>	Hofmann et al. (2008)	Fronndose form
<i>Charniodiscus</i>	<i>arboreus</i>	Glaessner and Daily (1959), Laflamme et al. (2004)	Arboreomorphs#
<i>Charniodiscus</i>	<i>concentricus</i>	Ford (1958, 1963)	Arboreomorphs#
<i>Charniodiscus</i>	<i>procerus</i>	Laflamme et al. (2004)	Arboreomorphs#
<i>Charniodiscus</i>	sp.	Hofmann et al. (2008)	Arboreomorphs#
<i>Charniodiscus</i>	<i>spinousus</i>	Laflamme et al. (2004)	Arboreomorphs#
<i>Hadrynichorde</i>	<i>catalinensis</i>	Hofmann et al. (2008)	Miscellanea
<i>Hadryniscalia</i>	<i>avalonica</i>	Hofmann et al. (2008)	Miscellanea
<i>Haootia</i>	<i>quadriformis</i>	Liu et al. (2014a)	Cnidarian?
<i>Thectardis</i>	<i>avalonensis</i>	Clapham et al. (2004), Sperling et al. (2011)	Sponge?
<i>Aspidella</i>	<i>terranoica</i>	Billings (1872), Gehling et al. (2000)	Discoid
<i>Cyclomedusa</i>	<i>davidii</i>	Boynton (2010)	Discoid
<i>Cyclomedusa</i>	<i>cliffi</i>	Boynton (2006)	Discoid
<i>Hiemalora</i>	<i>stellaris</i>	Fedonkin (1980), Hofmann et al. (2008)	Discoid#
<i>Triforillonia</i>	<i>costellae</i>	Gehling et al. (2000)	Discoid
<i>Palaeopascichmus</i>	<i>delicatus</i>	Palić (1976), Gehling et al. (2000), Antcliffe et al. (2011)	Protist
<i>Ivesheadiomorphs</i>		Boynton and Ford (1995), Hofmann et al. (2008), Liu et al. (2011)	Taphomorph
<i>Filaments</i>		Callow and Brasier (2009a), Liu et al. (2012)	Bacteria?

Branch structure has been an important consideration for Ediacaran workers when dealing with rangeomorph taxa, and a wide variety of terminology has been used to describe branching in the past (e.g. Pflug, 1972; Jenkins, 1992; Flude and Narbonne, 2008; Laflamme and Narbonne, 2008; Narbonne et al., 2009). A revised scheme for describing rangeomorph taxa was proposed by Brasier et al. (2012), and was used to amend the diagnoses of eight common genera, allowing their identification on the basis of branch architecture alone (Brasier et al., 2012). Morphological differences in the size and shape of rangeomorph taxa were suggested to be of use for species-level diagnoses (Brasier et al., 2012), when coupled with due consideration of likely intra-species variability. Distinction between so-called Charnid (undisplayed and rotated first order branches cf. Brasier et al., 2012) and Rangid (displayed first order branches) rangeomorph branching (see Narbonne et al., 2009) may also aid taxonomic differentiation, but the ecological and/or phylogenetic significance of this distinction remains to be explored. Most Avalonian rangeomorphs are unipolar (i.e. they possess one pole of growth), and have two rows of primary branches (cf. Brasier et al., 2012). Exceptions include *Bradgatia* (Fig. 2C), which may be multipolar, and *Pectinifrons* and *Fractofusus*, which are described as being bipolar (Brasier et al., 2012). In addition, the latter may have possessed three rows of primary branches (Gehling and Narbonne, 2007; Narbonne et al., 2014). A trifoliate structure would be highly unusual within the group. These taxonomic discussions all assume that branch architecture is a taxonomically robust feature in rangeomorphs, and was not subject to change during the life cycle of the organism, or via biostratigraphic processes. The observation that juvenile forms of several taxa show branching patterns similar to those seen in mature forms (Narbonne, 2004; Liu et al., 2012) would suggest that branch architecture is consistent throughout ontogeny.

Two rangeomorph genera, *Hapsidophyllas* and *Fronndophyllas* (Fig. 2H–I) were originally described as sharing a unique “hapsidophyllid” branching

structure, whereby rangeomorph sub-units combine to form larger “leaflet-like” structures (Bamforth and Narbonne, 2009). Branching structure in these taxa does seem to differ from that observed in other rangeomorphs (Fig. 2), but a paucity of exceptionally preserved hapsidophyllids currently presents a barrier to detailed comparisons.

Rangeomorphs can be broadly distinguished as either having been oriented upright in the water column in life (cf. Clapham and Narbonne, 2002; Ghisalberti et al., 2014, though see Grazhdankin et al., 2008) or, in the absence of a clear stem, holdfast or current alignment, as recumbent on the seafloor (e.g. *Fractofusus*; Fig. 2F–G and *Pectinifrons* Fig. 2J; Gehling and Narbonne, 2007; Bamforth et al., 2008). The earliest rangeomorph to possess a distinct stem is claimed to be *Culmofrons*, which first appears within the middle Briscall Formation of the Mistaken Point Ecological Reserve (Laflamme et al., 2012). Development of a stem has been considered an important functional innovation, permitting rangeomorphs both to exploit a considerably wider morphospace than would previously have been possible, and to compete effectively for nutrients in the water column (Laflamme et al., 2012). This basic construction is mirrored by *Charniodiscus* species (see Section 1.4.2), and also by forms similar to *Primocandelabrum* (Fig. 2K–L).

Rangeomorphs have been described from several younger and shallower localities across the globe, extending the range of this lineage beyond the time interval and facies recorded in the Newfoundland and U.K. successions (Jenkins, 1985; Grazhdankin et al., 2008; Hofmann and Mountjoy, 2010; Gehling and Droser, 2013; Narbonne et al., 2014). However, they occur with lower abundance and taxonomic diversity at these additional sites. Avalonian depositional environments thus appear to record the zenith of rangeomorph diversity, with only a handful of taxa, such as *Rangea* (e.g. Vickers-Rich et al., 2013), yet to be documented from the Avalon region. The reasons for the apparent demise of the group towards the end of the Ediacaran Period remain to be resolved (see Laflamme et al., 2013).

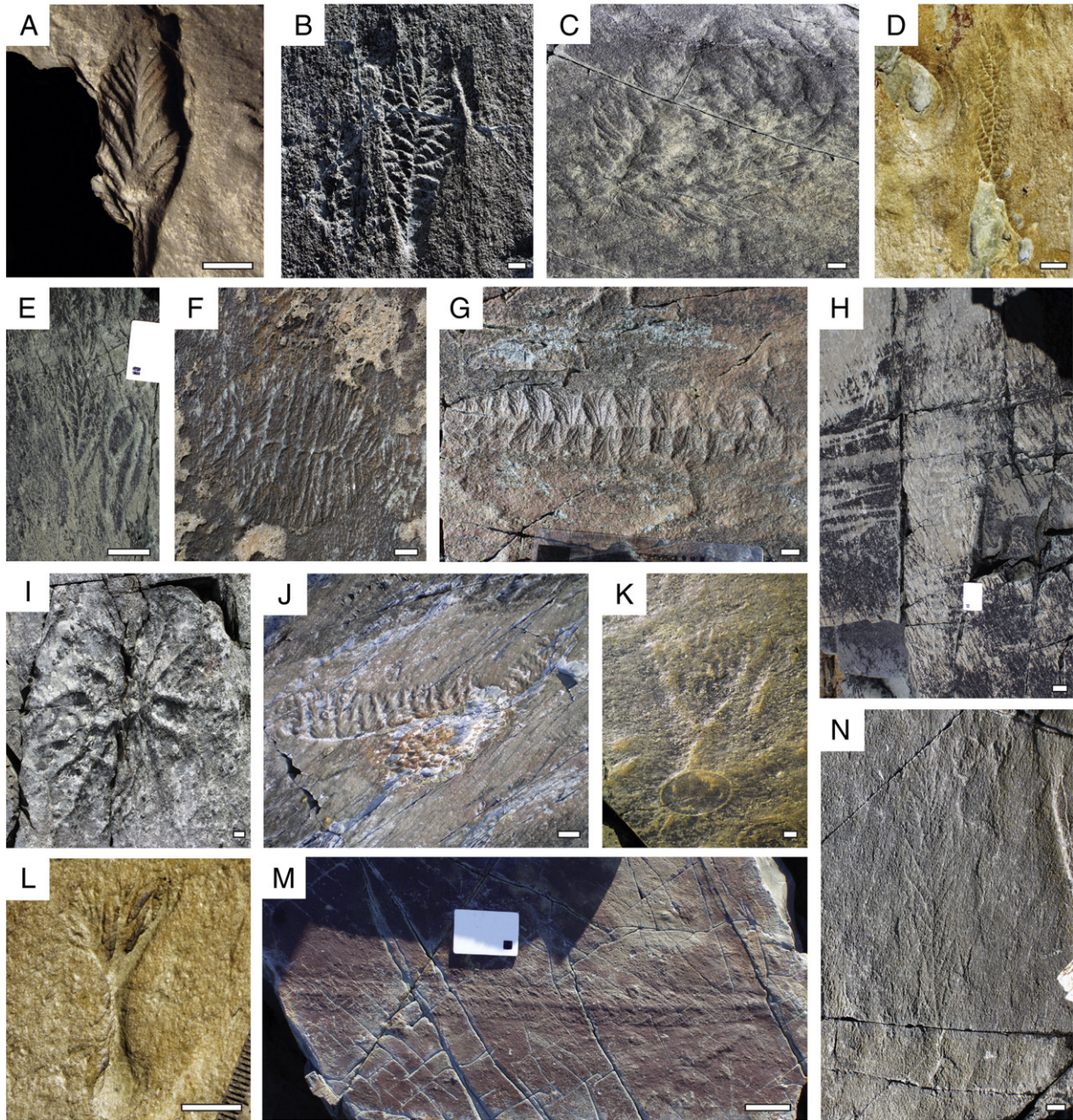


Fig. 2. Rangeomorph taxa from Avalonia. A: *Avalofractus abaculus* holotype, Spaniard's Bay, NL. B: *Beothukis mistakensis* holotype, MPER, NL. C: *Bradgatia linfordensis*, MPER, NL. D: *Charnia masoni*, Bonavista Peninsula, NL. E: *Culmofrons plumosa*, holotype, MPER, NL. F: *Fractofusus andersoni*, Bonavista Peninsula, NL. G: *Fractofusus misrai*, MPER, NL. H: *Frondophyllas grandis*, MPER, NL. I: *Hapsidophyllas flexibilis*, MPER, NL. J: *Pectinifrons abyssalis*, MPER, NL. K: *Primocandelabrum hiemalaranum*, Bonavista Peninsula, NL. L: *Primocandelabrum* sp., Bonavista Peninsula, NL. M: *Trepassia wardae* (incomplete), MPER, NL. N: *Vinlandia antecedens*, Bonavista Peninsula, NL. Scale bars = 10 mm, except E, H, J, M = 50 mm, and A = 5 mm.

Comparisons have been made between rangeomorphs and various biological groups including stem-group fungi (Peterson et al., 2003), algae (Ford, 1958), extinct Kingdoms or Phyla (Seilacher, 1989, 1992), and sessile stem- or crown-group metazoans (Clapham and Narbonne, 2002; Clapham et al., 2003; Narbonne, 2010). These suggested biological affinities stem from a mixture of morphological, developmental, and paleoecological observations. Affinities with cnidarian sea pens (cf. Glaessner, 1984; Jenkins, 1985) were challenged by an ontogenetic study suggesting that, in *Charnia masoni* (Fig. 2D), new branches were added sequentially at the tip of the frond, rather than at the base as in sea pens (Antcliffe and Brasier, 2007). However, that study only considered *Charnia*, and did not examine other rangeomorphs, or non-rangeomorph taxa (see

Section 1.4.2). Expansion of such approaches is therefore required to determine whether this growth mode is consistent within all rangeomorphs. Comparisons to stem-group fungi emphasised the sessile, sub-photic lifestyle, indeterminate growth, lack of taphonomic shrinkage and apparent growth zonation observed within certain rangeomorphs (Peterson et al., 2003). However, those authors caution that conclusive evidence for fungal biology, such as fungal hyphae with perforate cell walls, is required before such an interpretation can be accepted. Unfortunately, the siliciclastic sediments in which rangeomorphs are typically found rarely preserve impressions at the scale required to resolve such features. Whilst an algal affinity can be discounted on the basis of sub-photic environments, alternative hypotheses remain viable.

1.4.2. Non-rangeomorph frondose organisms

Several frondose taxa have been distinguished from the rangeomorphs by their apparent possession of uniform, parallel, *Arborea*-type branching (Laflamme and Narbonne, 2008), and a lack of observed rangeomorph elements. In such taxa, primary branches emanate from the stem and continue towards a distal rim. Some authors consider the primary branches to be held in place by a basal sheet, with sub-parallel secondary branches enclosed within a membrane (Laflamme and Narbonne, 2008). Such taxa have recently been termed arboreomorphs (e.g. Erwin et al., 2011; Laflamme et al., 2013), although an alternative nomenclature diagnoses fossils possessing a flattened foliate region (presumably, but not explicitly, without rangeomorph branching), a stem, and a holdfast structure, as frondomorphs (Grazhdankin, 2014). In Avalonia, species attributed to *Charniodiscus* (Fig. 3A–E) are the primary representatives of these broadly, but not directly, comparable groups. Arboreomorph/frondomorph taxa can be found globally (including in Australia, Russia, China and Canada) within both shallow- and deep-marine depositional environments.

Charniodiscus represents something of a taxonomic conundrum, in that the holotype specimen *C. concentricus* (Fig. 3B) from Charnwood Forest (Ford, 1958) is arguably morphologically dissimilar in its branching structure to the various *Charniodiscus* species subsequently described from Newfoundland (Fig. 3A, C–E; Laflamme et al., 2004). Future resolution of the taxonomic relationships within this genus would be extremely valuable. *Charniodiscus* specimens are unipolar, and

possess a prominent, often high-relief discoidal holdfast connected to a clear central stem that runs up the length of the frond (Laflamme et al., 2004). Shared alignment of fronds with respect to their discs on many bedding planes implies that they were anchored within the substrate by their holdfasts, and aligned by currents (e.g. Wood et al., 2003). The phylogenetic affinities of the arboreomorphs/frondomorphs have yet to be assessed, and similar forms amongst the Cambrian Burgess Shale and Chengjiang Lagerstätten (Conway Morris, 1993; Shu et al., 2006) need to be carefully compared.

The brush-like *Parviscopa* from the Bonavista Peninsula (Fig. 3F; Hofmann et al., 2008) neither displays rangeomorph branching nor resembles any other Avalonian taxon. Despite similarities to the Cambrian trace fossil *Oldhamia flabellata* (Hofmann et al., 2008), it is considered to be a body fossil. Its relationship to contemporaneous frondose taxa remains to be determined.

1.4.3. Other macrofossil taxa

A variety of additional macroscopic organisms known from Avalonian Ediacaran strata are neither rangeomorphs nor arboreomorphs/frondomorphs. These may include representatives of several phylogenetic groups, including metazoans, protozoans, and algae. Specimens of such taxa are typically rare, have received relatively little attention in the literature, and have been assigned to clades of low taxonomic diversity, but they are of immense importance for our interpretation of Ediacaran paleoecology. Apart from the palaeopascichnids (Fig. 4D;

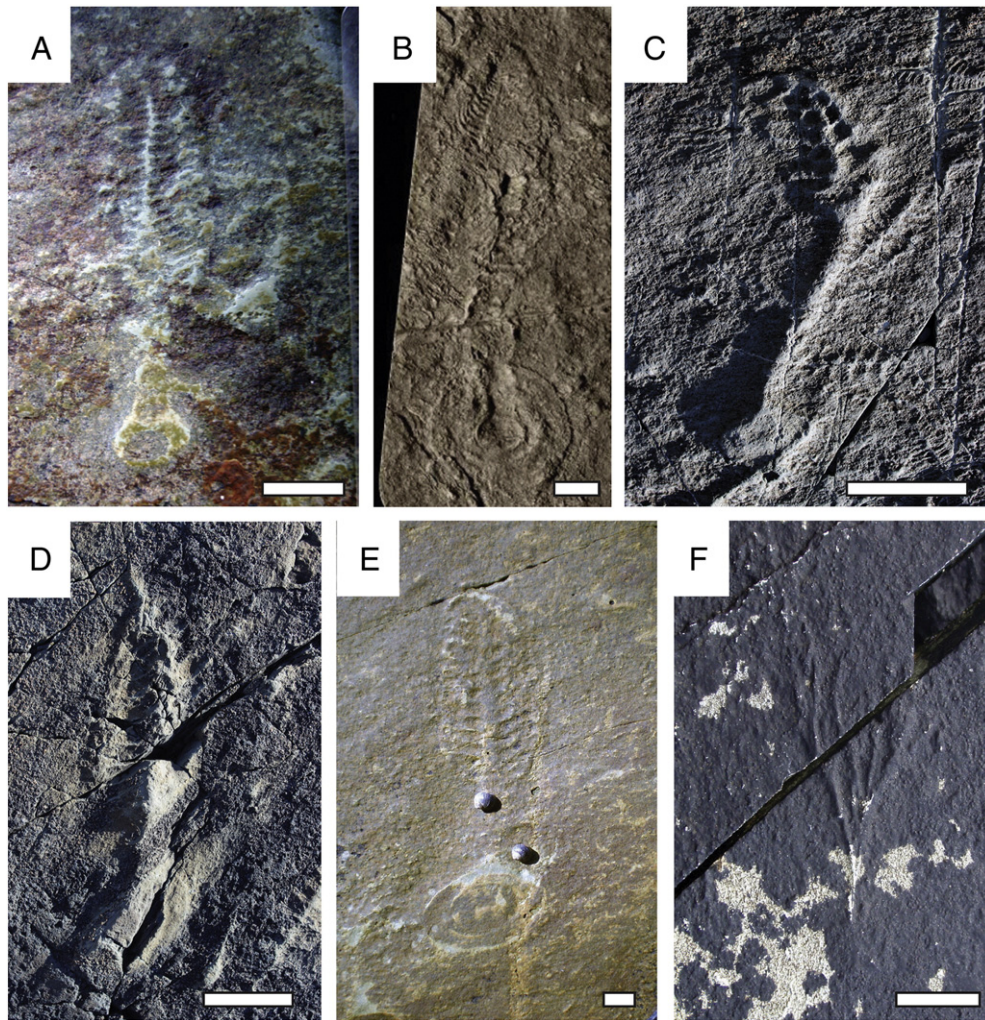


Fig. 3. Non-rangeomorph fronds from Avalonia. A: *Charniodiscus arboreus*, Bonavista Peninsula, NL. B: *Charniodiscus concentricus* (holotype), Leicestershire, U.K. C: *Charniodiscus procerus*, MPER, NL. D: *Charniodiscus spinosus*, MPER, NL. E: *Charniodiscus* sp., Bonavista Peninsula, NL. F: *Parviscopa bonavistensis*, Bonavista Peninsula, NL. Scale bars A, E and F = 10 mm, C–D = 50 mm, and B = 20 mm.

see [Grazhdankin, 2014](#)), all taxa discussed in this sub-section were apparently endemic to Avalonia and, like the rangeomorphs and arboreomorph/frondomorphs, are considered to be benthic. Macroscopic free-swimming organisms have yet to be documented from Avalonian deep-marine successions. The carbonised remains of tubular *Sabellidites* and vendotaenids from the uppermost Ediacaran of the Burin Peninsula (Member 1 of the Chapel Island Formation; [Narbonne et al., 1987](#)), are notable, but are not typical of the deep-marine Avalonian biota discussed in the rest of this review.

The ladder-like form *Hadryniscala* ([Fig. 4E](#)) and the string-like *Hadrynichorde* ([Fig. 4F](#)) both show morphological similarities to some modern algae ([Hofmann et al., 2008](#)), but such an algal affinity is currently unproven. Both taxa warrant further detailed study, but *Hadrynichorde* in particular requires attention, given that the holdfast of the holotype specimen appears to be attached to an effaced frond, and it is possible that the associated string (figured well in [Hofmann et al., 2008](#), fig. 22.3) is unrelated to the disc ([Fig. 4F](#)). *Thectardis* ([Fig. 4A](#)) is one of the lowest stratigraphically-occurring taxa within the Avalonian successions (appearing in the upper Drook Formation; [Clapham et al., 2004](#)), and can numerically dominate seafloor communities (e.g. bed PC of [Clapham et al., 2003](#)), although its abundance is diminished on younger bedding planes. A simple triangular form of relatively high topographic relief, *Thectardis* is of particular interest due to its interpretation by some authors as a poriferan ([Sperling et al., 2011](#)). Others consider it to be little more than a taphomorph of a frondose organism ([Antcliffe et al., 2014](#)), but insufficient morphological information is currently available to resolve this debate. Another

potential metazoan is the possible cnidarian *Haootia quadriformis* ([Fig. 4B](#)), which is known from two localities in the St. John's Group of Newfoundland. *Haootia* possesses a quadrate body plan with dichotomously dividing branches, and a regular arrangement of fibrous bundles that have been compared to muscular tissues ([Liu et al., 2014a](#)). This interpretation would make *Haootia* the oldest body fossil known to exhibit impressions of musculature. Assignment of *Haootia* to the Cnidaria may also imply the presence of predatory organisms within Avalonian ecosystems ([Liu et al., 2014a](#)).

Within the shallow-marine (but beneath storm-wave-base) settings of the upper Fermeuse Formation in Newfoundland ([Gehling et al., 2000](#)), serially chambered, soft-bodied impressions variously assigned to *Palaeopascichnus*, *Neonereites*, and *Yelovichnus* can be locally abundant ([Fig. 4D](#); [Gehling et al., 2000](#)). Although these palaeopascichnids are unknown from the deeper water, older units, they are the only Ediacaran macrofossils observed to continue almost up to the Ediacaran–Cambrian boundary in this region ([Narbonne et al., 1987](#)). They are locally abundant in other global Ediacaran shallow-marine settings (e.g. [Haines, 2000](#); [Grazhdankin et al., 2009](#)). *Palaeopascichnus* has been suggested to be allied to an unidentified protistan group on the basis of developmental analysis ([Antcliffe et al., 2011](#)). Several major Ediacaran morphotypes, such as the dickinsoniomorphs and erniettomorphs (cf. [Laflamme et al., 2013](#)), are not currently known from Newfoundland or the U.K., but the discovery of a *Namalia* specimen at Sekwi Brook ([Narbonne et al., 2014](#)) may demonstrate that members of the erniettomorphs at least were present in deep-marine environments prior to their appearance in shallower-water localities.

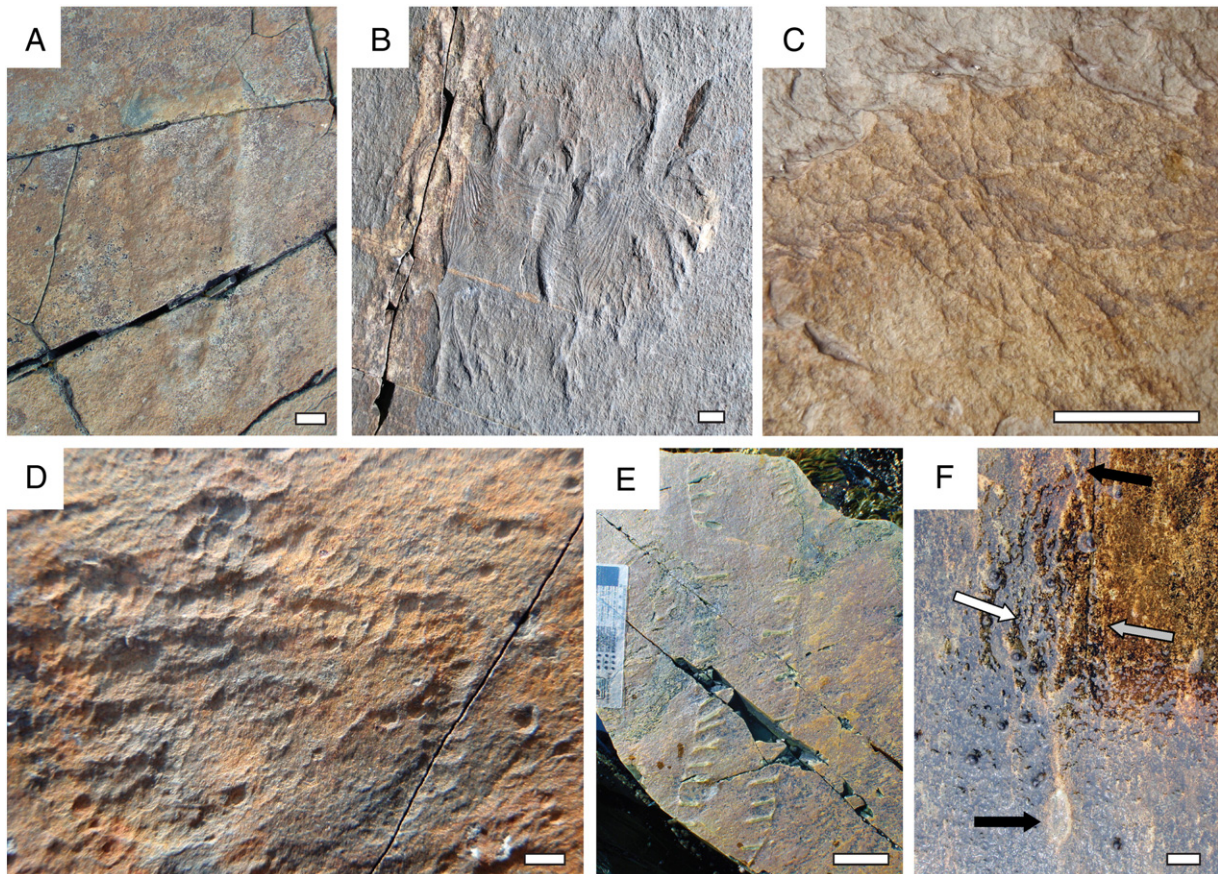


Fig. 4. Miscellaneous taxa from the late Ediacaran of Newfoundland. A: The purported sponge *Thectardis avalonensis* (cf. [Sperling et al., 2011](#)), MPER. B: *Haootia quadriformis* holotype, interpreted as a cnidarian ([Liu et al., 2014a](#)). C: Filamentous macrofossil impressions, Burnt Point, Bonavista Peninsula. D: *Palaeopascichnus delicatus*, a potential protist (cf. [Antcliffe et al., 2011](#)) from Ferryland. E: *Hadryniscala avalonica* holotype, Bonavista Peninsula. F: The basal portion of *Hadrynichorde catalinensis*, Bonavista Peninsula, showing what has been interpreted to be the attachment between a string (upper black arrow) and a holdfast disc (lower black arrow). However, it could be argued that the holdfast actually leads to an effaced frond (white arrow), and that the string instead continues as a discrete structure to the right (grey arrow). The position of the specimen in the tidal zone makes it difficult to distinguish between these possibilities at present. Scale bars = 10 mm except D = 20 mm, and E = 50 mm.

Irregularly-arranged lobate forms previously assigned to the genera *Ivesheadia*, *Blackbrookia*, *Pseudovendia* and *Shepshedia* have been synonymised within the Ivesheadiomorphs (Fig. 5E; Liu et al., 2011). Ivesheadiomorphs are considered to represent the effaced remnants (taphomorphs) of dead and decaying soft-bodied organisms on the seafloor (Liu et al., 2011). Since many frondose Ediacaran forms are thought to have been epi-benthic and tethered by their holdfast structures within the substrate (e.g. Seilacher, 1992; Narbonne and Gehling, 2003), it is reasonable to assume that they would have remained where they fell upon death (cf. Liu et al., 2011). The absence of vertical bioturbation in the ~565 Ma Ediacaran successions of Avalonia, combined with a paucity of evidence for macroscopic scavenging, detritivory, and predation in the Ediacaran Period in general (see Liu et al., 2011 and references therein), is an important taphonomic consideration. Without extended

heterotrophic food chains, autolysis and microbial degradation would have been major necrotic processes associated with the decay and removal of Ediacaran soft-bodied organisms (Liu et al., 2011). Heterotrophic microbes at and close to the sediment–water interface are likely to have mediated decomposition, utilising osmotrophic and/or saprophytic methods of feeding (Brasier et al., 2010). In such a scenario, decay processes may have taken considerably longer than is observed in modern marine environments (as supported by experimental data; Liu, 2011b unpublished thesis, University of Oxford), implying that organic matter in the form of dead organisms could have been a common phenomenon at the Ediacaran sediment–water interface, and that impressions of these deceased organisms would have been preservable.

Alternative interpretations view Ivesheadiomorphs as either discrete microbial colonies (Laflamme et al., 2011a), or as loading structures

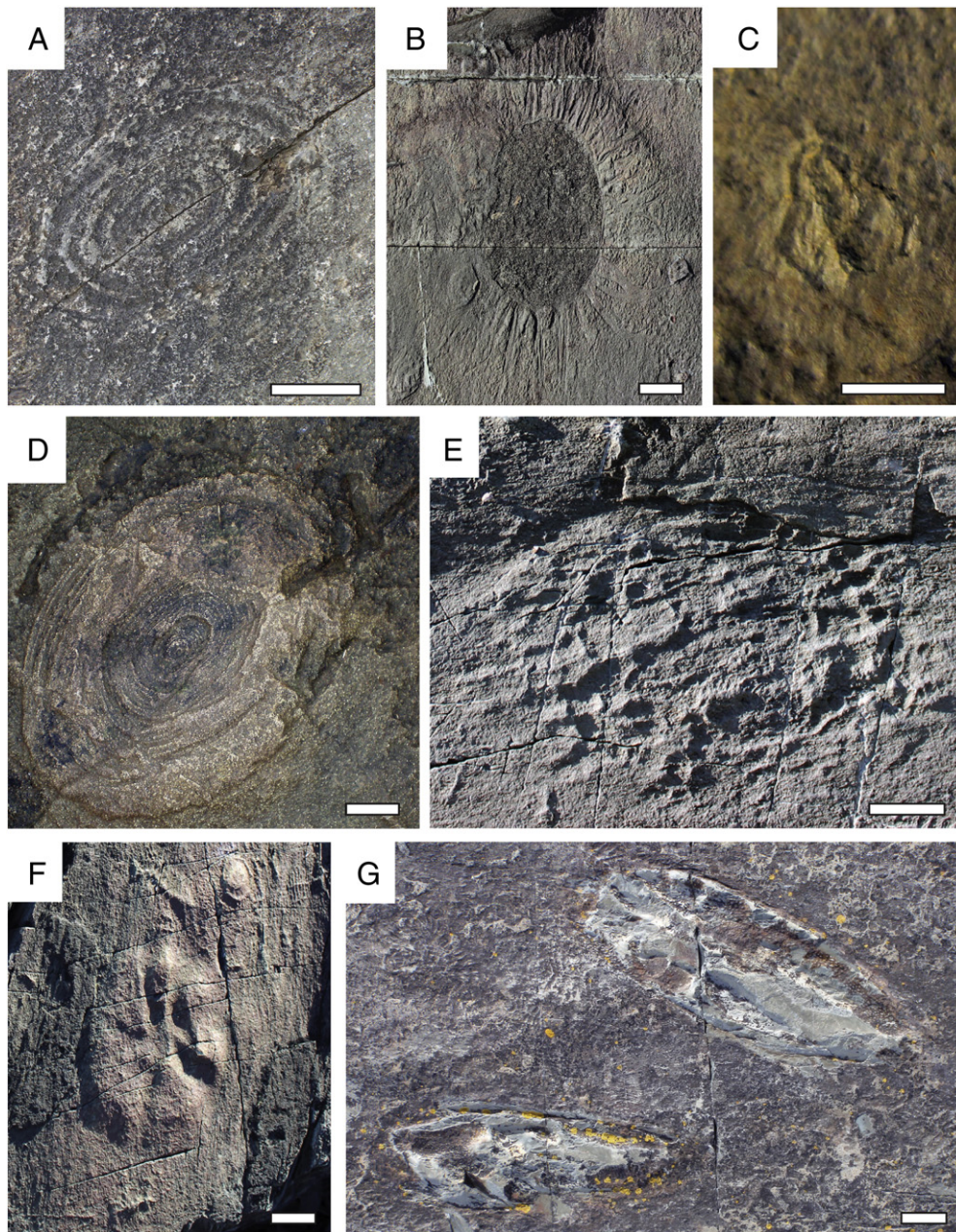


Fig. 5. Discoidal taxa from Avalonia. A: *Aspideella terranovica*, Bonavista Peninsula, NL. B: *Hiemalora stellaris*, Bonavista Peninsula, NL. C: *Triforillonia costellae*, Ferryland, NL. Image courtesy of L. Menon. D: *Cyclomedusa davidii*, Charmwood Forest, U.K. E: Ivesheadiomorph, MPER, NL. F: Lobate disc, MPER, NL. G: 'Blackbrookia', Bonavista Peninsula, NL. Scale bars = 10 mm, except A and E–G = 50 mm, and C = 5 mm.

related to the burial and decay of organisms in overlying sediment (Wilby et al., 2011). One of the strongest unresolved arguments against the taphomorph hypothesis is the difference in maximum size between the largest rangeomorphs published to date (which can reach lengths of over 1 m but are not known to have comparable widths, e.g. *Trepassey wardae*), and the largest ivesheadiomorphs (0.8 m diameter; Laflamme et al., 2011a). However, recent discoveries by one of us (AGL) have revealed well-preserved *Bradgatia* specimens of up to 0.8 m in diameter on the Bonavista Peninsula. When combined with comparably-sized multifoliate and unifoliate fronds in Charnwood Forest (Wilby et al., 2011), these specimens effectively remove this line of argument. On the basis of all available evidence (see also Liu et al., 2012), we consider the taphomorph hypothesis to remain the most parsimonious explanation for these structures. The possibility remains that not all impressions currently synonymised within the ivesheadiomorphs are taphomorphs. For example, “lobate discs” (Fig. 5F, cf. Clapham et al., 2003) and specimens assigned to *Blackbrookia* sp. (Fig. 5G; Hofmann et al., 2008) both exhibit more consistent structure and symmetry when compared to other ivesheadiomorphs, and warrant further study (Kenchington and Wilby, 2014).

1.4.4. Discoidal forms

Some of the most abundant Avalonian impressions are discoidal structures, and these can exhibit a variety of morphologies. They can be found alongside complete specimens of other recognisable taxa, or as assemblages entirely composed of discs. In the U.K., solitary discs are locally abundant. Those with multiple concentric rings are typically assigned to *Cyclomedusa davidii* (Fig. 5D; Boynton, 2010), whereas simpler discs with few or no concentric rings are assigned to *Cyclomedusa cliffi* (Boynton, 2006). Both taxa are likely to include frond holdfasts (as evidenced by two *C. cliffi* specimens with attached stems; Boynton, 2006), but microbial colonies could also potentially explain several simple irregular and unornamented variants (cf. Grazhdankin and Gerdes, 2007).

In Newfoundland, solitary discs range from the Drook Formation through to the Renew Head Formation (Hofmann et al., 2008), and have largely been assigned to two genera—*Aspidella* and *Hiemalora*—on the basis of their gross morphological features (e.g. Fig. 5A–B; Gehling et al., 2000; Hofmann et al., 2008). *Hiemalora* discs are circular to ovate in outline, typically up to ~6 cm in diameter, and possess multiple thread-like ‘rays’ that radiate from the margins of a featureless or concentrically-ringed structure (Fig. 5B; Hofmann et al., 2008). These rays are occasionally seen to branch, and have been proposed to be anchoring structures (Dzik, 2003), though alternative explanations as fungal hyphae or reproductive stolons have also been discussed (Hofmann et al., 2008). Most Newfoundland specimens have been assigned to *Hiemalora stellaris* (e.g. Fig. 5B; Hofmann et al., 2008), although *Mawsonites pleiomorphus* has alternatively been proposed (Grazhdankin, 2014). Some specimens of the rangeomorph genus *Primocandelabrum* can be found with a *Hiemalora*-type disc at their base (Fig. 2K; Hofmann et al., 2008), implying that *Hiemalora* is best regarded as an ‘organ-taxon’ preserving only the holdfast structure of a rangeomorph frond (cf. Serezhnikova, 2007).

Solitary discs that lack rays or extensions have generally been assigned to *Aspidella terranovica* (Gehling et al., 2000). *A. terranovica* was originally described from the Fermeuse Formation of Newfoundland (Billings, 1872) as an invaginated impression, but the taxon as currently accepted exhibits a wide variety of internal morphologies (Gehling et al., 2000). There has been much discussion about its biogenicity (most recently summarised in Boyce and Reynolds, 2008, fig. 3). Although it is generally considered to represent the holdfast structures of a variety of rangeomorph and arboreomorph/frondomorph taxa (Gehling et al., 2000), we consider it likely that *Aspidella* reflects several very different original entities, including holdfast discs, microbial colonies (cf. Grazhdankin and Gerdes, 2007), and discrete organisms (cf. MacGabhann, 2007). The sheer

density of discoidal specimens on some Fermeuse Formation bedding planes (e.g. Conway Morris, 1989) is seemingly at odds with the much lower densities of holdfast-bearing organisms observed within frondose assemblages (e.g. Clapham et al., 2003). However, these apparent densities could be a taphonomic artefact of bedding planes in the Fermeuse Formation being considerably thinner than those in other units, permitting individual discoidal impressions to be expressed over multiple laminae (cf. Gehling et al., 2000; though see MacGabhann, 2007 p. 303).

The majority of solitary discs within the Drook to Trepassey Formations are negative epirelief concentric forms with low topographic relief. Such fossils likely record the collapse of partially buried holdfasts, either preserving a composite impression, or the lower surface only. The original shape of holdfasts is debated, with many authors reconstructing them as bulbous in morphology (e.g. Narbonne, 2004; Laflamme and Narbonne, 2008), an interpretation supported by 3-D moulds of holdfasts from Spaniard's Bay (e.g. Narbonne et al., 2009; Brasier et al., 2013a). In contrast, others interpret a more flattened, discoidal or oblate shape for the holdfast (e.g. Steiner and Reitner, 2001). Holdfast shape may alternatively be species-specific. Since it is only possible to speculate about the identity of the original taxon to which a solitary disc belonged in a handful of cases, the presence of solitary discs presents significant barriers to accurate interpretation of the true original taxonomic composition of Ediacaran marine communities, not just in Avalonia, but worldwide (cf. MacGabhann, 2007).

Additional simple discoidal pits and mounds occurring in shallow/marginal-marine environments, for example those from the Long Mynd of Shropshire (Salter, 1856; McIlroy et al., 2005; Callow et al., 2011), are largely considered to be of microbial or sedimentary origin (see discussion in Liu, 2011a), and record a distinct facies association of global distribution (e.g. Kumar and Pandey, 2009; Lan and Chen, 2012; Liu et al., 2013a).

1.4.4.1. Triradial forms. The tri-lobed discoidal impression *Triforillonia costellae* (Fig. 5C) from the Fermeuse Formation of Newfoundland is a rare and seemingly endemic form of unknown biological affinity (Gehling et al., 2000), and is not considered by us to be a holdfast structure. It has three rounded, often-uneven lobes, is rarely greater than 30 mm in diameter, and is preserved on bedding planes alongside abundant *Aspidella* specimens. Both Laflamme (in Erwin et al., 2011), and Grazhdankin (2014) consider it to be a member of the Triradialomorph/Tribrachiomorph clade, and thus distinct from other discoidal forms in Avalonia.

1.4.5. Filamentous microfossils and microbial fabrics

Microbial mats are widely considered to have been a common component of Ediacaran marine ecosystems. In the absence of bioturbation, they are inferred to have played an important role in microfossil preservation (Gehling, 1999), and to have sustained a variety of mat-related modes of life that may have been absent in many Phanerozoic settings (e.g. Seilacher, 1999). Microbial mat features are commonly observed as wrinkle fabrics, textured organic surfaces, or microbially-induced sedimentary structures (e.g. Hagadorn and Bottjer, 1997; Noffke et al., 2002; Dornbos et al., 2006; Gehling and Droser, 2009). Although it is unusual to see mat fabrics and fossils preserved together on the same bedding plane in Avalonia, this does not preclude their presence. There are certain surfaces (e.g. Pigeon Cove in Newfoundland; Liu et al., 2012, or Memorial Crags in Leicestershire; Johnson, 2013), where lumpy, pustular surface textures interpreted as biomat structures, sometimes in combination with distinct petrographical features that may represent the pyritised remains of organic matter (Brasier et al., 2013a), co-occur with microfossil taxa. Microbial fabrics are more common in Avalonian marginal-marine environments. Mats have recently been recognised to persist across the Ediacaran–Cambrian boundary into the early Cambrian strata of Newfoundland's Burin Peninsula, where there is evidence that they suffered from the impact of increasing bioturbation (Buatois

et al., 2014). Stromatolites and thrombolites, common in some late Ediacaran successions (e.g. Grotzinger et al., 2000; Shapiro, 2004; Warren et al., 2011), are absent from late Ediacaran Avalonian clastic marine successions.

Macroscopic filamentous and tubular impressions have also been identified at multiple late Ediacaran localities (e.g. Steiner and Reitner, 2001; Cohen et al., 2009; Sappenfield et al., 2011; Z. Chen et al., 2014). Given their occurrence in largely shallow-marine depositional environments, interpretations as photosynthetic cyanobacteria (e.g. Steiner and Reitner, 2001; Hou et al., 2004), worms (e.g. Jensen et al., 2007), or algae (Gnilovskaya, 1983; Cohen et al., 2009) have been proposed. Recent discoveries in Newfoundland reveal assemblages of filamentous impressions 200–600 µm in width and up to 40 cm in length, preserved as positive epirelief casts (Fig. 4C), which appear to have formed dense fabrics over the seafloor (Callow and Brasier, 2009a; Liu et al., 2012). Filaments can be closely associated with macrofossils and, importantly, their inferred deep-marine depositional environment renders a photosynthetic life habit unlikely, whilst their large size rules out fungal and most bacterial comparisons.

1.4.6. Microfossils

Microfossils are rare in the siliciclastic successions of Newfoundland and the UK. In Newfoundland, organic-walled microfossils are restricted to simple spheres and filaments from a handful of localities in the Drook, Mall Bay, Fermeuse, Renewes Head and Cappahayden Formations (Hofmann et al., 1979), but are apparently absent from the deeper-marine Mistaken Point and Trepassey Formations. Charnwood Forest yields even less evidence for microfossil preservation (Peat, 1994), despite promising early reports (Tymofeyev et al., 1980). Investigations in the marginal-marine deposits of the Long Mynd, Shropshire, have been more rewarding, yielding spheroidal and filamentous forms preserved in at least three taphonomic modes (Peat, 1984; Callow and Brasier, 2009b). The paucity of microfossils in the Avalon region, particularly given the presence of a diverse microfossil biota in pre- and early Ediacaran sediments (e.g. Porter and Knoll, 2000; Knoll et al., 2006; Butterfield, 2009a; Bosak et al., 2011a,b; Cohen et al., 2011; Bosak et al., 2012), could be explained taphonomically; the substrates that most commonly contain Precambrian microfossils (carbonates, phosphates, and organic-rich shales) are typically absent in Avalonian depositional environments. Organic-walled microfossils are also likely to have been lost or degraded during Cambrian metamorphic events (see Section 1.2). However, an ecological driver cannot be ruled out. Improvements in microfossil sampling and preparation techniques since the cited early studies offer hope for future investigation of Avalonian material.

1.4.7. The potential for new taxa

Significant efforts have been made to name and officially document the major taxa within Avalonian settings, but a substantial number of undescribed forms remain. These include figured specimens such as the “dumbbell” and “gladius” of Wilby et al. (2011, figs. 2D–E), as well as other forms presently assigned to *Primocandelabrum* sp. on that bedding plane (Wilby et al., 2011). There are also the “ostrich feather” from Mistaken Point (Narbonne et al., 2012a, pl. I.1R), and several unnamed forms from the Bonavista Peninsula. Other specimens we have documented elsewhere in Newfoundland display self-similar rangeomorph branching, but in arrangements and associations that suggest they are likely to be new species or genera. Formal documentation of these specimens is required to fully appreciate the composition, dynamics and evolutionary progression of Avalonian macrobiotic ecosystems. Until the taxonomy of these forms is resolved, even basic quantitative paleoecological metrics that depend on taxonomic identification, such as species richness, cannot be calculated with certainty on many surfaces.

1.5. Summary of the Avalonian biotic assemblage

Rangeomorphs dominate Avalonian deep-marine ecosystems both in terms of abundance and taxonomic diversity, but it is clear that non-rangeomorph taxa are more varied and disparate than is generally discussed. Furthermore, a frondose morphology is not an exclusively rangeomorph trait (cf. Laflamme et al., 2013), and the presence of frondose morphologies in multiple lineages likely represents evolutionary convergence. The Avalon region, containing the oldest known examples of the Ediacara-type soft-bodied biota, exhibits lower diversity at generic and higher levels than younger Ediacaran shallow-marine biotic assemblages worldwide (e.g. Flinders Ranges and White Sea), despite the communities occupying similar ranges of morphospace (e.g. B. Shen et al., 2008). Convincing algal fossils are not currently known from the Avalonian record, microfossils are rare and low in diversity, and taxa related to *Kimberella*, *Dickinsonia*, *Ernieetta* and bilaterian organisms are currently not represented. Certain impressions and taxa are likely to be ‘organ taxa’ (e.g. *Hiemalora*), whilst others may represent multiple biological entities (e.g. *Aspidella*). There is still taxonomic work to do, but our knowledge of the paleobiology of this region is becoming ever more refined.

This brief overview of the geology and paleontology of the Ediacaran Avalon Terrane facilitates thorough discussion of recent paleoecological studies and approaches. Appreciation of environmental conditions and the degree of taxonomic completeness is important to accurately undertake meaningful paleoecological analyses. Although it has been said before (e.g. Peterson et al., 2003; Laflamme et al., 2013), it is worth re-emphasising that due to the phylogenetic variety likely to have been present within Avalonian ecosystems, individual taxa must be treated on a case-by-case basis, and should not be shoe-horned into one all-encompassing clade. The following sections detail recent advances made in Avalonian paleoecological understanding. We begin by assessing current knowledge of the modes of life of Ediacaran macro-organisms: their growth, feeding strategies, ability to locomote, and the ecological structure of their communities (Section 2). We then discuss the application of quantitative techniques to Avalonian paleocommunities, examining the biological and ecological insights they can provide (Section 3).

2. Recent Insights in Avalonian paleoecology

Paleoecology encompasses the study of past organisms, communities and ecosystems, and their interactions with the environment. It therefore incorporates study of a broad spectrum of topics. In recent years, paleoecological studies investigating the global late Ediacaran–Cambrian transition have discussed modes of life and feeding methods of the organisms (e.g. Droser et al., 2006; Laflamme et al., 2009; Xiao and Laflamme, 2009; Sperling et al., 2011), reproductive strategies (Droser and Gehling, 2008; Darroch et al., 2013), models of ecological succession (Clapham et al., 2003; Clapham, 2011), community composition and ecological structure (Grazhdankin and Ivantsov, 1996; Bottjer and Clapham, 2006; Droser et al., 2006), ichnological activity (Mángano and Buatois, 2014), and potential relationships between the biota and ambient environmental conditions (e.g. Fedonkin, 2003; Butterfield, 2009b; Lenton et al., 2014). Here we review current understanding of Avalonian taxa with respect to these areas.

2.1. Reproduction and growth

The uncertainty surrounding Avalonian macrofossil phylogenetic affinities, coupled with an apparent lack of preserved reproductive structures, has led to the reproductive strategies and early ontogeny of these organisms being poorly understood. Most studies into growth and reproduction have focused on rangeomorphs. Juvenile specimens of rangeomorphs are relatively rare (Narbonne, 2004), but where they do occur, specimens just a few millimetres in length are identical in morphology to larger fronds (Liu et al., 2012, 2013b). This observation

implies that simple asexual budding from mature fronds, as has been proposed for *Avalofractus* (Narbonne et al., 2009), is an unlikely reproductive strategy. The global distribution of rangeomorphs has been interpreted as potential evidence for a free-swimming or planktonic life stage in these organisms (as discussed in Darroch et al., 2013), although, as those authors note, no clear evidence for such larval stages has yet been found. Juvenile forms of non-rangeomorph taxa are even scarcer, and little is known at present about their growth or reproductive strategies.

Darroch et al. (2013) assessed models of size frequency distribution (using Bayesian Information Criterion) on five bedding plane assemblages from the Mistaken Point Ecological Reserve in Newfoundland. They demonstrated that the populations of four selected taxa (*Pectinifrons*, *Fractofusus*, *Thectardis* and *Beothukis*) represent single cohorts, and the rangeomorphs in particular exhibit wide variance in size, and right-skewed size-frequency distributions. These continuous distributions were taken to imply that rangeomorph reproduction was aseasonal, continuous, and sexual (Darroch et al., 2013), although the possibility of seasonal reproduction combined with slow growth rates could not be refuted. In contrast, the presence of a diverse assemblage of juvenile taxa colonising a bedding plane in the Drook Formation (see Liu et al., 2012) has been used by others to suggest that reproduction may have been seasonal, and consequently that the sedimentary environments may not have been as deep as is widely stated (Grazhdankin, 2014). However, modern deep-sea ecosystems are not aseasonal, and the presence of an entirely juvenile community of rangeomorphs may alternatively indicate episodic reproduction.

Thectardis differs from the rangeomorphs in exhibiting a normal, rather than log-normal, size-frequency distribution (Darroch et al., 2013). This difference potentially lends validity to the suggestion by Sperling et al. (2011) that *Thectardis* was a sponge (Darroch et al., 2013). These findings, whilst interesting, assume that size in these organisms can reliably be related to age and growth (cf. Laflamme et al., 2004). Whereas size is a sensible indicator of age for most marine organisms (Speakman, 2005), it is important to bear in mind that this correlation has yet to be proven for Ediacaran species. Several extant organisms, such as cnidarian actinians, can substantially alter their overall shape if food supply is limited, or if they are subjected to environmental or physical stresses, offering alternative explanations for size variability.

In terms of ontogeny, Avalonian juvenile specimens can be compared with larger individuals of the same taxon to determine growth patterns and pathways, and to distinguish features that change with growth from reliable taxonomic characters (e.g. Laflamme et al., 2004). Studies of *Charnia masoni* argue that it both added new primary branches distally, and inflated these as it grew during life (Antcliffe and Brasier, 2007; Liu et al., 2012, 2013b). Similarly, *Fractofusus* appears to have grown by both addition and inflation of primary branches (Laflamme et al., 2009), with this combination of accretion and inflation mirrored by seemingly unrelated tubular body fossils later in the Ediacaran Period (e.g. *Wutubus*, Z. Chen et al., 2014). However, there is significant scope to expand such studies to consider other Avalonian taxa. It has been suggested that *Bradgatia* (Fig. 2C) may have changed its overall morphology during growth, progressing from an elongate 'I'-shape towards an 'O'-shaped gross morphology at maturity (Flude and Narbonne, 2008). An alternative explanation proposes that certain juvenile *Bradgatia* possess elongate morphologies not because of their age, but because they were aligned and streamlined by a particularly strong current prior to burial (Brasier et al., 2013a). Combining these hypotheses, we envisage that the presumably smaller volume of juvenile *Bradgatia* relative to 'bushier' mature forms may have preferentially facilitated current alignment. Suggestions that juvenile rangeomorphs might have been enclosed within a protective sheath (Narbonne et al., 2009) have been questioned by sedimentological analyses of bedding planes from Spaniard's Bay, with the perceived sheaths alternatively interpreted as abiogenic scour marks created by high-energy currents (Brasier et al., 2013a).

One Avalonian organism whose growth differs distinctly from that of the rangeomorphs is *Palaeopascichnus*, previously considered by some to be a possible xenophyophore (Seilacher et al., 2003). Its arcuate, gradually-expanding chambers exhibit surprising attributes, such as the ability for individual chains to merge, bifurcation of chambers upon reaching a critical size threshold, and occasional "chaotic" chambers that are interpreted to be a response to damage and repair (Antcliffe et al., 2011). This suite of attributes is not considered to be compatible with known protozoan or metazoan growth plans, and therefore it has been proposed that *Palaeopascichnus* was a eukaryote of unknown affinity (Antcliffe et al., 2011).

Going forward, studies of growth in multiple Ediacaran taxa would greatly inform our inferences regarding their phylogenetic affinities. Such studies are still in their infancy, but even application of existing techniques to the full suite of taxa currently described would significantly benefit our understanding of growth and development.

2.2. Feeding strategies

Discussion of feeding strategies in late Ediacaran organisms has largely relied upon observations gleaned from the morphology of body fossils. Unlike in the Flinders Ranges and the White Sea, where features interpreted as grazing traces have been taken to suggest active feeding on microbial mats in shallow-marine environments (e.g. *Radulichnus* and *Epibaion*; Seilacher, 1999; Ivantsov, 2010, 2011, 2013; though see McIlroy et al., 2009), Avalonian assemblages are yet to yield ichnological evidence for feeding behaviour.

For many Avalonian taxa, feeding strategies have not been discussed in great detail. Interpretation of *Thectardis* as a sponge implies that it may have predominantly been a filter feeder, though extraction of DOC from the water column was also considered (cf. Sperling et al., 2011). Recent discoveries suggesting the presence of possible cnidarian-grade organisms in Avalonian benthic ecosystems, either indirectly through locomotion traces (Liu et al., 2010a; Menon et al., 2013) or directly as body fossils (Van Iten et al., 2013; Liu et al., 2014a), may imply the presence of macroscopic predators. Such feeding strategies would be of great ecological and evolutionary significance.

Early descriptions of rangeomorphs as possible sea pens (Glaessner, 1984) saw them widely interpreted as filter feeders, a hypothesis apparently supported (though not exclusively) by the tiered structure of their communities (Clapham and Narbonne, 2002). However, rangeomorph fossils lack evidence for pores (where particles could be ingested by the organisms), or for zooids or polyps, even in specimens with morphological features observable at resolutions of 0.1 mm. Such structures are required by many modern metazoan filter feeders to extract food particles from the water column macrophagously (cf. Narbonne, 2004; Laflamme and Narbonne, 2008), casting doubt on the interpretation that rangeomorphs fed in this manner. However, sub-millimetric structures interpreted as zooids in the Cambrian frondose organism *Thaumaptilon* (Conway Morris, 1993) demonstrate that zooids could feasibly have been of a finer scale than is preserved in available Ediacaran specimens. Furthermore, feeding sites such as the foramen in foraminifera can be as small as 2 µm in diameter (Be et al., 1980), two orders of magnitude finer than structures observable on even the best preserved Ediacaran microfossils found to date. In contrast, discussion of the arboreomorph/frondomorph *Charniodiscus* has often noted its similarity to *Thaumaptilon*, leading to the suggestion that *Charniodiscus* may have been a filter feeder (e.g. Laflamme et al., 2004; Laflamme and Narbonne, 2008). Again, evidence for clear zooids or polyps is currently lacking, but the much lower surface areas of *Charniodiscus* species compared to contemporaneous rangeomorphs may indicate different methods of feeding.

In the absence of morphological evidence for filter feeding structures or pores, osmotrophy—the absorption of dissolved organic carbon through an outer membrane—has been proposed as the primary mechanism of nutrition for rangeomorphs (Laflamme et al., 2009). An

osmotrophic feeding strategy is also consistent with the high surface area to volume (SA/V) ratios of many rangeomorph taxa. There are, however, a number of unresolved questions surrounding this hypothesis, based on morphological, biological and geochemical grounds. Although the following points often use rangeomorphs as a case study, they are also applicable to other late Ediacaran deep-marine taxa.

2.2.1. Osmotrophy and organic carbon in the Ediacaran ocean

Rangeomorphs seemingly do not always make use of their maximum surface area. Interpretation of several taxa as reclining on the seafloor (e.g. *Fractofusus*) would suggest they held as much as half of their surface area in close or even direct contact with the substrate. Also, several rangeomorph taxa possess furled and/or undisplayed branches (where distal branch margins are tucked against neighbouring branches; cf. *Brasier et al., 2012*), which would appear to reduce the surface area of the branches in contact with the water column. Both of these features would appear paradoxical in osmotrophic organisms that should benefit from maximal exposure of their surface area to the water column, the purported source of their nutrition. If the recumbent organisms were instead extracting nutrients from the sediment or a microbial mat, a lack of evidence for locomotion in such forms makes it difficult to explain how they might continue to access such nutrients over the course of their lifespan without exhausting their supply.

It is also worth exploring whether Ediacaran fronds would have been physically capable of utilising osmotrophy as a feeding strategy. To investigate this, *Laflamme et al. (2009)* compared characters in modern osmotrophic organisms with those observed in Ediacaran fossils. In order for SA/V ratios of modelled Ediacaran organisms (*Pteridinium* and *Fractofusus*) to be consistent with those of extant osmotrophic bacteria, their metabolically active layer cannot exceed 0.01 mm in thickness; the remainder of the organism must be filled with metabolically inert material such as sediment or fluid (*Laflamme et al., 2009*). For the erniettomorph *Pteridinium*, this equates to around 98.72% of its volume. Such a value is a greater proportion of inert material even than is found in extant *Thiomargarita* (98.41% for a 750 µm diameter cell with a 2 µm thick wall; values from *Schulz and Jorgensen, 2001*). Although there is evidence for some degree of 'hollowness' in certain Ediacaran organisms (*Narbonne et al., 1997; Laflamme et al., 2009; Vickers-Rich et al., 2013*), the extent required for SA/V ratios to be consistent with those modelled for modern osmotrophs seems unlikely on a number of grounds. First, unless the cell membrane or wall is composed of extremely tough material, it might be expected that a far greater proportion of punctured, wrinkled or otherwise distorted fossil specimens (cf. *Meyer et al., 2014a*) would be observed if their metabolically-active layer was as thin as is proposed by modelling. A tough integument, however, would presumably have hindered absorption of DOC. Secondly, the alternative possibility that the rangeomorph branches were open to the water column at one end—in the manner of an open pipe (raised by *Laflamme et al., 2009*)—would predict preservation of some specimens with sediment infilling the distal (open) ends of the branches; such specimens are not currently known. Although the *Laflamme et al.* modelled SA/V values are considered by some workers to be very conservative (e.g. *Sperling et al., 2011*), they raise questions about whether the nutritional requirements of rangeomorphs could have been met by osmotrophy alone.

A variety of options exist for the use of osmotrophy in combination with other feeding strategies. Extant organisms as disparate as sea urchin larvae (*Shilling and Manahan, 1990*), dinoflagellates (*Glibert and Legrand, 2006*) and algae (e.g. *Vincent and Goldman, 1980; Gervais, 1997*) have been shown to be capable of osmotrophy, but most of these organisms use it facultatively to supplement photosynthesis (*Glibert and Legrand, 2006*) or endocytosis (*Stephens, 1988*; often to provide a source of nitrogen), or as a means of subsisting through unfavourable conditions. Whilst photosynthesis can be dismissed by the deep-water setting of the Avalonian biota, endocytosis remains a viable option.

Another consideration is whether DOC concentrations in the Ediacaran oceans would have been high enough to support dense osmotrophic communities. At present, DOC in the deep oceans (> 900 m) can reach concentrations of up to 48.1 µM, but is more typically around 40 µM (*Hansell and Carlson, 1998; Benner, 2002; Hansell et al., 2009*), even in oxygen minimum zones (*Benner, 2002*). It has been suggested on the basis of carbon isotopic data that late Ediacaran DOC concentrations were 2–3 orders of magnitude higher than in modern oceans (*Rothman et al., 2003*), suggesting that DOC concentrations may have been adequate to support large osmotrophic communities. However, as has been noted by *Bristow and Kennedy (2008)*, aside from the carbon isotopic data there is no independent geological evidence for such high DOC concentrations. The contour currents widely considered to have been present in many Avalonian settings may also have brought enriched concentrations of nutrients to the benthic communities. Modern examples such as Antarctic circumpolar current support high density biotic communities (e.g. *Gili et al., 2006*), but the organisms present are largely suspension feeding organisms. Whether such contour currents could increase DOC locally is questionable, since although the overall flux of organic matter entering the community would increase, the currents would also arguably remove it at a similar rate. Contour currents would therefore have served to refresh the organic matter pool, but may not have appreciably increased local carbon concentrations.

Just as important for proposed osmotrophy is the utility of available organic matter (OM) for metabolism by either microbes or higher organisms, which is dependent on whether the organic compounds are labile, or recalcitrant (e.g. *Westrich and Berner, 1984; Kristensen, 2000*). Below a few hundred metres in depth, modern ocean DOC is dominated by refractory and semi-labile components (*Hansell and Carlson, 1998*), which are difficult to exploit (*Barber, 1968*). Around 15% of modern DOC comprises dissolved carbohydrates (*Benner, 2002*), whereas only about 1% comprises labile OM such as glucose, amino acids and other compounds that can be taken up by osmotrophs (*Stephens, 1988*). Unless labile carbon existed in abundance in the deep oceans, osmotrophs in the Ediacaran Period would presumably have had to produce their own labile compounds. In the modern oceans, labile material may be sourced from enzymatic breakdown of larger compounds by aerobic micro-organisms, protozoans, and/or marine fungi (cf. *Gooday et al., 1990; Hyde et al., 1998*). In contrast, anaerobic microbes are typically reliant on other organisms oxidising large compounds to create labile material (*Kristensen, 2000*). Heterotrophic bacteria and marine fungi degrade recalcitrant OM by excreting enzymes and absorbing the digestion products (*Hyde et al., 1998; Schulz and Jorgensen, 2001*). The return gained from these digestion products, at least in bacteria, only exceeds the metabolic expenditure on enzymes within a limited radial distance from the cell. This distance is a function of OM concentration, and typically does not exceed 10 µm for heterotrophic bacteria (*Schulz and Jorgensen, 2001*). Consequently, smaller cell sizes are favoured at lower OM concentrations, since the cells have a greater effective foraging distance proportional to their size (*Schulz and Jorgensen, 2001*). Given these considerations, it seems unlikely that osmotrophic organisms obtaining their labile monomers via exo-enzymatic breakdown of recalcitrant matter would have thrived in environments affected by persistent currents (contour or turbidite), as was the case in Avalonian settings (cf. *Wood et al., 2003*). Such currents would have continually refreshed the water surrounding the organism, potentially removing any enzymes produced. We therefore consider that Avalonian macro-organisms would not have been able to break down recalcitrant organic matter exo-enzymatically in these environments, and suggest they would have required that a sufficient source of labile DOC already existed in the water column if they were indeed osmotrophs.

Sperling et al. (2011) proposed an elegant model by which labile organic carbon could be transferred to the Ediacaran deep ocean. They postulate that DOC aggregates, termed marine snow, would have sunk more slowly in the Proterozoic than in the Phanerozoic due to their smaller particle size (arising from the dominance of bacterially-

sourced DOC, and the absence of biomineralizing organisms such as diatoms and coccoliths to add ballast). The organic aggregates have accordingly been suggested to have had longer time to be broken down into labile DOC in the water column via bacterial/viral lysis and solubilisation (Sperling et al., 2011). However, as these authors note, over half of modern DOC, particularly the most labile fraction, is produced by zooplankton, whose presence in the Neoproterozoic oceans is yet to be confirmed (cf. Butterfield, 1997). Additionally, this proposed mechanism does not account for bacterial utilisation of labile DOC during its journey through the water column, nor for the fact that bacteria are likely to have been the dominant marine osmotrophs at this time (outcompeting eukaryotes as in modern environments, due to their greater surface area; Wright and Hobbie, 1966; Kamjunke et al., 2008). Thus, it is unclear whether any labile DOC created during slow sinking of particulate matter would actually reach the depths at which Avalonian Ediacaran taxa lived. On the basis of this discussion, the questions of whether there was sufficient carbon to support large osmotrophs, whether it was in a suitable form for utilisation, and whether the morphology of the organisms was suited to effective osmotrophy, remain to be answered.

Finally, recent fluid dynamic modelling of rangeomorph communities has been taken to support osmotrophy as the primary rangeomorph metabolic pathway (Ghisalberti et al., 2014). Those authors propose that interaction between bottom-currents and the tiered frondose communities created a velocity profile in the water column, with taller organisms perceived to have access to flows of higher velocity, permitting faster rates of nutrient uptake. This flow profile is suggested to have been a major driver for the development of ecological tiering in rangeomorph communities (Ghisalberti et al., 2014, fig. S3). Mixing in the vicinity of the fronds (both rangeomorphs and arboreomorph/frondomorphs) is considered to have been supplemented by morphologically-driven oscillations in certain organisms (Singer et al., 2012). There is, however, no requirement in the model for the substance taken up from the water column to be DOC. Indeed, given our discussion of the effect of currents on sites of enzymatic DOC break-down, higher velocities may have been counter-productive for osmotrophs. Therefore, whilst the modelled canopy flows may have been a contributory factor in structuring frondose communities in terms of their height above the sediment-water interface and how they interacted with one another, they do not provide conclusive evidence for osmotrophy.

On the basis of the discussions in this section, we suggest that it would be premature to uncritically accept osmotrophy as the most likely feeding method used by rangeomorphs. The arguments for osmotrophic feeding in the rangeomorphs focus on their high SA/V ratios, fluid dynamic arguments, and a lack of evidence for pores or filter feeding apparatus (cf. Laflamme et al., 2009; Ghisalberti et al., 2014). Biological arguments against obligate osmotrophic feeding habits include the paradox of furled frond architectures, recumbent forms, implausibly thin metabolically active zones (in modelled organisms), and a paucity of modern obligate osmotrophic marine macro-organisms. Further questions are introduced by the observation that pores in modern filter feeders can be smaller than could possibly be observed in existing Ediacaran specimens, by uncertainties surrounding the concentrations and utility of DOC at that time, and by the fact that fluid dynamic models do not unequivocally exclude alternative feeding strategies. For these reasons, we regard it as unlikely that rangeomorphs met their metabolic requirements exclusively by osmotrophic feeding. It may be time to reconsider alternative feeding strategies, such as chemoautotrophy, symbiosis, or filter feeding (Jenkins and Gehling, 1978; Glaessner, 1984; McMenamin, 1998), perhaps by phagotrophy or pinocytosis. However, several of these alternative feeding modes face similar challenges to osmotrophy in that nutrients need to be absorbed across the body surface. Detailed consideration of the physical and biological challenges faced by each of these feeding strategies is required if we are to determine the feeding methods of Avalonian taxa.

2.2.2. Alternative food sources

Assuming that the majority of Ediacaran organic matter was sourced from shallower depths, once carbon reached the deep ocean, it could be recycled locally by microbial activity (though in the absence of bioturbating organisms, it may have remained at the sediment-water interface as a nutrient resource for a considerable length of time). However, the late Ediacaran witnessed the first appearance of a novel source of organic material in marine benthic settings—Ediacaran macro-organisms themselves. Prior to their appearance, marine snow and microbial mats would have been the major sources of organic matter at mid- to deep ocean depths. When buried beneath event beds such as tuffs, communities of Ediacaran macro-organisms would have been broken down by microbes and decayed, with carbon recycled through the microbial communities, or trapped in the sediment and subsequently lost during burial. However, if individuals died between sedimentation events and their remains persisted on the seafloor for long periods (weeks to months as hypothesised by Liu et al., 2011), they would have decayed gradually via microbial and autolytic processes in direct contact with the water column. The amount of material released into the water column may not have been particularly large—binding of organic matter by growth of microbial mats, and the requirements of the microbial communities themselves, may have diminished the release of DOC. Consequently, whilst carcasses may have created ‘hotspots’ of localised microbial growth, they are unlikely to have released sufficient nutrients to sustain large communities of living osmotrophic macrobiota. Although microbial mats would also have constituted a prominent source of organic matter on the seafloor, much of this would have been confined within the microbial loop (Butterfield, 1997), and therefore would remain unavailable for use by macro-organisms. ‘Sloppy’ (incomplete) feeding by modern copepods and zooplankton when digesting large phytodetritus particles is one pathway by which DOC levels can be raised in experimental systems (Møller and Nielsen, 2001), but the presence of such organisms is yet to be demonstrated in Ediacaran communities. Whilst we are not suggesting that putrefying material played a significant role in sustaining Avalonian macro-organisms or microbial communities, we propose that the presence of large concentrations of organic matter on the Ediacaran seafloor may have supplemented local DOC levels in the deep oceans, and potentially impacted global carbon cycling. Eventually, the evolution of motile metazoans with the ability to locate food sources would have led to wider exploitation of macro-organism carcasses as a food source. Investigation of spatial associations, hinted at in the paleoecological studies of Clapham et al. (2003), could be used to test and constrain ecological models relating to hypotheses regarding decomposing matter as a source of nutrition.

2.3. Aspects of community structure

Considerable efforts have been made to understand Ediacaran macrobiotic communities via comparisons with modern ecosystems. Studies have assessed species richness and diversity indices, as well as physical aspects of the communities such as population size distributions and tiering. In addition to augmenting our knowledge of Ediacaran ecological structure, these methods may provide an alternative approach by which to constrain the biological affinities of Ediacaran macro-organisms.

Communities from Mistaken Point exhibit a range of population structures (Clapham et al., 2003), varying between “frond-poor” (typically dominated by species inferred to have reclined on the seafloor, for example *Fractofusus*) such as the ‘D’ Surface at Mistaken Point, and “frond-rich” (typically dominated by species, both rangeomorph and arboreomorph/frondomorph, interpreted to have been upright in the water column such as *Charniodiscus* or *Charnia*), as on the ‘E’ Surface and Lower Mistaken Point (Q- and R-mode cluster analysis; Clapham et al., 2003). Bray–Curtis similarity analysis has further shown that variability in community composition is significantly lower within

individual surfaces (e.g. three different outcrops of the 'E' Surface) than between surfaces (Clapham et al., 2003). Analysis of thin sections through the studied bedding planes revealed no variability in sedimentological texture or composition (Clapham et al., 2003), whilst a purely taphonomic explanation for observed community composition can be refuted by principal components analysis (PCA), detrended correspondence analysis (DCA), and non-metric multidimensional scaling (NMDS) ordinations (Clapham et al., 2003). Furthermore, evolutionary effects are considered to have had only a small impact on community structure, since a broad but weak correlation with stratigraphic position has been determined (Clapham et al., 2003; Clapham, 2011). Observed differences in community composition were thus interpreted to result from ecological and environmental variability (Clapham et al., 2003; Clapham, 2011), with variability between bedding plane communities taken to reflect different stages along an ecological succession; frond-poor communities such as the 'D' Surface are interpreted as early succession communities, diverse communities with both fronds and low-lying species (e.g. the 'E' Surface) considered as mid-succession stages, and the frond-rich assemblages represent late stage/climax communities (e.g. Lower Mistaken Point; Clapham et al., 2003).

The successional change from low-lying species to upright frondose species is coupled with the development of a tiered ecosystem structure, whereby different taxa occupy different levels of vertical space in the water column (Clapham and Narbonne, 2002). The formation of tiered communities is considered to have been facilitated by the development of a distinct stem (Laflamme et al., 2012). The advent of tiering may have permitted the Ediacaran macrobiota to compete to exploit resources within higher levels of the water column (Xiao and Laflamme, 2009), driving associated canopy flows (cf. Ghisalberti et al., 2014). Experimental work subjecting replica fronds to flow regimes in a flume tank suggests that some frondose morphological features may have evolved to minimise drag, and to capture and channel fluids across the frond surface (Singer et al., 2012). In *Charniodiscus procerus* (Fig. 3C), the asymmetry of the frond (with respect to the stem) has been hypothesised to be an adaptation designed to improve mixing of water in the vicinity of the frond, an activity that has been suggested to support osmotrophy over filter-feeding (Singer et al., 2012). However, those authors suggested that this may alternatively reflect either an adaptation to remove waste products, or a respiratory function.

In contrast to the vertical tiering, evidence for lateral competition is limited, with only 2 out of 32 possible pairs of taxa at Mistaken Point showing signs of spatial segregation, and only two taxa showing intraspecific spatial segregation (Clapham et al., 2003). Comparison of Mistaken Point communities with modern deep-sea benthic slope metazoan communities found that they exhibited similar levels of ecosystem complexity (in terms of species richness, abundance, diversity values and spatial patterns; Clapham et al., 2003). This observation needs to be interpreted with caution, since other influences may alternatively be responsible for the observed similarities (see Section 3.2).

Appreciation of time averaging within the communities provides additional insights, since it permits the recognition of secondary community succession on certain bedding planes (i.e. the recolonization of the substrate following the apparent demise of a previous community; Liu et al., 2012, 2013b), and the impact of taphomorphs on observed community structure. On the majority of studied Mistaken Point bedding planes, distinct Ivesheadiomorphs (interpreted as fully-effaced taphomorphs; cf. Liu et al., 2011) form a relatively small proportion of the community, varying between 0.34% at Bristy Cove to 7.8% at Shingle Head, whereas Pigeon Cove exhibits a notably high proportion of 33.33% (Clapham, 2011). Additionally, many specimens show partial effacement, where the original organism is still identifiable (Liu et al., 2011). The differential influence of partially- as opposed to fully-effaced specimens on paleoecological studies may be substantial. Taphomorphs had the potential to impact their community twice—when living, and when dead. If all impressions we see on bedding surfaces are interpreted to record the life positions of organisms, the preserved spatial distributions

should reflect reasonably well the spatial relationships of the community. The interactions between an organism and its community take time to manifest, and so the length of time that has passed since an individual's death will control whether the observed relationships reflect the impact of the individual on the community over its lifetime, or its impact following death. Fully-effaced taphomorphs may have had a dominantly decay-related influence on the community (potentially as a nutrient source), whilst partially-effaced taphomorphs may be viewed as having had negligible post-mortem effect. Whilst this time lag enables us to more confidently interpret spatial information in cases where the organism has not been dead for very long (i.e. for partially-effaced specimens), additional caution is required when considering other aspects of community paleoecology such as standing biomass.

2.4. Evidence for locomotion

Trace fossils provide an independent line of evidence for metazoans in Ediacaran ecosystems, and have been reported from a variety of facies and locations across the globe. It is now widely accepted that horizontal surface locomotion traces are present amongst Ediacaran fossil assemblages of ≤ 555 Ma (e.g. Crimes and Germs, 1982; Seilacher et al., 2005; Jensen et al., 2006; Carbone and Narbonne, 2014). These examples are augmented by claims of limited vertical movement (Chen et al., 2013; Meyer et al., 2014b), and potentially even full bioturbation (Rogov et al., 2012; though see Brasier et al., 2013b; Gámez Vintaned and Zhuravlev, 2013).

Evidence for locomotion in Avalonian marine settings was historically restricted to the Cambrian boundary sections of Newfoundland's Burin Peninsula (Crimes and Anderson, 1985), and the Swithland Slates of Leicestershire (e.g. Bland and Goldring, 1995). The discovery of horizontal surface traces within the Mistaken Point Formation at ~ 565 Ma (Liu et al., 2010a) extended the ichnological record in Newfoundland by ~ 20 million years. The Mistaken Point assemblage yields almost 90 individual impressions assignable to at least two ichnotaxa, showing similarities to *Helminthoidichnites* and *Archaeonassa* (Liu et al., 2014b). The *Archaeonassa*-like variants comprise concave-forward hemispherical sediment lobes, a terminal discoidal impression, and marginal ridges interpreted to record lateral sediment displacement (Liu et al., 2010a). These characters are consistent with movement over the sediment surface by muscular metazoans locomoting in a similar way to modern actinian cnidarians (Liu et al., 2010a). Meanwhile, the *Helminthoidichnites*-like morphotypes are simple surface grooves ≤ 4 mm in width, with lateral ridges of sediment (Liu et al., 2014b). Further surface traces have since been found in the younger, shallower, Fermeuse Formation (e.g. Menon et al., 2013; Liu and McIlroy, 2015), with some demonstrated to be associated with the type-morph of *Aspidella terranovica* (Menon et al., 2013). Importantly, several impressions within the Fermeuse Formation appear to truncate sedimentary laminae in vertical section, and have thus been interpreted as vertical equilibration traces formed by organisms shuffling upwards through the sediment in response to small sedimentary influxes (Menon et al., 2013), a suggestion not too dissimilar to that made by MacGabhann (2007, p. 303). Although we do not currently know the identities of the trace makers, these traces suggest that motile, probably muscular organisms were present within late Ediacaran Avalonian marine ecosystems.

It must be emphasised that there is currently no evidence that known Ediacaran organisms other than those responsible for the type (invaginated) morph of *A. terranovica* (Menon et al., 2013) were capable of active movement. Rangeomorphs, arboreomorph/frondomorphs, and the majority of the miscellaneous taxa abundant on these bedding planes are still interpreted as sessile and immotile. Furthermore, evidence for locomotion in other Avalonian Ediacaran localities (Fig. 1B) remains scarce, with a handful of surface impressions from Carmarthen-shire (Cope and Bevins, 1993), and possible circular depressions from the Long Mynd (McIlroy et al., 2005), being the only other plausible

examples (Liu and McIlroy, 2015). Movement remains one of the key lines of evidence for the presence of metazoans in the Neoproterozoic, and late Ediacaran ichnology is a rapidly expanding field (reviewed in Liu and McIlroy, 2015). Evidence for additional interactions between taxa would be valuable in determining levels of ecological complexity within these ecosystems.

2.5. Geographic distribution of taxa and endemism

Variations in the biological composition of the Avalon, White Sea, and Nama assemblages have been discussed in detail by several authors (e.g. Waggoner, 2003; Gehling and Droser, 2013; Laflamme et al., 2013). In Avalonia, variation in taxonomic composition between the ‘eastern Avalonia’ sites of Charnwood Forest, and the ‘western Avalonia’ Newfoundland localities, was recently reduced by the discovery of hundreds of new fossils in Charnwood Forest (Wilby et al., 2011). Now, as many as 60% of macrofossil taxa are known to be common to both regions (Wilby et al., 2011), but 40% are not. This apparent difference is not considered to be due to differences in the age of the sites, since radiometric U–Pb dating of both successions suggests they were deposited broadly contemporaneously (Benus, 1988; Noble et al., in press). Notable absentees from Charnwood include prostrate or reclining forms such as *Fractofusus* (often the dominant taxon on Newfoundland bedding planes) and *Pectinifrons*, both of which lack holdfast discs (Wilby et al., 2011). Possible reasons for the apparent differences may include variation in nutrient availability, physical environment, depositional regime, or microbial mat communities (Wilby et al., 2011). When considering these differences, it is important to note the discrepancy between the number of bedding planes available for study in these regions: Newfoundland possesses over 200 individual fossil-bearing surfaces whereas, even with recent discoveries of new sites (Bowers, 2013; Johnson, 2013), the number of Charnwood sites remains below 30. However, in both localities, only a handful of fossil-bearing bedding planes have an areal extent greater than a few square metres, hindering a full evaluation of taxonomic diversity in many cases. With such a sampling bias, and taking into account intra-bed variation in community composition (e.g. Clapham et al., 2003; Wilby et al., 2011), we should be wary of interpreting the apparent absence of taxa in Charnwood as a real geographic distinction. Indeed, the casting study detailed in Wilby et al. (2011) revealed nine taxa new to the Charnwood assemblage from just one bedding plane.

2.6. Paleocological synthesis

The recent studies into Ediacaran fossil assemblages discussed here-in (e.g. Fig. 6) are enhancing our understanding of late Neoproterozoic ecology and evolution. They reveal environments where diverse biological components combined to create strong, thriving ecosystems whose like persisted for around 20 million years. Studies into growth, reproduction, locomotion and feeding strategies are progressively improving our knowledge of the biology of some Ediacaran organisms, but non-rangeomorph taxa are yet to receive anywhere near as much attention, and significant questions remain to be addressed. For example, how reliable are these insights, are the paleocological metrics being measured and assessed appropriate for Ediacaran assemblages, and are existing interpretations and attendant inferences robust? The following section discusses the methodology that underpins quantitative paleocological studies, and reflects upon some of the previous conclusions such studies have reached.

3. Considerations when assessing Avalonian paleoecology

The exceptional preservation of in situ ecosystems observed in Avalonia is rare in the wider fossil record, and offers the opportunity to employ a host of modern quantitative ecological techniques on fossil assemblages. Many factors, both original and secondary, can influence



Fig. 6. A view of the ‘E’ Surface (Queens, cf. Clapham et al., 2003) bedding plane, Mistaken Point, showing the well-preserved, dense assemblages of Ediacaran macrofossils.

paleoecological data and subsequent analyses. In order to meaningfully interpret the paleoecology of a fossil community, these factors (and their effects on datasets) must be considered and addressed.

3.1. The importance of facies

Detailed studies at Ediacaran fossil localities in Russia and Australia have revealed the important role played by facies in shaping observed community structure and composition, with certain taxa and species associations found to be confined to specific depositional environments (Grazhdankin, 2004; Gehling and Droser, 2013). To date, there have been few attempts to conduct similar work in the Avalon Terrane, largely due to the limited degree of sedimentological variation described within its deep-water turbiditic sequences. Although several facies and facies associations have been recognised (Wood et al., 2003; Ichaso et al., 2007; Mason et al., 2013), these typically differ only in the thickness of turbidites and the relative abundance of mudstones and volcanic ashes, and they broadly correspond to the defined stratigraphic formations and members (cf. Williams and King, 1979; Hofmann et al., 2008).

Two primary substrates are encountered within the fossil-bearing units of the Conception and St. John’s Groups: turbidites, typically capped by a Bouma-type T_e mudstone; and discrete hemipelagites (facies F4 of Ichaso et al., 2007). Fossils are almost exclusively found on the hemipelagite surfaces, which are inferred to record sedimentation by contour currents in the intervals between turbidity flows (Ichaso et al., 2007). It is only in the finely inter-bedded siltstones and sandstones of the Fermeuse Formation that we see evidence for organisms preserved in abundance on coarser substrates. As a result, assessment of a possible link between fossil communities and facies in the Conception and St. John’s Group is difficult. However, until we can appreciate the potential effect of subtle differences in sedimentology on preserved

fossil communities, we should not dismiss the possibility that facies may play a role in governing Avalonian community structure.

3.2. Application of ecological studies to Avalonia

In Newfoundland, quantitative paleoecological analyses (e.g. Darroch et al., 2013; Ghisalberti et al., 2014) have principally used the dataset collected by Clapham et al. (2003; see also Clapham, 2011) from the Mistaken Point Ecological Reserve. This dataset is the most comprehensive currently available from Avalonian sites. The approach that underpinned the Clapham et al. studies is threefold:

- i) Identify beds that provide faithful representations of in situ communities hosting abundant specimens.
- ii) Document and measure paleontological data from those surfaces, recording information such as taxonomic identifications, fossil dimensions, orientations, areal extent, and spatial positions.
- iii) Interpret this data via use of statistical techniques and metrics commonly employed in modern ecological studies, comparing the values obtained both between different Ediacaran bedding planes and against values observed in modern communities.

Taphonomic, temporal, and methodological biases and assumptions can be introduced at each stage. Consideration of these issues and their impact can facilitate more faithful interpretations of paleoecological data.

3.2.1. Perceived fidelity of Ediacaran community reconstructions

In this sub-section, we discuss the most influential effects of taphonomy and time averaging upon the interpretation of paleoecological data. Some aspects covered in detail elsewhere, such as variation in organism densities between different outcrops of the same surface (Clapham et al., 2003; Droser et al., 2006), are omitted here.

3.2.1.1. Taphonomic influences on paleoecology. If fossil assemblages are to be trusted as paleoecologically informative, an accurate understanding of the vagaries of preservation of organic material is required. A thorough knowledge of not only the fossils and the rocks they are found in, but also the chemical, physical and biological processes that have led to fossilisation of the organisms—their taphonomic history (cf. Briggs, 1995)—is essential. It is extremely rare for fossil assemblages to preserve all of the organisms (micro- or macro-) present in a community (e.g. Conway Morris, 1985; Butterfield, 2003) and, despite the late Ediacaran being noted for its widespread exceptional preservation of soft tissues, the same is true of this interval. For example, although abundant trace fossils at Australian Ediacaran sites record the presence of probable bilaterian metazoans, the body fossils of the organisms responsible for such simple locomotion traces (as opposed to *Epibaion* or *Kimberichnus*) are yet to be reported (Droser et al., 2006). Although there are far fewer traces in the Avalon region, there is a similar absence of body fossil evidence for trace makers (Liu et al., 2010a). Thus a purely literal reading of data, even from beds with exceptional fossil preservation, could be misleading. Furthermore, when considering early animal evolution it should be remembered that some of the earliest animals may have been meiofaunal, and of a size-range that yields a virtually non-existent fossil record (Sperling, 2013).

In Avalonia, taphonomic biases are also introduced by the quality of preservational fidelity, which varies markedly between bedding planes and geological units, and even across individual bedding surfaces (cf. Clapham et al., 2003). These biases do not necessarily preclude paleoecological analysis, because differences in community composition have been shown to be smaller between outcrops from the same horizon than between different horizons (Clapham et al., 2003). Those authors did, however, demonstrate that the quality of preservation directly correlates with observed fossil densities, and therefore surfaces

exhibiting higher-quality preservation are preferred for paleoecological studies.

Preservational differences between bedding planes result from a combination of factors, likely including primary factors such as the grain size of the casting medium (Gehling et al., 2005; Liu et al., 2012) and the thickness of smothering sediment (Narbonne and Gehling, 2003; Laflamme et al., 2007), as well as folding, fracturing, cleavage development and more recent weathering and erosion. For example, unweathered ash on a surface can obscure fossil impressions, presenting a barrier to location and identification of certain specimens, particularly those of low topographic relief.

There are two aspects to community composition: the species present, and its abundance. Both are affected by taphonomic variation, but to different degrees. Species–area curves can be used to estimate whether a bedding surface is likely to preserve all species present at the time of burial, whilst for individual species, size distribution curves can indicate the likelihood of whether the whole population was preserved. The Mistaken Point ‘E’ Surface is considered to be amongst the best global assemblages of Ediacaran macrofossils, with both species–area curves (Clapham et al., 2003) and species size distributions (Darroch et al., 2013) indicating that the vast majority of macro-organisms on these surfaces have likely been preserved and documented. However, there are fewer small individuals on the surface than are expected from size-distribution analysis, and many of those present are difficult to identify to genus or species level. We are, of course, limited to studying the beds available to us, but paleoecological studies must incorporate an estimate of how complete the record is likely to be, and of which species or size classes are likely to be absent or reduced in number. The effect any missing data may have on interpretations of the paleoecological data should also be stated. The use of a metric to quantify preservational quality, such as smallest morphological feature preserved (cf. Clapham et al., 2003), is appropriate. Local variations in this parameter should be noted and taken into account in subsequent paleoecological discussion. Furthermore, factors such as differential ash coverage or modern weathering processes can be incorporated into statistical analyses, leading to a more realistic description of the original community.

3.2.1.2. The importance of time averaging. Ediacaran bedding planes in Newfoundland (e.g. Fig. 6) have previously been interpreted to record ‘snapshots’ of living communities of sessile organisms that were smothered by volcanic ash and cast as they had appeared in life at the moment of burial (e.g. Seilacher, 1992; Clapham et al., 2003). Accordingly, the assumption that all organisms were alive at the time of burial has been used to support the use of modern ecological metrics to assess the paleoecology of Ediacaran fossil communities (e.g. Clapham et al., 2003).

An apparent lack of evidence for either post-mortem transport or the presence of infauna in the Avalonian successions has been taken to suggest that post-mortem mixing of multiple generations of populations did not occur (Clapham et al., 2003; Wood et al., 2003; Bottjer and Clapham, 2006). Documentation of a spectrum of preservational fidelity of taxa on individual bedding planes (see Ivesheadiomorphs, Section 1.4.3), which cannot be explained by secondary causes (cf. Section 3.2.1.1), conversely implies that organisms may have perished and lain decaying on the seafloor prior to obrution (Liu et al., 2011). Therefore, it can be argued that Avalonian fossil assemblages record composite ecosystems that included both living and deceased soft-bodied organisms preserved together on the seafloor (e.g. Fig. 7). Ecological studies should accordingly attempt to consider the proportions of dead versus live organisms in analyses, to ensure that more faithful measures (of factors such as biomass) are made (taking into account our previous discussion; Section 2.2.1). The scale of the influence of taphonomic variation on paleoecological interpretation depends on the questions being asked. For example, inclusion of taphomorphs may severely overestimate biomass estimates, but will have little impact on calculations of species richness.



Fig. 7. Reconstruction of a typical densely-populated, benthic Avalonian community, dominated by rangeomorphs and arboreomorphs/frondomorphs. In this aphotic environment, lighting is necessarily artificial. White mottling represents microbial populations, the largest and most highly textured of which are developed on decaying organisms (Ivesheadiomorphs). Illustration by CGK.

3.2.2. Obtaining Ediacaran paleoecological data

Once a suitable study site has been chosen, collecting data from Ediacaran bedding planes for paleoecological studies is relatively straightforward. Perhaps the most important process (at least with regard to obtaining accurate quantitative data) is the restoration of the bedding surface and its fossils to their original shape, to remove effects of tectonic distortion (retrodeformation; see Wood et al., 2003). Many Avalonian bedding planes, particularly those around Mistaken Point, have undergone some degree of tectonic deformation. However, it has been demonstrated that individual discoidal fossils (which have typically been used as strain indicators for retrodeformation methods) can provide conflicting strain readings, either because they were not originally circular (contrary to the assumption and requirement of the retrodeformation technique), or due to tectonic strain being non-uniform over short distances (Liu et al., 2011, fig. 11). The former possibility is most plausible within the beds of the upper Fermeuse Formation, since multiple different discoidal morphotypes are present, potentially representing a variety of original organisms (MacGabhann, 2007). In units of the Conception Group, there is less confusion about the origin of solitary discs (since the vast majority are holdfast structures of frondose organisms; Section 1.4.4), and their use as strain indicators can arguably be undertaken with more confidence. However, the uniformity of structural tectonic deformation is often not constrained, and deserves serious attention. The choice of ‘disc’ is also important, since some impressions used previously (e.g. Ivesheadiomorphs) cannot necessarily be regarded as originally circular (Liu et al., 2011). Ideally, independent, non-biological strain indicators such as crystallographic fabrics (Law, 1990) or sedimentological features (e.g. Ramsay and Huber, 1983) should be utilised, and the data used in the calculations presented and justified to ensure reproducibility of analysis.

Taxonomic identification is not always straightforward, since the quality of preservation can often make it difficult to say anything more about a specimen than that it is a frond, or a holdfast. Sampling biases can also be introduced by the fact that certain taxa are easier for observers to identify from poorly-preserved specimens. Taxa with a characteristic high-relief gross morphology, for example the tapering zig-zag midline and perpendicular ridges of *Fractofusus* species, are more readily identifiable to a generic level when partially buried by ash than are unipolar fronds. The perceived influence of these variables

and their likely effect on datasets should be explicitly discussed in quantitative paleoecological studies.

Furthermore, detailed study of growth cycles and morphological variation within known taxa is required to determine whether our current taxonomic understanding is robust (cf. Droser et al., 2006). In the absence of formal descriptions, use of informal taxonomic groupings (e.g. “feather dusters”; Clapham et al., 2003) is valid if no alternative formal classification scheme exists, as long as the taxa are clearly described to ensure their consistent identification.

3.2.3. Caveats to the application of quantitative approaches to Avalonian paleoecology

Application of modern quantitative ecological techniques to Avalonian ecosystems has great potential, but only if the inherent biases (Section 3.2.1) are taken into account. This caveat is particularly important when comparing ancient and modern ecosystems. Paleoeological analysis shares many problems with modern ecological analysis, but the unknowns in the past are much greater, and correspondingly more caution is needed. Different ecological questions are affected by biases in different ways, and understanding which uncertainties are manageable, and which are unmanageable, is key to maximising the volume of information extracted from the bedding surfaces whilst minimising over-interpretation.

Three measures, namely population density, species richness, and species diversity indices, summarise the problems faced in this sort of analysis. Limitations associated with more complicated analyses generally propagate from the limitations of the simpler measures on which they are based (e.g. cluster analyses such as DCA rely on accurate measures of the species richness and proportions within communities).

Population density: Population density is strongly influenced by taphonomic biases. The two beds showing the highest fossil densities in the study of Mistaken Point fossil assemblages (Clapham et al., 2003, beds BC and E) also exhibit the highest fidelity of preservation, with morphological features of <0.5 mm resolution being preserved (Clapham et al., 2003). Those authors noted that fossil densities on the Mistaken Point ‘E’ Surface varied from 31.9 individuals per m² at Water Cove (where preservation is relatively poor and variable across the surface), to 39.7–56.5 individuals per m² on the ‘Yale’ and ‘Queens’ surfaces respectively (where preservation is best and can range up to

150 ind./m²). The use of a mean value for fossil density allowed those authors to claim that fossil density across the 'E' Surface fell within the range typical for modern animal communities from modern continental slopes (Clapham et al., 2003, fig. 9). However, the quoted highest values on that surface (as well as those at Bristy Cove) are considerably higher than those seen in the cited animal communities (e.g. Clapham et al., 2003, p. 541), thus undermining such comparisons.

Assessing the 'completeness' of fossil assemblages is difficult in the Ediacaran, not only because an unknown number of taxa have not been preserved as siliciclastic moulds and casts (due to original taphonomic biases), but also due to later variability in erosional processes preferentially removing or concealing certain taxa (Section 3.2.1.1). Small specimens are disproportionately affected by taphonomic biases (e.g. they can be preferentially lost to currents due to being less-well anchored in the substrate; see Tarhan et al., 2010), and they are also relatively easy for observers to miss on bedding planes. Assessment of size frequency distributions (cf. Darroch et al., 2013) may permit recognition of beds where a substantial number of small specimens are missing, potentially indicating that the communities are not complete, and assisting interpretation of population density data.

Species richness: Species richness is a measure of the number of distinct taxonomic species within a community, and is thus directly dependent upon taxonomic definitions. Cumulative sampling curves comparing species richness to randomly sub-sampled areas suggest most Mistaken Point bedding surfaces were fully sampled (Clapham et al., 2003, fig. 3; Droser et al., 2006, fig. 4A). As previously discussed, recent discoveries from those same bedding planes (e.g. Section 1.4.7) demonstrate that an as yet unknown quantity of rare taxa remain to be officially documented. The problem of taxonomic definitions is by no means unique to the Ediacaran (e.g. Magurran, 2004), but it is exacerbated by the relatively low species richness of Avalonian communities compared both to other Ediacaran ecosystems (Erwin et al., 2011), and to many modern ecosystems (Roberts et al., 2002). As such, the addition (or subtraction) of a species in Avalonian paleoecological studies has a relatively large impact on species richness and diversity measures. Ediacaran species richness is also hindered by a lack of agreement as to what constitute generic and species level characteristics in many Ediacaran organisms. Species richness data should, therefore, be interpreted as a minimum estimate of original diversity until all Ediacaran macrofossils from an assemblage have been described (Droser et al., 2006), and comparisons between Ediacaran and modern communities should consequently be undertaken with great care. However, comparisons between Ediacaran communities, rather than with modern communities, are subject to much more similar and quantifiable biases, so species richness comparisons can be considered to be more instructive.

Shannon diversity indices: The Shannon diversity index (Shannon, 1948) is a measure of both the diversity and evenness (which quantifies

the dominance of species within a population) of a population. The index is calculated using the formula:

$$H' = -\sum_{i=1}^S (p_i \ln p_i)$$

p_i	the relative abundance of each species, $\frac{n_i}{N}$
n_i	the number of individuals in species i
N	the total number of all individuals
S	species richness

Even if we could be confident that values of species richness and total individuals do accurately reflect the ancient communities, use of this particular metric has some important caveats. Assemblages from four Conception Group bedding planes were found by Clapham et al. (2003, fig. 9) to fall within the "typical" range of Shannon diversity values for modern animal communities. However, the range of Shannon diversity values stated to characterise modern marine benthic animal communities (0.05–3.7 = extreme, 0.8–2.5 = typical; Clapham et al., 2003) encompasses the vast majority of values obtainable from any community with a species richness of < 30 (Fig. 8), regardless of the biological affinities of its constituent organisms. The maximum possible diversity value, H'_{\max} , is equal to the natural logarithm of the species richness ($H'_{\max} = \ln S$). Therefore, the quoted "typical" range of Shannon diversity values proposed for modern animal ecosystems by Clapham et al. (2003) cannot possibly be exceeded in any given biological community unless the species richness of that community is ≥ 13 ($S = 13$ results in a H'_{\max} value of 2.56). Furthermore, such a population would also require maximum evenness within the community, which is not considered to be present in any of the studied Mistaken Point communities (Droser et al., 2006, fig. 4). Because all Mistaken Point localities discussed in the original study exhibit species richness values of ≤ 12 (Clapham et al., 2003, table 2), their assemblages necessarily fall within the normal to depauperate range of values from modern animal communities (<2.5). Interpreting the similarity between the Shannon diversity index of the Mistaken Point assemblage and modern animal communities to arise from a common ancestry or biology is therefore misleading. The range of documented Mistaken Point Shannon diversity index values is merely a function of the species richness of the measured assemblages, and any conclusions drawn should therefore be regarded with caution.

The most striking claim to result from the quantitative paleoecological studies of Mistaken Point is the suggestion that, because the fossil communities share attributes of their community structure with modern animal communities and exhibit features such as epifaunal tiering, certain Ediacaran organisms were most likely to have been animals, or of animal-grade (Narbonne, 2005). However, there are several

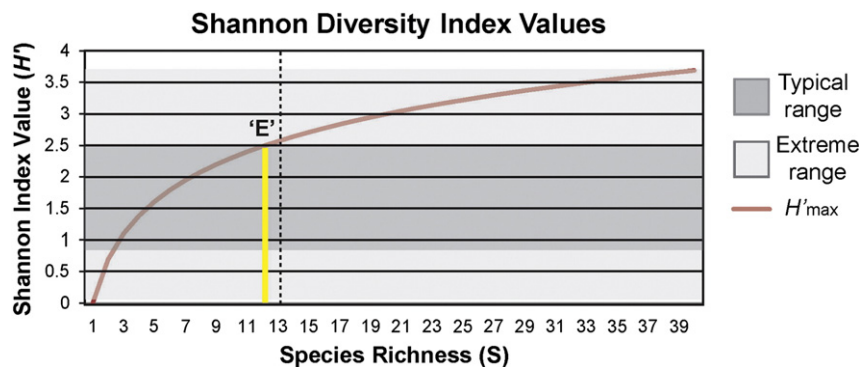


Fig. 8. Graphical illustration of the problems of low species richness in comparison of Shannon Diversity Indices from fossil communities with those of modern benthic metazoans. The red line illustrates the maximum value of H' obtainable for a population of given species richness (S). The yellow bar shows the range of values of H' possible for a community with a species richness of 12 (as was the case for the 'E' Surface studied by Clapham et al., 2003), demonstrating that all possible values fall within the typical to extreme ranges of H' observed in modern benthic marine communities (grey boxes; see Clapham et al., 2003 for references to metazoan community ranges).

methodological and biological reasons for caution in the acceptance of this assertion. First, the inherent variation in the biological composition of modern ecosystems suggests that, even if metazoans were present in Ediacaran ecosystems (Section 1.4), there exists the distinct possibility that they shared the ecosystem with non-metazoan macro-organisms (cf. Xiao and Laflamme, 2009), as well as with microbial populations. Secondly, the suggestion that the inferred epifaunal tiering of Ediacaran frondose communities is a characteristic feature of animal-grade organisms has been questioned elsewhere: tiering is a simple ecological strategy that limits vertical competition, and is not unique to metazoan ecosystems (cf. Sperling et al., 2007). Thirdly, as discussed herein, the use of modern ecological metrics to assess the paleoecology of Ediacaran ecosystems (including simple measures of species richness, Shannon diversity indices, and multivariate analyses; Clapham et al., 2003; Clapham, 2011) requires caution. Such metrics are useful for gaining an appreciation of how an ecosystem is structured, and for constraining biological hypotheses about behaviour, reproduction, and feeding strategies, but their use as indicators of specific phylogenetic groups in an ancient ecosystem is subject to substantial interpretational caveats. At the very least, data from fossil assemblages should be compared to those from multiple disparate biological groups. In the Ediacaran, consideration should also be made of the possibility that some of the organisms may belong to now-extinct clades (e.g. Vendobionta; Seilacher, 1992), which adds another level of uncertainty to direct comparisons with modern ecosystems.

Furthermore, it is important to appreciate that although Ediacaran bedding planes are commonly regarded as ‘snapshots’ of communities, the temporal resolution of these snapshots is poor (for example, at Mistaken Point ~100 fossil-bearing surfaces span around 20 million years of sedimentation, unequally distributed throughout the stratigraphy). Clapham (2011) found a weak correspondence between community position and stratigraphic position (using DCA), implying probable evolutionary controls on Mistaken Point community composition. However, at this sampling resolution it is difficult to differentiate between short term influences such as ecological succession (or the influences of short-term climatic changes, ocean circulation, seasonality, or Milankovitch cyclicity), and longer-timescale processes such as evolution and large-scale climate change.

3.3. Summary of paleoecological considerations

Analytical and statistical paleoecology is informative, but only when considered in the context of the preservational environment from which the data has been gleaned. Comparisons between extant and fossil biological communities should ideally: (1) focus on bedding plane assemblages exhibiting exceptional quality of preservation in order to minimise taphonomic biases; (2) assess the limitations of ecological parameters in terms of taphonomic and methodological biases; (3) possess a complete and taxonomically accurate dataset for the fossil assemblage, or provide an informed discussion of what may be missing; (4) present statistical data from multiple modern ecosystems for comparison; and (5) state, incorporate and, ideally, quantify all sources of taxonomic, taphonomic, and methodological bias. In this way, it is hoped that future quantitative paleoecological studies may provide valuable and meaningful insights into Ediacaran biological communities.

4. Conclusions

Recent discoveries and paleoecological insights are refining our views of Avalonian ecosystems. These settings hosted diverse communities comprised of a wide range of higher-order biological groups, which may have exerted a significant influence on their surroundings in terms of nutrient cycling, geochemistry, and substrate colonisation. A combination of physiological and paleoecological lines of evidence, alongside detailed ontogenetic, anatomical and behavioural studies,

are constraining the possible biological interpretations for these organisms. However, we propose that, in light of biological and geochemical considerations, it is time to revisit existing hypotheses for feeding in Ediacaran taxa.

Our datasets are now reaching a standard that will permit detailed quantitative analysis of Ediacaran paleoecological patterns, and appreciation of the inherent biases in such analyses will assist in improving the accuracy of paleoecological investigations. Given the uncertainties surrounding the phylogenetic placement of Ediacaran macro-organisms, paleoecological analyses would benefit from comparisons with multiple modern phylogenetic groups. Context is also critical, and a holistic appreciation of all aspects of Ediacaran taphonomy, environments, and geochemistry is required to correctly interpret biological patterns. Although we may not be able to accept these assemblages as perfect snapshots of Ediacaran communities, an appreciation of the biases affecting Ediacaran fossils serves to refine our understanding of these biotas.

In the last 30 years or so, we have moved from viewing Ediacaran macrofossils as recording the remains of animals (cf. Glaessner, 1984), to viewing them as an extinct Kingdom (Seilacher, 1989), to comparing them with a vast range of other biological groups (e.g. Seilacher and Pfluger, 1994; Peterson et al., 2003) and to interpreting them as diverse communities containing many if not all of these groups (e.g. Xiao and Laflamme, 2009). To avoid future confusion and unhelpful generalisations, careful and consistent application of terminology across the field, and an agreed taxonomic framework for the description of Ediacaran taxa, are now required (cf. Brasier et al., 2012; MacGabhann, 2014). Our interpretations of the phylogenetic position of Ediacaran organisms now extend beyond morphological comparisons to consider interdisciplinary information regarding feeding, respiration, reproduction and locomotion, obtained from both quantitative and qualitative analyses. This information is supplemented by increasingly rigorous and innovative geochemical, sedimentological, and taphonomic investigations, providing the clearest picture yet of Ediacaran marine conditions. Careful application of the techniques described herein, allied with appreciation of the atypical (from a Phanerozoic perspective) nature of the Ediacaran biosphere, will continue to expand our paleoecological understanding. The next 30 years will surely witness further transformations in our understanding of this most fascinating interval of Earth history.

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