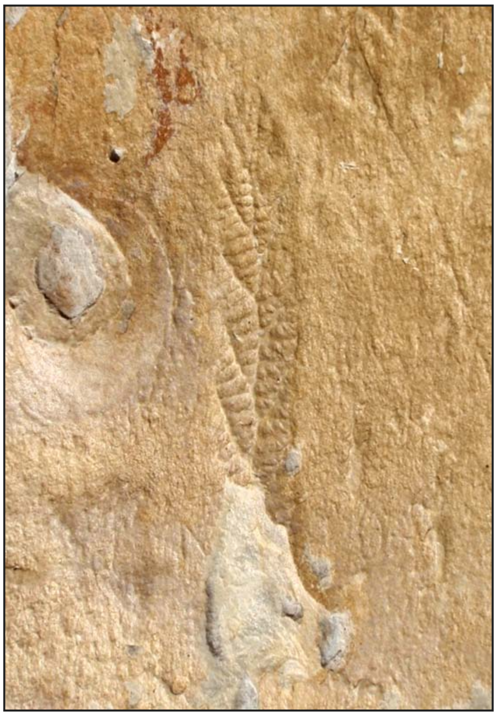
UNDERSTANDING THE EDIACARAN ASSEMBLAGES OF AVALONIA:

A PALAEOENVIRONMENTAL, TAPHONOMIC AND ONTOGENETIC STUDY



ALEXANDER G. S. C. LIU

EXETER COLLEGE

Submitted for consideration for the degree of Doctor of Philosophy, Trinity Term 2011

Department of Earth Sciences, University of Oxford

DEDICATION

To my parents, with love

Thank you for everything

Image: Close-up image of an exceptionally preserved Ediacaran rangeomorph, possibly aff. *Bradgatia*, from the 'MUN surface', locality PU9. Trepassey Formation, near Port Union, Bonavista Peninsula, Newfoundland, Canada. Image width = 25 mm.

Front cover image: *Charnia* specimen, from the 'MUN surface'. Trepassey Formation, near Port Union, Bonavista Peninsula, Newfoundland, Canada.

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ALEXANDER G. S. C. LIU, EXETER COLLEGE

DEGREE OF DOCTOR OF PHILOSOPHY, TRINITY TERM 2011

SHORT ABSTRACT

The Ediacaran Period, stretching from 635–542 million years ago, is one of the most dynamic intervals in the history of life. It witnessed the rapid transition from a microbially-dominated world, which had existed undisturbed for almost three billion years, to a Phanerozoic biosphere that is greatly modified by the interactions between macro-organisms and Earth surface systems. Ediacaran successions worldwide contain enigmatic assemblages of fossilised soft-bodied organisms. Determining the biological affinities of these fossils represents one of the major challenges in modern palaeontology.

This thesis addresses some of the fundamental questions surrounding the Ediacara biota of the Avalon region from taphonomic, ontogenetic and palaeoenvironmental perspectives. Up-to-date stratigraphic ranges are produced for Avalonian macro-organisms, documenting spatial and temporal trends in their occurrence. New fossil assemblages are described, which include populations of juvenile rangeomorphs, and one of the earliest examples of community succession in the fossil record. The previously unexplained fossil *Ivesheadia* Boynton and Ford 1996 is re-described as a taphomorph, preserving the remains of Ediacaran macro-organisms that had died and undergone microbial decay on the seafloor prior to burial. This hypothesis implies considerable time-averaging of Avalonian palaeocommunities, and consequently suggests that the preserved fossil assemblages do not represent census populations of living organisms at the time of burial. Microbial decay is experimentally demonstrated to replicate aspects of *Ivesheadia*-type morphology, supporting the arguments presented herein for the preservation of microbially-induced taphomorphs during the Ediacaran.

Finally, the discovery of the oldest evidence for metazoan locomotion, from 565Ma horizons at Mistaken Point in Newfoundland, suggests that motile macro-organisms were present amongst the Ediacara biota, ~20Myrs before the Cambrian boundary. This portrayal of Ediacaran palaeobiology views the deep-marine Avalonian ecosystems as diverse assemblages of both macro- and micro-organisms. Such palaeoenvironments preserve rare evidence of organisms capable of locomotion, and are likely to have included metazoans.

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EXTENDED ABSTRACT

The initial evolution of the Kingdom Animalia is a subject of substantial scientific and philosophical interest. The first definite members of animal phyla appear in the Cambrian Period, but the assemblage of fossils that immediately precedes them has long been considered enigmatic. Fossil-bearing horizons of the Ediacaran Period, 635–542 Ma, preserve soft-bodied macro-organisms that cannot be readily assigned to modern phyla. The morphological peculiarity of Ediacaran macro-fossils, and a lack of preserved primary organic material, makes them highly intriguing. Determining whether the Ediacara biota were the earliest animals in the fossil record, or a more primitive or even entirely extinct biological group, remains one of the most controversial and stimulating topics in modern palaeontology.

Initial studies of the Ediacara biota attempted to elucidate biological information through morphological analogies, and the study of depositional environments. More recent research has explored modes of growth, ecosystem structure, and patterns of diversity in an attempt to decode the Ediacara biota. Whilst these are all important factors for us to consider in order to fully understand this ancient group, it could be argued that our knowledge of the basic facets

of Ediacaran palaeobiology is currently incomplete. Global correlation of Ediacaran successions is yet to be accomplished, and questions persist regarding many of the depositional environments and taphonomic regimes in which these fossils are found. Furthermore, the late Neoproterozoic was a time of immense change in the biosphere, where classic uniformitarian thinking cannot necessarily be directly applied. Tectonic and climatic upheavals, unusual oceanic and atmospheric chemistry, and a wide variety of palaeoecological innovations all transpired during this Period. These factors demand consideration when assessing any proposed explanation of the Ediacara biota.

This work concentrates on the Avalon biotic assemblage, which at the time this doctoral project began was considered the oldest macro-fossil assemblage on Earth. An extensive amount of new research has been published in the intervening years, demonstrating both the significance currently ascribed to Neoproterozoic geoscience, and indicating the amount we still have to learn. Herein, a multifaceted approach to Ediacaran palaeobiology is utilised, to test previous palaeontological hypotheses, and document new discoveries. In particular, the taphonomy and palaeoecology of the Avalonian bedding plane assemblages are investigated, resulting in a substantial reappraisal of our views of Avalonian palaeoenvironments.

Two of the key questions regarding the Ediacara biota are exactly when, and why, they first evolved. Previously, the first macro-organisms in the fossil record were considered to appear ~579 Ma, just three million years after the end of the Gaskiers glacial event. This geological coincidence has been proposed to be causal, with a glacially-induced rise in atmospheric oxygen levels thought to have pushed marine dissolved oxygen concentrations over the threshold necessary for the evolution of large, complex multi-cellular organisms. Documentation of a new assemblage of small frondose Ediacaran organisms from the Drook Formation of Pigeon Cove, Newfoundland, suggests that the earliest known macro-organisms may have been substantially more diverse than previously thought. This hints at a possible hidden history of Ediacaran evolution prior to the Gaskiers event. When combined with new evidence from Chinese localities, which document algal macro-fossils ~600 Ma, and a recent critique of the link between oxygen and animal evolution, it appears that the Gaskiers glacials may not have been such a significant factor the evolution of the Ediacara biota.

If we are to identify the processes governing the initial evolution and radiation of the Ediacara biota, we must first elucidate the patterns concealed within the fossil data, and any biases therein. Following a wide-ranging survey of Avalonian bedding planes, detailed stratigraphic ranges for the organisms of the Avalon region have been constructed. This enables Pigeon Cove and other new assemblages to be placed into a temporal and biological context, revealing several interesting and previously unreported findings. Such ranges also provide a point of reference for discussions of Ediacaran diversification and evolution.

The rangeomorph fronds of Pigeon Cove are the smallest to be described from the Avalon region. Interpreted as juveniles, they inform us about the early growth stages of rangeomorph taxa. From the limited amount of morphological detail preserved in these specimens, it can be demonstrated that taxa such as *Charnia masoni* Ford 1958 and *Trepassia wardae* Narbonne et al. 2009 initially do not possess a full complement of primary branches. They progressively add their branches distally, undergoing both inflation and addition throughout their lifetime. Potential juvenile *Charniodiscus* Ford 1958 specimens, when combined with a consistent bedding plane orientation for the entire assemblage, suggest that young rangeomorphs also possessed a basal holdfast disc.

The nature of Ediacaran fossils and the biostratigraphic patterns they reveal can arguably only be correctly interpreted once the taxonomy of a given biotic assemblage has been defined. This requires rules for distinguishing between the taxa and their defining morphological taxobases to be formulated, tested and confirmed, a process only now being attempted. Many current Avalonian taxonomic diagnoses include morphological characteristics and measurements that have been corrected for tectonic deformation, using a technique called retrodeformation. Although it is clear that tectonic deformation has secondarily altered fossil morphology, and should be considered in order to obtain the true original morphology of the fossil, prior studies have not necessarily undertaken this process in a repeatable, testable manner. Rules are proposed herein to rectify this problem, encouraging researchers to state the amount of strain removed from specimens, so that future workers can replicate/re-work original studies and datasets.

Previous taxonomic treatment of the Ediacara biota has also been highly provincial in nature, with multiple taxa described in duplicate from various geographic terranes. Taxonomic ‘housekeeping’ is thus required to constrain true Ediacaran macrofossil diversity and disparity, and one factor that must be accounted for in doing this is the effect of taphonomy upon fossil morphology. A spectrum of preservational fidelity has been observed on several Avalonian bedding planes. Individual taxa can be well-preserved, showing all of the characteristic features of their species, or they can appear progressively effaced, until only irregular, lobate impressions with the gross morphology of an Ediacaran taxon remain. The fossil genera *Ivesheadia* Boynton and Ford 1996, *Shepshedia* Boynton and Ford 1995, *Blackbrookia* Boynton and Ford 1995, and *Pseudovendia* Boynton and Ford 1979 are considered to represent the effaced end-members of this taphonomic spectrum. Such impressions are consistently irregular, and composed of asymmetrically-arranged lobes, ridges and troughs, often preserved in high positive epirelief. Importantly, a small proportion of specimens possess regions of high-fidelity rangeomorph branching within their structure, and/or the gross morphology of other well known Ediacaran taxa. While they have variously been described as medusoids, pseudofossils, arthropods and enigmas in the past, this new review of their morphologies interprets them as taphomorphs of other members of the

Ediacara biota, rather than taxa in their own right. They have been synonymised within the taphonomic grouping ‘Ivesheadiomorpha’ to reflect this view.

Preservational differences between well-preserved and effaced individuals are not found to be related to tectonic, erosional or weathering profiles, with both forms found interspersed on individual bedding planes. This taphonomic gradation is here suggested to be the result of microbial decay acting upon Ediacaran macro-organisms prior to burial. Avalonian benthic ecosystems are regarded to have lacked pervasive bioturbation, scavenging, and macro-predation. Therefore, when organisms died on the sea-bed, they would often remain where they fell for a substantial period of time. Autolysis and microbial degradation are envisaged to have been the only processes available during the Ediacaran Period to remove dead organic material. Such microbial activity would have gradually effaced specimens on the seafloor, removing the fine detail of their morphology, whilst possibly trapping and binding sediment from the water column onto the surface of the carcasses, thus enhancing their overall topography. In this way, the spectrum of preservational fidelity on Avalonian bedding planes can be explained, with the temporal extent of decay being responsible for the observed gradation in preservational quality. The term ‘effaced preservation’ is coined to describe the preservation of partially decayed organisms on the ancient sediment-water interface in this manner.

Experiments to replicate conditions on the Avalonian seafloor have been constructed, utilising a variety of organic tissues in experimental aquaria. These are designed to assess the plausibility of microbially-induced effaced preservation – whether it can produce the features of effacement typically observed in ivesheadiomorphs – and the preservation potential of such features in the rock record. Microbial decay of modern metazoan organic matter in the laboratory is found to replicate effaced features seen on Ediacaran bedding planes in the field. Surface morphology is experimentally shown to be gradually effaced over time, with lobate structures developed, and substantial variation in gross morphology obtained. Fossilization of such microbially-induced morphologies is demonstrated to be possible, but further investigation is required to confirm these preliminary observations.

Recognition of effaced preservation in Avalonian fossil assemblages has important implications for studies of palaeoecology in Avalonian ecosystems. Prior studies have suggested that the community structure of Ediacaran palaeocommunities is similar to that of modern epibenthic animal communities. Such studies assume that Avalonian bedding planes faithfully record snapshots of living ‘census’ communities at the time of burial. If the suggestion that dead and decaying organisms are preserved within these assemblages is considered, such an assumption becomes invalid. The data upon which those previous conclusions are based are reanalysed herein, taking into account time-averaging of palaeocommunities resulting from the preservation of both decaying and living organisms. Such a revision refutes the earlier conclusions, and also highlights issues surrounding the applicability of modern ecological measures to fossil ecosystems. In addition, much of the perceived biomass preserved on the Avalonian seafloor is here argued to be necromass, composed of dead and decaying organisms. This interpretation has important implications for nutrient cycling and metabolism on the deep marine seafloor.

Many previous studies into the biological affinities of the Ediacara biota have interpreted them as sessile groups, due to a lack of evidence for locomotion or bioturbation on fossil-bearing bedding planes. The discovery of an assemblage of surface locomotory traces from the Mistaken Point Formation, slightly younger than 565 Ma, reveals the oldest documented evidence for probable metazoan locomotion in the fossil record. The candidate traces, from the upper surface of a deep-water turbidite deposit, possess internal arcuate structures that are interpreted to record the posterior edge of a circular body moving across the sediment-water interface. A negative-relief circular impression is sometimes found at the termination of the trace, inferred to represent the body impression of the trace maker. The traces possess a variety of morphological features that rule out interpretations as abiogenic structures, tubular body fossils, or known Proterozoic trace fossils. Comparison is made with structures produced by extant metazoans, and it is considered that they are analogous to features produced by modern actinian cnidarians or gastropods. A survey of Avalonian fossil sites reveals that ichnofossils, although rare, were present across the Avalon terrane. It is therefore regarded as likely that total group metazoans were present in these settings ~565 Ma.

Finally, the effaced preservation hypothesis implies that microbes played an important role in the preservation and recycling of organic material in Ediacaran deep-marine ecosystems. Fossil evidence for their presence within Avalonian strata has until recently been limited to microbial mats and occasional individual spheroids or filaments. Herein, it is shown that macroscopic filaments, inferred to be microbial, were a common and potentially integral component of the Avalonian benthic community. Specific microbial affinities for these impressions remain to be confirmed, but the Ediacaran microbial biota is here argued to have been widespread and diverse in the Avalon region, and is considered to have participated in a variety of interactions with the macro-organisms in their ecosystems.

These findings combine to reveal new insights into the Ediacara biota of the Avalon terrane. Fossil assemblages record the remains of organisms both living, and dead, at the time of burial. They also document a spectrum of microbial effacement of decaying organisms, along with a host of previously unreported impressions likely to be microbial in origin. Avalonian deep marine ecosystems thus contained diverse communities of macro-organisms, living alongside numerous microbial taxa. Interactions between the microbial populations and the macrobiota extend into the realms of taphonomy, structural support, and potentially even nutrition. Rare components of the Ediacaran macrobiota were capable of locomotion along the sediment-water interface, and are likely to represent some of the earliest large organisms to

possess muscular tissue, potentially being of metazoan grade. This work expands our knowledge of life on Earth during this unique interval, and further refines our interpretations of the earliest macroscopic organisms. In this way, it is hoped that it will form a valuable contribution towards understanding the mysteries of the enigmatic Ediacara biota.

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CHAPTER 1
AN INTRODUCTION TO THE EDIACARAN PERIOD

“For my part, following out Lyell's metaphor, I look at the natural geological record, as a history of the world imperfectly kept, and written in a changing dialect; of this history we possess the last volume alone, relating only to two or three countries. Of this volume, only here and there a short chapter has been preserved; and of each page, only here and there a few lines. Each word of the slowly-changing language, in which the history is supposed to be written, being more or less different in the interrupted succession of chapters, may represent the apparently abruptly changed forms of life, entombed in our consecutive, but widely separated, formations”.

Darwin, 1859, pp. 310–311.

PREFACE

Despite only being formally defined in the last decade, the Ediacaran Period is widely recognised as one of the most important intervals in the history of our planet. The events it witnessed had extensive effects on the biosphere, and greatly influenced the development of the modern natural world. This chapter introduces the Ediacaran Period within the context of the Precambrian–Cambrian transition, and reviews the history of research into Ediacaran geology and palaeontology. Ediacaran biotic assemblages are described, with particular reference to those of Avalonia – an ancient micro-continent comprised of what is now maritime Canada, the north-eastern United States, and parts of the United Kingdom. Previously published hypotheses regarding Avalonian communities and ecosystems are discussed. The work compiled within this thesis is then introduced, detailing how studies into the palaeoecology, ontogeny and taphonomy of the Ediacara biota have enhanced our understanding of the Ediacaran Period and its biotic communities.

THE EDIACARAN PERIOD

Ratified as recently as 2004 (Knoll et al., 2004, 2006), the Ediacaran Period is the youngest period of the Proterozoic eon. Beginning at the base of the cap carbonate that marks the end of the Marinoan Snowball Earth event 635 Ma (Knoll et al., 2004), it was preceded by some of the most severe climatic perturbations in Earth's history, the extensive and long-lasting Cryogenian glaciations. Some workers hypothesise that these glaciations covered the entire planet in a shroud of ice for millions of years at a time, impacting strongly upon the subsequent evolution of the biosphere (Hoffman et al., 1998). The enormous physical and climatic changes occurring prior to the base of the Ediacaran are matched in scale by the biological revolution that took place at its end – the so called 'Cambrian Explosion' of metazoan diversity and disparity, ~ 542–520 Ma (Brasier, 2009). Sandwiched between these extraordinary events, the Ediacaran Period encompasses the transition between the microbe-dominated Proterozoic ecosystems, and the metazoan-dominated ecosystems of the Phanerozoic (Clapham et al., 2003). Ediacaran successions therefore record the critical interval over which multicellular life on Earth diversified into large macroscopic forms. The most striking fossils from this period are the unusual Ediacara biota, soft-bodied organisms that can reach almost two metres in length, but do not closely resemble any modern taxa. Determining the biological affinities of the Ediacaran organisms, and their place in the history of life on Earth, is the subject of this research.

EDIACARAN RESEARCH: AN OVERVIEW

Precambrian palaeontology is a relatively recently developed field. Due to the apparent lack of shells and bones in rocks of Precambrian age, early scientists considered such rocks to be 'azoic' (a term defined by Murchison, 1845, to describe crystalline rocks beneath his basal

Silurian zone), and therefore devoid of life. From a pre-1900s viewpoint, animals first appeared and diversified in what is now the Cambrian Period. The lack of animal fossils in older rocks seemingly represented a true absence of organisms. Despite this, and contrary to the general conceptions of his illustrious peers, Charles Darwin had recognised by 1859 that the history of life on Earth must have stretched back prior to the Cambrian (Darwin, 1859, pg. 307):

> *"if my theory be true, it is indisputable that before the lowest Silurian* [now Cambrian] *stratum was deposited, long periods elapsed, as long as, or probably far longer than, the whole interval from the Silurian age to the present day; and that during these vast, yet quite unknown, periods of time, the world swarmed with living creatures."*

The discrepancy between Darwin's expectations, based on evolutionary theory, and the sparse fossil record, presented a paradox now commonly referred to as Darwin's Dilemma (e.g. Brasier, 2009). Solving this dilemma has only been possible through subsequent palaeontological discoveries, with the Ediacara biota (a term used herein to denote the macro-organisms present during the late Ediacaran Period, and not specifically the fossil assemblage of the Ediacara Hills, Australia) an integral part of this narrative.

The first fossils to be described from definitively Precambrian rocks came from the Longmynd of Shropshire even as Darwin was writing the Origin –*Arenicolites didymus* in 1856 (originally described as trace fossils; Salter, 1856, 1857). Regrettably, the true importance of these finds was not immediately recognised (Callow et al., Submitted). Large 'rings' preserved in a slate quarry in rural Leicestershire, England, were noted in 1866 (Ansted, 1866) and again in 1877 (Hill and Bonney, 1877), but their palaeontological importance was not realised at the time. The discoidal impression *Aspidella terranovica*

Billings 1872 from downtown St John’s, Newfoundland, Canada, was also discovered in 1866 (Billings, 1872), but after this date there was a substantial lull in Precambrian palaeontological finds. Discoveries by Reginald Sprigg and Martin Glaessner in the Ediacara Hills of South Australia (Sprigg, 1947; Glaessner, 1958), and Hans Pflug and Georg Gürich in Namibia (Gürich, 1933; Pflug, 1966), demonstrated that fossilised macro-organisms did exist in Precambrian rocks. The first U.K. discovery important enough to achieve global attention occurred in 1958; that of an Ediacaran frond by schoolchildren in Charnwood Forest, Leicestershire, from the same quarry in which Ansted’s ‘ring structures’ were described (Ford, 1958). This frond, named *Charnia masoni* Ford 1958 in honour of its discoverer and location, is one of the most recognisable and cosmopolitan Ediacaran taxa (Antcliffe and Brasier, 2008; Plate 1.1A).

Since these initial discoveries, the field of Ediacaran palaeobiology has expanded enormously, and it is now one of the most controversial and exciting areas of palaeontology (Edgecombe, 2009). Macrofossils of soft-bodied organisms range from >579 Ma, right up to and possibly even across the Ediacaran–Cambrian boundary (e.g. Conway Morris, 1993; Jensen et al., 1998). A diverse microfossil assemblage including acritarchs, algal eukaryotes, and potential opisthokont embryos has been documented from Ediacaran horizons (e.g. Xiao et al., 1998; Fedonkin et al., 2007a; Yuan et al., 2011; see also Chapter 7). The Period also contains the first abundant trace fossils (reviewed in Jensen et al., 2006), and the earliest macroscopic biomineralizing organisms (e.g. Germs, 1972).

Over 100 Ediacaran macrofossil species have been described to date, with many more awaiting official classification, and the biota is known from more than 35 localities worldwide (Fedonkin et al., 2007a). Despite this, the fundamental biology of Ediacaran fossils – their taxonomic affinities, modes of life, and evolutionary or ontogenetic pathways – in many cases

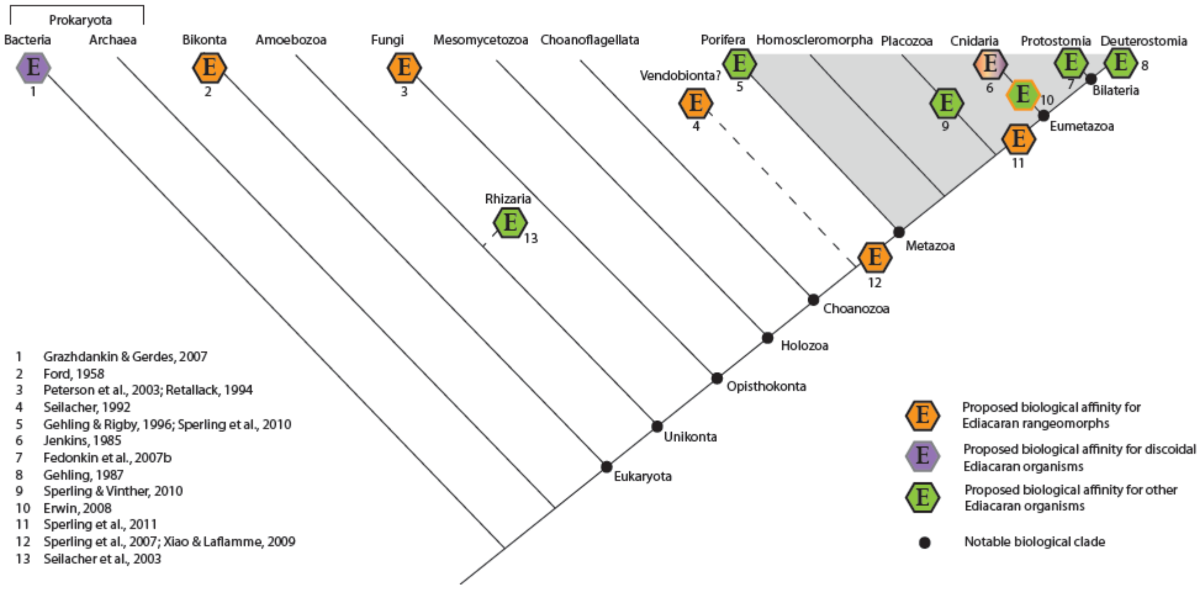

Fig. 1.1. Cladogram showing previously proposed phylogenetic affinities of the Ediacara biota. The cladogram shows the relevant major groupings in the tree of life, with relative branch positions based on the data of Sperling et al., 2009 (their fig. 2) and Cavalier-Smith, 2010 (his fig. 6). Ediacaran macro-organisms have been postulated to belong to groups spread throughout the cladogram. The metazoa are shaded to highlight the fact that proposed affinities occur both within and outside of the metazoan clade. The extinct Kingdom Vendobionta (Seilacher, 1992) is here inserted as a branch prior to the base of the metazoa, a position that is entirely arbitrary and simply added to demonstrate one possible location for a hypothetical clade. The placement of the Rhizaria, to which xenophyophores belong, is also dubious, and its position off the amoebozoa (Cavalier-Smith, 2002) is just one of several competing possibilities (e.g. Burki et al., 2007).

remains unresolved. There is no other period in the geological record where a single group of fossils could be proposed to be animals (Sprigg, 1947; Dzik, 2003; Fedonkin and Ivantsov, 2007), algae (Ford, 1958), lichens (Retallack, 1994), chemoautotrophs (McMenamin, 1998), fungi (Peterson et al., 2003), protists (Seilacher et al., 2003), microbial colonies (Grazhdankin and Gerdes, 2007), stem-group opisthokonts (Sperling and Vinther, 2010), placozoans (Rozhnov, 2010), and their own unique but now extinct Kingdom (Seilacher, 1992), and where all of these possibilities are supported by varying degrees of fossil evidence (Fig. 1.1). Even individual organisms have been assigned to multiple Kingdoms (see the discussion of

Dickinsonia in Xiao et al., 2010). Such a variety of interpretations highlights the difficulties involved in attempting to classify organisms with no obvious living descendents within modern taxonomic groups (Conway Morris, 1985). The personal viewpoint of the writer, and one that is becoming increasingly widespread (e.g. Xiao and Laflamme, 2009), is that rather than attempting to force all Ediacaran macrofossils into one group, we should appreciate that representatives of multiple extant biological groups, and several extinct clades, were likely present amongst the Ediacara biota. Together, these organisms constructed a rich and diverse ecosystem that was successful for ~40 million years, until the radiation of modern metazoan groups at the base of the Cambrian Period (Fig. 1.2). To call such long-ranging taxa ‘failed experiments’ in evolution (e.g. Narbonne et al., 2009) is thus both unhelpful and untrue. The correct approach should be to determine the affinities of specific individual taxa on a case by case basis, in order to build up a picture of the fascinating and complex biological communities and interactions seen in these assemblages.

THE AVALON BIOTA

Ediacaran fossils worldwide have been found by cluster analysis to form three distinct assemblages, defined by palaeogeographic and biotic parameters (Waggoner, 2003). These assemblages, the Avalon, White Sea and Nama, are commonly used to describe the biotic groupings seen in the Ediacaran macro-biota (Fig. 1.2). A widely-held view is that these assemblages are defined by taphonomy and evolution, with each biota being replaced by that of the next assemblage over time (Narbonne, 2005). Conversely, environment of deposition may have been a significant factor in defining the biota of these provinces (Grazhdankin, 2004), as demonstrated, for example, by the presence of rangeomorph taxa (largely

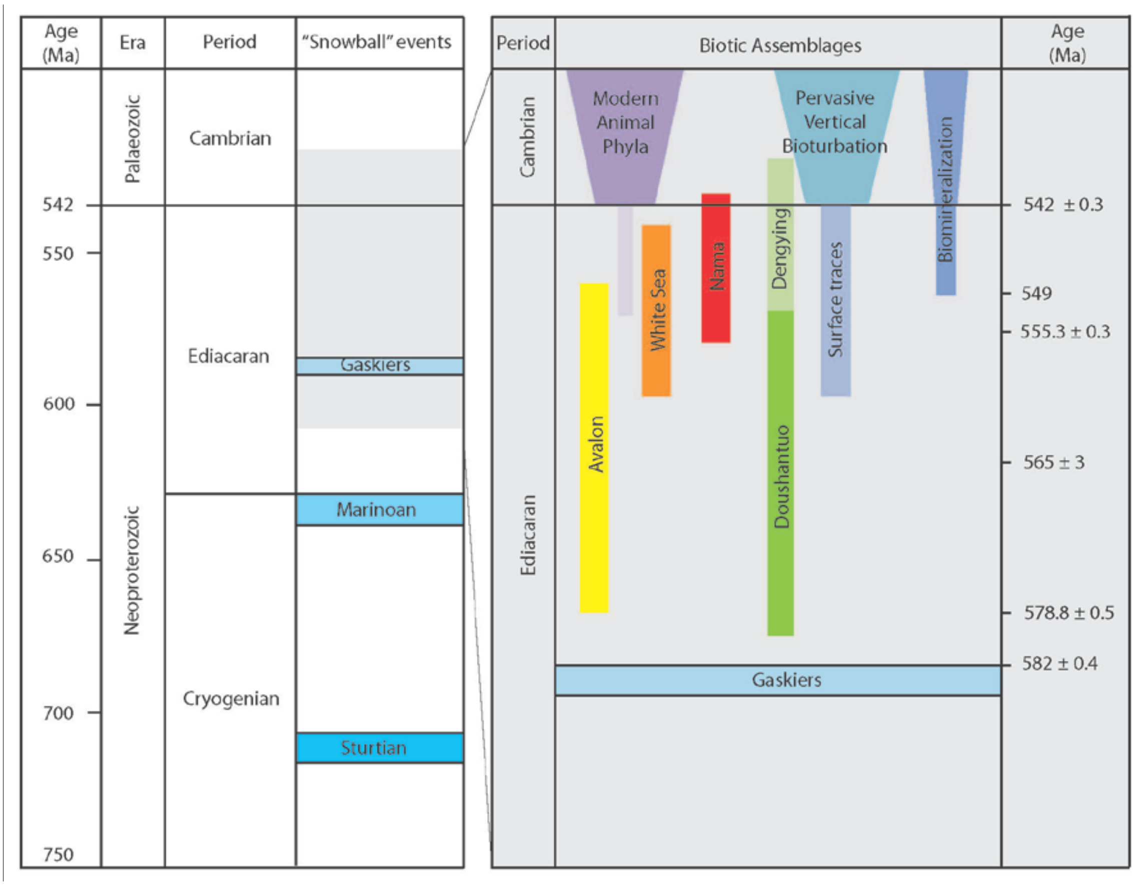

Fig. 1.2. The position of the Ediacaran Period in the geological column, and stratigraphic ranges for biotic assemblages (following Waggoner, 2003, though see Grazhdankin, 2004), and biological radiations. Dates obtained by radiometric dating techniques at far right are taken from Benus, 1988, Grotzinger et al., 1995, Martin et al., 2000, Gradstein et al., 2004, Condon et al., 2005 and Van Kranendonk et al., 2008. The range of the Avalon assemblage, the focus of this thesis, is in yellow. Note the radiations of biomineralization, vertical bioturbation and modern animal phyla in the Cambrian. Data from Russian sections (not included in the original Waggoner study) are also included, collated from Grazhdankin, 2004. Horizontal blue bars indicate the occurrence of "Snowball Earth" global glaciation events.

Avalonian) in Siberia (White Sea; Grazhdankin et al., 2008), and the Miette Formation of Canada (part of Laurentia during the Ediacaran Period; Hofmann and Mountjoy, 2010). Therefore, these assemblages may not represent an evolutionary trajectory as previously considered (Fig. 1.2). This terminology for grouping similar biotic assemblages will undoubtedly require future revision (to include recently discovered successions from China for example, summarised in Zhu et al., 2007), and its relevance to evolutionary patterns is arguably questionable. Despite this, the Waggoner (2003) assemblage terminology remains useful when describing the fossil populations and preservational styles exhibited by these regions.

The oldest assemblage, and the one upon which this thesis is focused, is the Avalon assemblage. Avalonian fossil-bearing successions of the Conception Group of Newfoundland, and the Charnian Supergroup of Leicestershire, are characterised by deep marine (>1 km; see Chapter 6) siliciclastic and volcaniclastic turbidites. These are considered to have been deposited on a slope or within a subsiding back-arc basin, in the vicinity of a volcanic island arc (Carney et al., 2000; Wood et al., 2003). Influxes of volcanic ash or remobilised volcaniclastic sediments regularly smothered the seafloor ecosystems, preserving the impressions of soft-bodied Ediacaran organisms on bedding planes as casts or moulds (Gehling, 1999; Narbonne, 2005; Chapter 3). Shallower water, more proximal depositional settings are seen in the upper levels of the St John’s Group in Newfoundland, and in the Longmyndian Supergroup of Shropshire, U.K. These shallower successions are both thought

PLATE 1.1. Key Ediacaran taxa from around the globe. **A**: *Charnia masoni* (holotype) from Charnwood Forest, U.K. **B**: *Fractofusus misrai*, from the Mistaken Point Formation, MP2, Mistaken Point, Newfoundland. **C**: *Kimberella* sp., White Sea assemblage, Russia. **D**: *Funisia dorothea*, from the Flinders Ranges of South Australia, taken from Droser and Gehling, 2008. **E**: *Pteridinium* sp. from Namibia. **F**: *Dickinsonia costata*, from the Flinders Ranges of Australia. Specimen housed in the collections of Adelaide University. **G**: *Ernietta* sp. from Namibia. **H**: *Eoandromeda*, preserved as a carbonaceous impression from the Upper Doushantuo Fmn., south China. Photograph courtesy of Maoyan Zhu. **I**: Thin section through an embryo from the Doushantuo Fmn., China; from Callow and Brasier, 2009a, fig. 2A. **J**: *Primocandelabrum* sp., a rangeomorph organism from the MUN Surface, Trepassey Formation, Bonavista Peninsula, Newfoundland, Canada. See Appendix D for all GPS co-ordinates of beds studied during the writer’s 2007–2010 field seasons. All images (unless stated) are from the Brasier Group image archive. Scale bar in A and E = 50 mm. Scale bar in B, C, D, F, G, H and J = 10 mm. Scale bar in I = 100 µm.

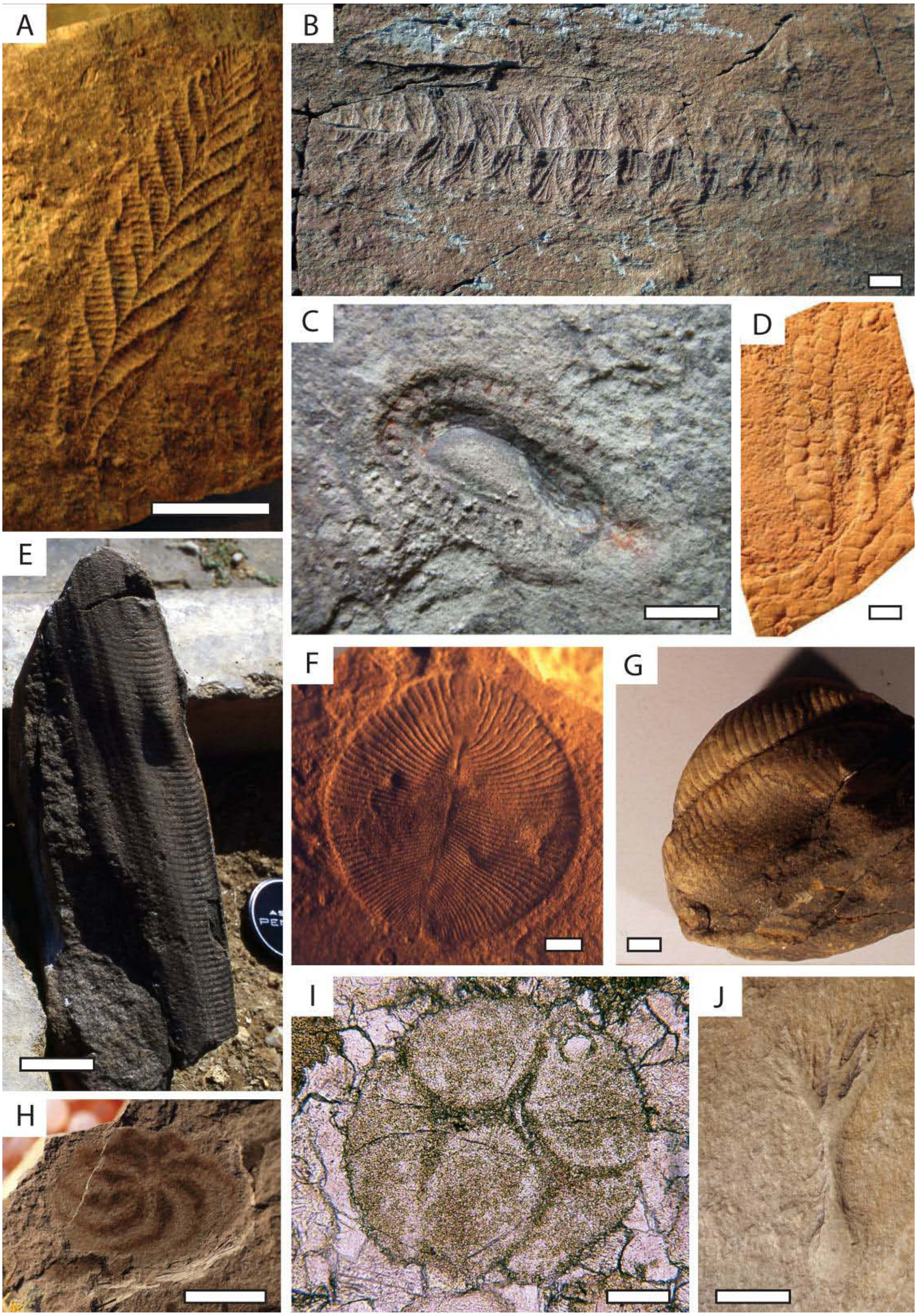

PLATE 1.1

to have been younger than those of the Conception Group and Charnwood Forest respectively, and contain fossil assemblages that differ significantly from those preserved in deep-water palaeoenvironments (Chapter 2).

The earliest Avalonian macrofossils are found in beds dated at 578.8 ± 0.5 Ma (Narbonne and Gehling, 2003; Van Kranendonk et al., 2008), appearing just 3 Myrs after the deposition of the Gaskiers diamictite. This temporal correlation has been used to suggest that the Gaskiers glaciation was a primary factor in the initial evolution and radiation of the Ediacara biota (e.g. Narbonne and Gehling, 2003). Such a relationship, although convenient, may not be correct. The global extent of the Gaskiers event is controversial, and an increasing body of evidence suggests that it was a series of regional, short glaciations, rather than one extended global episode (e.g. Herbert et al., 2010). Therefore, a thorough understanding of both global climatic events, and the temporal nature of the biota, is required to critically test such hypotheses.

The White Sea assemblage is slightly younger at ~560–545Ma, and outcrops in the White Sea and Siberian regions of Russia, as well as in the Flinders Ranges of South Australia (Fedonkin et al., 2007a). There, shallow marine, coarse-grained siliciclastic sediments, and occasionally carbonates, preserve the impressions of soft-bodied organisms. Proposed bilaterian feeding and mining trace fossils also make their first appearance in the fossil record (Jensen et al., 2006 and references therein, though see also Chapter 6). The iconic fossil *Dickinsonia* occurs here (Plate 1.1F), along with the possible stem-group mollusc *Kimberella* (Plate 1.1C; Fedonkin et al., 2007b), and a diverse population of macroscopic tubular organisms (e.g. *Funisia dorothea*; Plate 1.1D; Droser and Gehling, 2008).

Finally, the Nama assemblage of Namibia, and also potentially Spain (Jensen et al., 2007) and California/Nevada (Hagadorn and Waggoner, 2000), is the youngest Ediacaran biotic assemblage, at 549–542 Ma (Grotzinger et al., 1995). Nama fossils are commonly found preserved in three dimensions both on and within shallow marine event beds (Grazhdankin and Seilacher, 2002). The Nama rocks contain distinctive vendobiont organisms such as *Ernietta* (Plate 1.1G) and *Pteridinium* (Plate 1.1E), and some of the earliest biomineralising macro-organisms in the fossil record, *Cloudina* and *Namacalathus* (Grotzinger et al., 2000).

The Doushantuo and Dengying Formations from the Yangtze Platform of China, dated at 580–551Ma (Condon et al., 2005), contain black shales and phosphorites with abundant microfossils, including acritarchs, algae, cyanobacteria, and possible animal embryos (Plate 1.1I; Xiao et al., 1998). Occasionally, carbonaceous and pyritized impressions of macroscopic body fossils also occur (Xiao et al., 2002). These south China sections show some similarities with the Nama assemblage, including shared tubular body fossil taxa (Waggoner, 2003), but the presence of the body fossil *Eoandromeda* (Plate 1.1H) in both China and Australia could imply at least a temporal relationship with the White Sea assemblage (Zhu et al., 2008; Fig. 1.2). Further east, the Lantian Formation of China may contain the oldest macro-fossils in the Ediacaran Period, carbonaceous impressions thought to include algae, roughly 600 Ma (Yuan et al., 2011). The Lantian rocks do not, however, contain any elements of the classic Ediacara biota. Unfortunately, a scarcity of precise radiometric dates for many Ediacaran sections prevents reliable chronological correlation of these geographically disparate assemblages. The Avalon assemblage is regarded as the oldest of the three Waggoner assemblages, and is unique amongst them in containing diverse macro-organisms that are inferred to have lived in deep-marine settings (e.g. Narbonne, 2005). Until the Chinese dates can be confirmed, Avalonian beds are therefore an obvious place to look in order to research the initial evolution and radiation of large and complex organisms in the Ediacaran Period.

WERE ANIMALS PRESENT AMONGST THE AVALON BIOTA?

Determining whether true metazoans were present in Ediacaran ecosystems is a matter of substantial debate, due to the philosophical and scientific importance conferred upon the origins of animal life. In the White Sea assemblage, the mollusc-like organism *Kimberella* (Plate 1.1C; Fedonkin et al., 2007b), and a variety of bilaterian locomotion and grazing traces (e.g. *Helminthoidichnites,* scratch-marks attributed to *Radulichnus,* "under-mat mining traces"; Jensen et al., 2006), indicate that organisms likely to have possessed muscular tissue were present in these environments. In contrast, definitive fossil evidence for metazoans in older rocks is scarce, and is mainly derived from microfossils (though see Seilacher et al., 1998; Bengtson et al., 2007; Maloof et al., 2010). The possible animal embryos described from phosphorite deposits of the Doushantuo Formation (Xiao et al., 1998) are contentious. These spheroidal microfossils, about 500 µm in diameter and possessing clear sub-divisions interpreted as 'cells', have since been subjected to scrutiny. Some workers consider them to be the remains of giant sulfur bacteria (Bailey et al., 2007), but the consensus opinion seems to be that they are embryos (though not necessarily metazoan), and research into this area is ongoing (e.g. Hagadorn et al., 2006; Xiao et al., 2007; Yin et al., 2007). More recently, large acritarchs >100 µm in diameter from early and middle Ediacaran successions have been interpreted as animal resting cysts, based on morphological comparisons with modern invertebrate forms (Cohen et al., 2009a). This potentially pushes evidence for the presence of animals back almost to the Marinoan glaciation, but the accompanying body fossil record of possible metazoans during this period is sparse (see also Chapter 7). Avalonian taxa either show too little morphological detail to be definitively identified as metazoans, or do not fit easily into extant taxonomic groupings. Trace fossil evidence in these rocks is also minimal, with the vast majority of proposed Ediacaran and older ichnofossils reinterpreted as either body fossils or abiogenic impressions in recent reviews (Jensen et al., 2005, 2006).

Over the past decade, study of the Avalonian fossils has focused on their palaeoecology (Clapham and Narbonne, 2002; Clapham et al., 2003), their construction and modes of growth (Antcliffe and Brasier, 2007a, 2007b; Brasier and Antcliffe, 2009; Narbonne et al., 2009), their diet (Xiao and Laflamme, 2009), and the continuous task of documenting new finds and taxa (e.g. Laflamme et al., 2004; Bamforth et al., 2008; Hofmann et al., 2008; Bamforth and Narbonne, 2009; Narbonne et al., 2009; Brasier and Antcliffe, 2009). Debate continues as to whether Avalonian organisms were metazoans. The enigmatic triangular form *Thectardis avalonensis* Clapham et al. 2004 (Fig. 1.3H) is a good example of the problems inherent in trying to assign a taxon with few defining features to a modern biological group. *Thectardis* has recently been suggested to be a sponge, based upon a similar gross morphology to modern sponges (which, it is claimed, possess distinct morphometric characteristics intrinsically linked to the mechanics of their water canal system; Sperling et al., 2011). Similar shape metrics are unfortunately the only positive evidence suggested in support of this interpretation; key crown-group sponge characteristics such as ostea, spicules, a central osculum or obvious asymmetry have never been found associated with *Thectardis* specimens. Therefore, although the theoretical and structural-analogue approach of Sperling et al. should be commended, it remains impossible to objectively determine whether or not *Thectardis* was a poriferan based on current available information. With so few diagnostic morphological traits to work with, difficulty in identifying Ediacaran biological affinities remains.

Thectardis and a few other oddities apart (such as the possible xenophyophore *Palaeopascichnus*; Seilacher et al., 2003; Fig. 1.3F), the Avalon biota is mainly comprised of a mixture of discoidal and frondose fossils (Figs. 1.3–1.5). The discs come in a range of shapes and sizes, and also commonly occur in the White Sea assemblages (e.g. Gehling et al., 2000, table 1). Many discs possess radiating or concentric grooves, which are interpreted by some workers to be the result of tissue shrinkage following burial and desiccation (Gehling et al., 2000), and by others as characteristic features of microbial colonies (Grazhdankin and Gerdes, 2007). The various discoidal taxa, such as *Aspidella*, *Hiemalora*, *Beltanelliformis* and

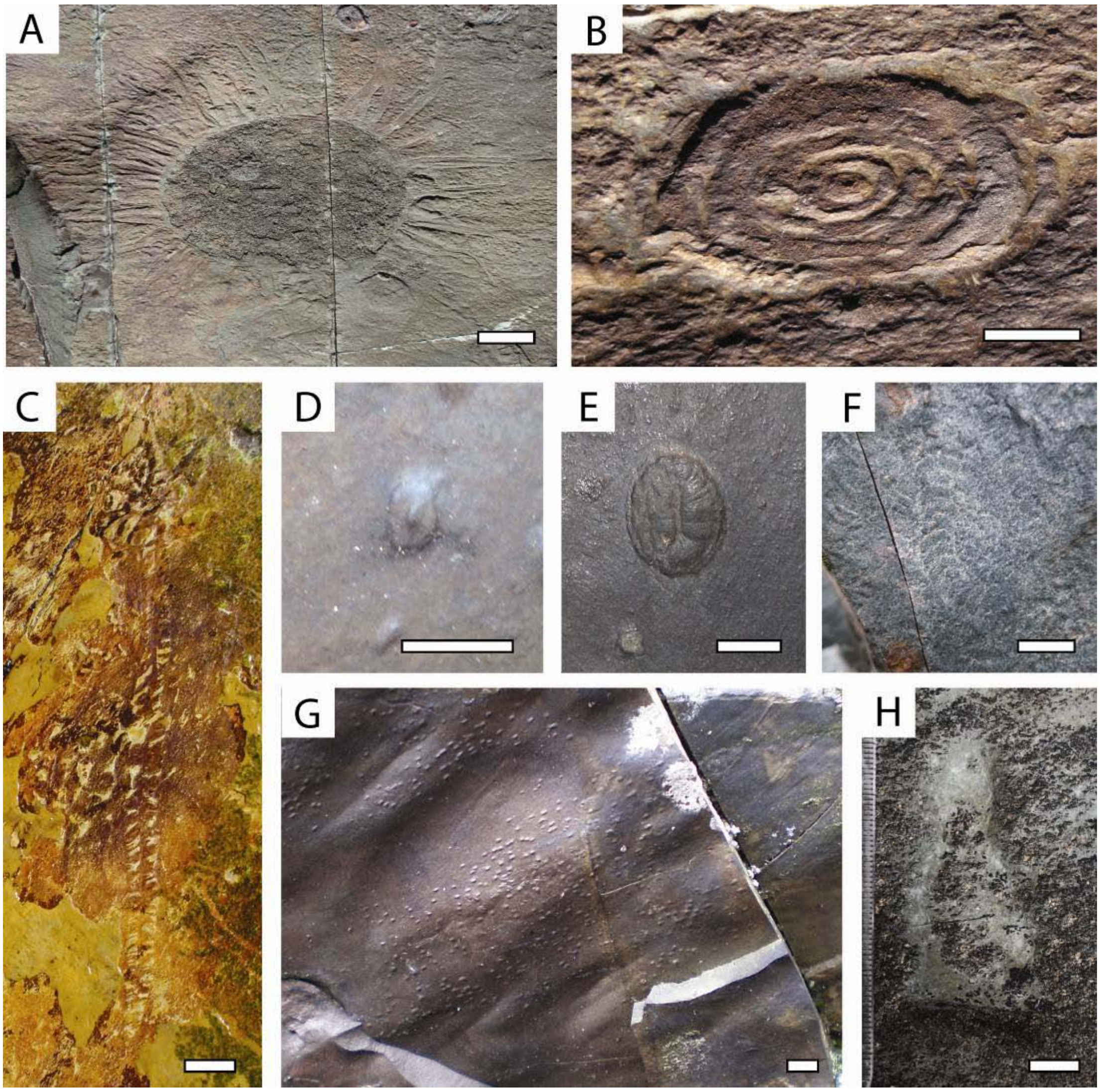

Fig. 1.3. Discoidal fossils and other unusual forms from the Avalon biota. **A**: *Hiemalora stellaris*, Mistaken Point Fmn., Murphy's Cove, Bonavista Peninsula, NL. **B**: Concentric morph of *Aspidella terranovica*, Fermeuse Fmn., Bonavista Peninsula, NL. **C**: *Hadryniscala avalonica*, MUN surface, Trepassey Fmn., Bonavista Peninsula, NL. **D**: *Medusinites* aff. *asteroides*, Burway Fmn., Longmynd, Shropshire, U.K. **E**: Invaginated morph of *Aspidella terranovica*, Fermeuse Fmn., Ferryland, NL. **F**: *Palaeopascichnus delicatus*, Fermeuse Fmn., Ferryland, NL. **G**: *Beltanelliformis minuate*, Synald's Fmn., Ashes Hollow, Longmynd, Shropshire, U.K. **H**: *Thectardis avalonensis*, Mistaken Point Fmn., Mistaken Point, NL. Image H courtesy of Jack Matthews. All scale bars = 10 mm except C, where the scale bar = 100 mm. Images A–C, F and H show the top surfaces of beds; D, E and G image bed bases.

Medusinites (Fig. 1.3A–B, D–E, G), can range in diameter from 1 mm to 0.4–0.5 m in places, though typically they are 20–100 mm. *Aspidella* has been interpreted to be the holdfast disc for many of the frondose organisms in these assemblages (Gehling et al., 2000). Similarly, *Hiemalora* with its radiating rays (Fig. 1.3A) was suggested as the holdfast organ for a benthic organism (Serezhnikova, 2007), a hypothesis confirmed by field observations linking it to *Primocandelabrum* specimens (Hofmann et al., 2008). Therefore, it is highly likely that, despite their very different appearance, many discoidal taxa may be related to frondose specimens, with taphonomic factors largely responsible for determining the proportion of the whole organism ultimately preserved (Laflamme et al., 2011). It must be noted, however, that the considerable morphological variation observed in *Aspidella* morphs (Gehling et al., 2000) may indicate over-synonymisation of the clade (McIlroy et al., 2005).

Fig. 1.4. Spectacular preservation of rangeomorph branching in the multifoliate rangeomorph *Bradgatia*, preserved on the top surface of a bedding plane. Note the self-similarity of the frondose packages, which repeat at smaller scales along each branch of the structure. This specimen comes from the MUN Surface (Appendix D2), Trepassey Formation, Bonavista Peninsula, Newfoundland, Canada. Scale bar represents 10 mm.

The Avalonian fossils that attract most debate are the rangeomorph fronds. These organisms are composed of small, self-similar frondose units (termed rangeomorph units, Narbonne 2004; Fig. 1.4), which can be combined in different arrangements and architectures to produce a myriad of overall morphologies (Brasier and Antcliffe, 2009; Narbonne et al., 2009; Pl. 1.2). The rangeomorphs include such taxa as *Charnia*, *Bradgatia*, *Fractofusus*, *Pectinifrons*, *Beothukis*, *Avalofractus* and *Trepassia*, and fossils of these organisms dominate many Avalonian bedding planes (Clapham et al., 2003; Pl. 1.2). Other organisms with a similar gross morphology but with slightly different styles of branching are also present, such as *Charniodiscus*, *Primocandelabrum*, *Hapsidophyllas* and *Frondophyllas* (Pl. 1.2). The morphologies of all of these organisms are unlike anything seen in modern animal groups, and therefore they have attracted substantial speculation regarding their biotic affinities. Past interpretations for rangeomorph taxa range from seaweeds (Ford, 1958) and crown-group animals (Jenkins, 1985), to 'failed experiments' in multicellular evolution (Narbonne, 2004; Narbonne et al., 2009), and most recently, stem-group animals (Narbonne, 2010).

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PLATE 1.2. Frondose fossils of the Avalon biota. **A**: *Beothukis mistakensis*, Trepassey Fmn., locality PU9 (MUN surface), Bonavista Peninsula, NL. **B**: *Avalofractus abaculus*, Trepassey Fmn., BC1, Upper Island Cove, NL. This specimen is housed in The Rooms Provincial Museum, St John's, NL: NFM F-754. **C**: *Charniodiscus* sp. Hofmann et al., 2008, Mistaken Point Fmn., PU4, Murphy's Cove, Bonavista Peninsula, NL. **D**: *Hapsidophyllas flexibilis*, Mistaken Point Fmn., MP1, Watern Cove, Mistaken Point, NL. **E**: *Bradgatia linfordensis*, Fermeuse Fmn., LC2, Little Catalina, Bonavista Peninsula, NL. **F**: *Pectinifrons abyssalis*, Mistaken Point Fmn., MP N, Mistaken Point, NL. **G**: *Primocandelabrum hiemaloranum*, Mistaken Point Fmn., PU4, Murphy's Cove, Bonavista Peninsula, NL. **H**: *Charnia masoni*, Trepassey Fmn., MUN surface, Bonavista Peninsula, NL. **I**: *Trepassia wardae*, Drook Formation, CW1, Daley's Cove, NL. Scale bars in A, B, C and H = 10 mm. Scale bars in D, E, G and I = 50 mm, and in F = 100 mm. All images show the top surfaces of bedding planes.

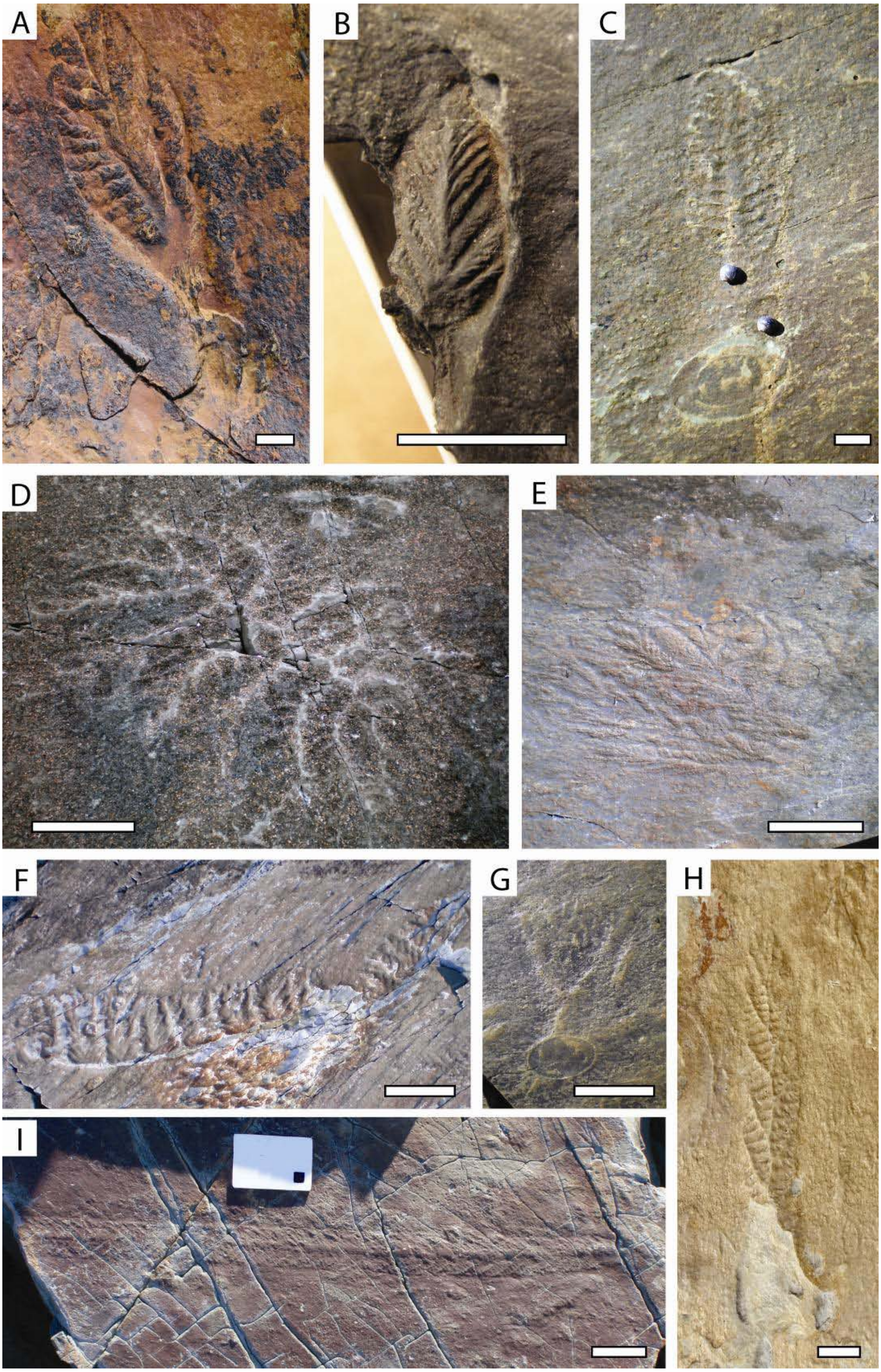

PLATE 1.2

The deep marine depositional environments postulated for the Avalonian successions (e.g. Wood et al., 2003) discount the possibility that these organisms (preserved *in situ* on the seafloor) were photosynthetic in life. Apparent analogies between rangeomorph fronds and modern plant leaves are therefore likely to be indicative of a convergent functional role rather than a biological ancestry (Laflamme and Narbonne, 2008). This has encouraged researchers to probe the metabolic requirements of rangeomorphs, with suggestions that, rather than viewing them as sessile filter feeders (e.g. Narbonne, 2005), they may in fact have been osmotrophs, absorbing nutrients directly from the water column (Laflamme et al., 2009).

Recent work examining the composition of sediments associated with *Aspidella* from the Fermeuse Formation of Newfoundland suggests that the organisms may have incorporated sediment within their bodies during life, in a similar way to modern deep marine xenophyophores (Laflamme et al., 2011; though see also Seilacher, 1992; Seilacher et al., 2003). Rangeomorphs may therefore represent a very different type of organism to anything we are familiar with today, though further research into their biology and taphonomy is required. It remains to be seen whether frondose taxa considered by some to be non-rangeomorph fronds (e.g. *Charniodiscus*; Narbonne *pers. comm*. 2009) could also have been osmotrophs.

Although research is beginning to uncover many of the secrets surrounding the enigmatic Ediacaran organisms, there is still work to do. The presence (or absence) of metazoans in the Avalon assemblage remains to be verified. We must also ensure that the new taxonomy being developed is robust, and determine whether apparent morphological differences between species are truly taxonomic in origin. Such issues must be resolved before we can put the Ediacara biota into its true Precambrian–Cambrian evolutionary context.

THE CONTEXT FOR THE EDIACARAN PERIOD

To fully understand the biological changes occurring in the Ediacaran Period, it is essential to appreciate the scale of the global geological events happening at that time. The late Neoproterozoic was an interval of immense change in the biosphere. Not only was life developing a series of biological innovations that would culminate in the appearance and dominance of metazoans in marine ecosystems, but numerous chemical and physical changes were also taking place.

The Cryogenian glaciations

Thick glacial diamictites deposited synchronously on multiple continents at all palaeolatitudes suggest that widespread and long-lived glacial events affected the planet more than once, both before and during the Ediacaran Period (e.g. Hoffman et al., 1998; Fig. 1.2). The most extreme interpretation of these observations envisages the planet being totally enveloped in ice for millions of years in a 'Snowball Earth' event (Kirschvink, 1992). The Earth could have been released from such glacial conditions only after the gradual increase in atmospheric CO_2, caused by global volcanism, had reached a level high enough to trigger a runaway greenhouse effect (Kirschvink, 1992; Hoffman et al., 1998). Contrary to this view, a raft of data incompatible with a full 'snowball' hypothesis has emerged in recent years, and a less severe but equally influential 'slushball' model, positing extreme polar glaciations but not full global ice coverage, is gaining support (e.g. Kilner et al., 2005; Dobrzinsky and Bahlburg, 2007; Allen and Etienne, 2008; Etienne et al., 2009). The most recent studies are revealing subtle differences in the scale and nature of the individual glacials, with the Sturtian and Marinoan events being the largest and longest (Dobrzinsky and Bahlburg, 2007; Kasemann et al., 2010). Importantly, the younger Gaskiers glacial may turn out to be a series of smaller, regional glaciations, rather than one single global event (Chumakov, 2009; Herbert et al., 2010).

Indeed, it is substantially shorter in duration (~1 Myr) than the other ‘snowballs’, often lacks a cap carbonate, and exhibits atypical carbon isotope trends through its stratigraphy (Narbonne et al., 2005). While the debate over the spatial extent and correlation of these glaciations will continue, their long durations (on the order of 10^5–10^6 years; Kilner et al., 2005), and associated physical and chemical changes recorded in marine sediments, imply that they had a significant effect on the biosphere. They have therefore been postulated to be responsible for many of the major biotic events in the Precambrian (e.g. Boyle et al., 2007; Chumakov, 2010). Global facies occurrences have suggested that climate over the remainder of the Ediacaran Period (following the glacials) was warm and humid (Chumakov, 2007).

The break-up of Rodinia

The supercontinent of Rodinia (McMenamin and McMenamin, 1990), which formed gradually during the early Neoproterozoic (Li et al., 2008), had mostly rifted apart by the Ediacaran Period. Such Cryogenian rifting events (Bogdanova et al., 2009) may be related to the Sturtian and Marinoan ‘snowball’ events (Dalziel, 1997), but they occurred too early to have influenced the Avalonian biotic diversification. Of greater consequence is a second supercontinent, Pannotia, thought by some to have existed during the Ediacaran Period. Pannotia formed ~650 Ma, and began to break apart again around 560 Ma (Scotese, 2009). Such rifting would have greatly increased the distribution of shallow marine shelves and slopes, and raised the sea level (e.g. Brasier, 1992). This tectonic activity could therefore have provided abundant unoccupied ecospace for organisms to radiate into, and potentially stimulated both the Ediacaran and Cambrian biological radiations (cf. McIlroy and Logan, 1999; Brasier and Lindsay, 2001).

During the Ediacaran Period, the fossil-bearing bedding planes of Newfoundland and the central U.K. lay off the micro-continent of Avalonia, a terrane that was likely located on the edge of the Cadomian arc subduction zone, in the vicinity of the Florida, Amazonia and West Africa cratons (Fig. 1.5; Li et al., 2008). Avalonia consisted of regions in the modern day United Kingdom, eastern Newfoundland and parts of New Brunswick and Nova Scotia in Canada, and parts of New England, U.S.A. (Landing, 1996; Thompson et al., 2007). Although Avalonia is thought to have been located at roughly 60° south during the Ediacaran Period (Pisarevsky et al., 2008), it should be noted that palaeogeographic reconstructions this far back in time are considered rather imprecise (Torsvik, 2003; Li et al., 2008). There is also reason to believe that the Earth's magnetic field during the late Neoproterozoic may have been distinctly non-uniformitarian, hampering attempts to determine true palaeogeographic positions (Abrajevitch and Van der Voo, 2010).

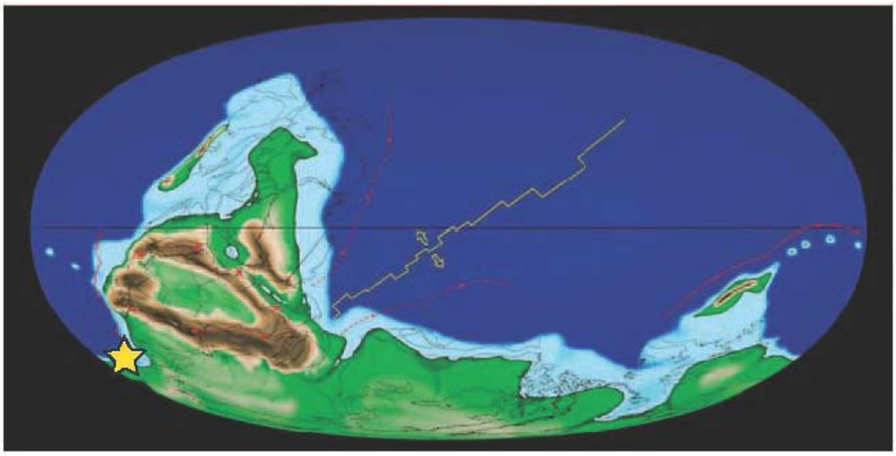

Fig. 1.5. One possible palaeogeographic reconstruction for the Ediacaran Period, plotted on an oval projection for 600 Ma modified from Scotese, 2009. The position of Avalonia (gold star) is debated (see McKerrow et al., 1992; Samson et al., 2005; Pisarevsky et al., 2008 and Li et al., 2008 for alternative reconstructions). Here Avalonia is located off the West African and Amazonian cratons, a position that is consistent in most palaeogeographic reconstructions. The proposed latitude of Avalonia can however vary in the literature from almost on the South Pole (Samson et al., 2005) to as low as 38°S (Thompson et al., 2007).

Widespread geochemical perturbations

Late Neoproterozoic geochemical data show the largest negative shift in stable carbon isotopes in the geological record (>10‰), known as the Shuram/Wonoka excursion (e.g. Le Guerroue, 2010). This is identified in sections from Oman and Australia (Halverson et al., 2005), and reveals large-scale perturbations to the global carbon cycle (Le Guerroue et al., 2006; Le Guerroue, 2010). The exact date at which this occurred is still debated, due to multiple excursions and a dearth of dated sections. Some workers correlate the Shuram event to glaciations of Gaskiers age (though both the Marinoan and Sturtian carbonate deposits also show large negative carbon isotope anomalies), while others consider it to be around 551 Ma (Condon et al., 2005). The relationship between this chemical shift and the glaciations, and more importantly with the biota, remains to be determined. The global nature of the Shuram event also needs to be validated (Bristow and Kennedy, 2008). Ecosystem engineering is one potential way in which the biota may have caused these chemical perturbations, with changes in macroecology enforcing top-down controls upon the chemistry of the oceans (Butterfield, 2011). There is evidence from carbon and sulfur stable isotope records for a rise in deep marine oxygen levels through the Ediacaran Period (Fike et al., 2006). Further geochemical analyses exploring iron speciation during the late Ediacaran Period reveal a ferruginous and often sulfidic water column (Canfield et al., 2008). An apparent pulse of oxygenation to the deep oceans is thought to have immediately followed the Gaskiers glacial event in Newfoundland (Canfield et al., 2007). This perceived rise in oxygen in deep-marine ecosystems has previously been proposed as a causal factor for the appearance of the first large macro-organisms in Ediacaran palaeoenvironments just three million years later (Cloud Jr., 1968; Narbonne and Gehling, 2003; Catling et al., 2005; Canfield et al., 2007). Although almost all modern animals require oxygen in order to survive (Narbonne, 2010), the hypothesis that the rise in global oxygen levels is a forcing factor in the evolution of metazoans has received criticism (Budd, 2008; Butterfield, 2009a). In the absence of direct proxies for absolute oxygen levels, it is difficult to quantify the exact timing and magnitude of a Proterozoic atmospheric oxygen rise. Even then, there is no way to be certain that in a non-uniformitarian world, the chemistry of the deep oceans would follow that of the atmosphere (Butterfield, 2009a). Evidence for large-scale carbon burial in the form of black shale deposits directly above the Marinoan/Nantuo diamictite levels in China could reveal one way in which huge quantities of oxygen could have been released into the biosphere (Jiang et al., 2010). A reduction in marine salinity and ocean temperatures through the late Neoproterozoic could also have permitted an increase in dissolved oxygen concentrations (Meng et al., 2011). The data obtained from the Avalon region in support of a link between oxygen levels and the initial evolution of the Ediacara biota (Canfield et al., 2007) should be treated with caution on the grounds that it is a regional, not global, study (though similar patterns have more recently been recorded from NW Canada and China; Shen et al., 2008a). The temporal range of that studied interval also does not extend far enough before the Gaskiers glacial to accurately constrain oxygen levels prior to that event. Therefore, it is considered that further work is required to confirm a causal relationship between oxygen levels and the evolution of complex multicellular life.

The response of biology

All of these events – the breakup of Rodinia, the Shuram/Wonoka carbon isotope excursion, the Snowball Earth glaciations, and the apparent oxygenation of the deep oceans – occurred broadly simultaneously with the first appearance of the Ediacara biota. The extent to which they are related remains to be determined, but it is likely that feedbacks governed by one or several of these events are responsible for triggering the others (McIlroy and Logan, 1999).

Determining the exact feedbacks and forcings involved in the evolution of macroscopic multicellularity is one of the ultimate goals in Ediacaran research.

It is important here to distinguish between macro-organisms and multicellularity. Multicellularity had evolved at a microscopic level, maybe multiple times, prior to the Ediacaran Period. A recent review recognises nine different groups of multicellular organisms fossilised in rocks older than 635 Ma (Butterfield, 2009b), while a diverse array of eukaryotic microfossils are described from older units (e.g. Sergeev and Schopf., 2010). Prior to the Ediacaran Period, multicellular life is most widely represented by the acritarchs, a group of spherical organic-walled microfossils of uncertain biological affinity (Vidal and Moczydlowska-Vidal, 1997). Possible biomineralization may also have evolved in some eukaryote lineages ~750 Ma (Porter et al., 2003). The fossil record of complex multicellular macroscopic organisms does not begin until the mid-late Ediacaran with the Avalon assemblage (Narbonne and Gehling, 2003; though note the Lantian biota of south China, Yuan et al., 2011). Although several workers have proposed a biological ‘bottleneck’ during the ‘Snowball Earth’ events, with the climatic changes reducing global biotic diversity (e.g. Hoffman et al., 1998; Narbonne and Gehling, 2003), the survival of numerous eukaryotic clades through these events questions the validity of this claim (Porter, 2004).

NEW FINDINGS FROM THE AVALON BIOTA

The research presented herein approaches the biological affinities of Ediacaran organisms from the standpoints of taphonomy, ontogeny and palaeoecology. Much uncertainty surrounds both the biology of the Ediacara biota, and exactly what observed morphological differences between taxa may represent (see discussion in Brasier and Antcliffe, 2004). Understanding the principles governing the preservation, morphology and distribution of these fossils is therefore crucial if we are to constrain the true biology, behavioural capabilities, and evolutionary histories of the original organisms they record.

Ontogeny (Chapter 2)

Understanding the ontogeny of an organism can inform us regarding its biological affinity, since ontogeny often recapitulates phylogeny (cf. Antcliffe and Brasier, 2007a). The morphology of an organism is commonly controlled by functions or processes that are integral to the survival of the individual (Thompson, 1961). Morphological development as an organism grows from juvenile to adult can inform us about the behaviour and even the evolutionary relationships between individual species, and can be used to test the various phylogenetic hypotheses that have been proposed. The description of an assemblage of potentially juvenile rangeomorph fronds from the lowest fossil-bearing beds of the Drook Formation in Newfoundland, Canada, provides new insights into the ontogeny and reproductive processes utilised by these organisms (Chapter 2). Their age, at ~579 Ma, suggests that substantial rangeomorph diversity existed just 3 Myrs after the end of the Gaskiers glaciation. The question of whether this morphological diversity truly represents taxonomic variation is discussed, along with the implications this assemblage has for the timing of evolutionary events. Stratigraphic range charts are also constructed for taxa from Avalonian localities to identify possible evolutionary or ecological patterns within the biotic assemblages.

Taphonomy (Chapters 3–4)

A thorough understanding of taphonomy is vital if we are to accurately quantify the biological diversity and disparity of a fossil assemblage. We must be able to distinguish between true morphological features preserved as fossils, and those features that have been introduced after the death of an organism by biological, erosive, tectonic or chemical processes. The recognition of effaced preservation, a term presented herein to describe the process by which microbial degradation of macro-organisms effaces their resultant morphologies, has important implications for nutrient cycling and biotic diversity in Ediacaran assemblages (Chapters 3–5; Liu et al., 2011). Laboratory testing of this hypothesis, utilising a combination of experimental taphonomy and novel applications of computer tomography (CT) x-ray imaging, represents an important advance in applying laboratory techniques to Ediacaran successions (Chapter 4). The consequences of this hypothesis for taxonomy are discussed (Chapter 3). The proposal of 'tapho-taxa' within the Avalonian fossil assemblages represents a paradigm shift in our views of Ediacaran communities, and demonstrates that there is still much to learn about the mechanisms by which organisms were preserved on the Avalonian seafloor. Petrological and sedimentological studies further illuminate our understanding of Avalonian taphonomy and depositional environments.

Palaeoecology (Chapters 5–6)

Like any good research, Ediacaran palaeontology must have strong foundations if the exciting findings within it are to stand the test of time. Therefore, until we obtain a complete understanding of what is being preserved, how it is being preserved, and when it existed, we should exercise caution when attempting to fit the Ediacara biota into the bigger evolutionary story. Previous palaeoecological studies have considered the Avalonian bedding plane assemblages to record census populations of organisms alive at the time of burial. They have then used this assumption to validate research into the community structure of the organisms (measuring parameters such as species richness and diversity; Clapham and Narbonne, 2002; Clapham et al., 2003). Work comparing the taxonomic standing diversity of the Avalon region with White Sea and Nama assemblages (Shen et al., 2008b), whilst reaching interesting conclusions, also cannot hope to identify true evolutionary patterns until accurate taxonomic registers are obtained. Importantly, such studies were undertaken *before* the majority of organisms on the bedding planes had been formally described or identified, and without consideration of the time-averaging of populations, as revealed by the effaced preservation hypothesis (Liu et al., 2011). In light of effaced preservation, the palaeoecology studies of Clapham et al. (2003) are revisited and revised, revealing that, contrary to previous conclusions, the Mistaken Point fossil assemblages cannot be said to possess similar community structural attributes to modern animal ecosystems (Chapter 5).

The recognition that microbial organisms living alongside Ediacaran macro-organisms played a crucial role in the preservation of the Ediacara biota is not new (e.g. Gehling, 1999; Laflamme et al., 2011), but the interaction of microbes with deceased organisms is previously undocumented (Chapters 3–5). Microbes interacting both with the sediment and their larger neighbours on Ediacaran bedding planes have also been discovered, representing a previously unrecognised aspect of Ediacaran ecosystem dynamics (Chapters 2, 4 and 7). The role of microbes in the preservation, stabilisation, and even nutrition of the Ediacaran macro-biota is explored.

Finally, evidence for behaviour can further inform our concepts of what these organisms were biologically capable of doing. Recognition of ~565 million year old locomotory trace fossils within the Avalon assemblages of Mistaken Point in Newfoundland, reveals that novel behavioural innovations were developing in communities and environments previously considered entirely sessile (Chapter 6; Liu et al., 2010a). Moreover, the structure of these fossilized impressions strongly suggests that their creator possessed muscular tissue, and therefore was likely to have been of metazoan grade. This discovery creates an ichnofossil gap in the fossil record, with under-mat miner traces from the White Sea biota being the next known ichnofossils ~10 Myrs later. Other unreported trace fossils from several Avalonian successions are also described (Chapter 6), demonstrating that evidence for motile macro-organisms, although relatively rare, is present throughout the Avalon terrane.

SUMMARY

To elaborate upon Lyell's metaphor, the discovery of fossils in Precambrian rocks has unearthed further, albeit more fragmentary, volumes of the "history of the world" that were unavailable to Darwin and Lyell in the mid-1800s (pg. 1). These fossils provide extensive insights into the evolution of the biosphere, and the place of all living things within it. The ultimate aim of this study is to test and enhance our knowledge of ancient Ediacaran palaeocommunities, thereby furthering our understanding of the evolution of complex life on Earth.

The findings of this thesis do much to revise our views of Ediacaran ecosystems. Avalonian bedding planes do not record census populations of sessile, filter-feeding macro-organisms, considered to be animals by virtue of their tiered community structure (*sensu* Narbonne, 2005). Rather, they preserve diverse assemblages of living and deceased organisms, potentially including motile metazoans, and microbial prokaryotes and eukaryotes. Together, these Avalonian fossils document the unique interval over which macro-organisms first appeared and asserted themselves in marine environments. The evolutionary and ecological milestones documented in Ediacaran strata subsequently paved the way for the metazoan Phanerozoic biosphere, which has existed successfully through to the present day.

CHAPTER 2

THE DEVELOPMENT AND STRATIGRAPHIC RANGES OF AVALONIAN MACRO-ORGANISMS

PREFACE

Knowledge of the stratigraphic ranges over which individual Ediacaran taxa occur is currently inadequate. The dearth of radiometric dates from many successions, and limited correlation between geographically dispersed localities, has inhibited attempts to obtain detailed global ranges. Similarly, the ontogenetic development of the Ediacara biota, considered to be of critical importance in determining the biological affinities of the organisms (Brasier and Antcliffe, 2004; Antcliffe and Brasier, 2008), and fundamental to distinguishing between taxonomic entities, has received little attention.

This chapter examines a previously unreported assemblage of rangeomorph and filamentous fossils from a surface at Pigeon Cove on the Avalon Peninsula of Newfoundland. These findings are being written up for publication with Jack Matthews, Duncan McIlroy, and Martin Brasier under the title "*Juvenile Ediacaran organisms from Newfoundland increase the diversity of the oldest Avalonian macroscopic fossil assemblages*", for submission to the *Journal of the Geological Society, London*. The frondose forms, all less than three centimetres in length, are considered to represent the juvenile growth stages of Ediacaran organisms, including *Charnia* spp. and *Trepassia* spp. This is the first discovery of a large population of juvenile rangeomorph fossils from Ediacaran rocks, providing insights into the ontogeny of the earliest members of the Ediacaran macrobiota. The occurrence of these fossils, alongside a population of large ivesheadiomorph taxa (see Chapter 3; Liu et al., 2011), represents one of the oldest documented examples of secondary community succession, recording a pioneer community colonizing an ecosystem inferred to have previously been relatively mature. Sinuous filamentous fossils from Pigeon Cove are described for the first time, preserving a little-studied component of Ediacaran macrofossil assemblages in Newfoundland. Similar forms from other bedding surfaces on the Bonavista and Avalon Peninsulas are also described, and comparisons are made with a variety of extant and fossil filamentous organisms.

The Pigeon Cove assemblage may extend the stratigraphic ranges of several taxa, increasing the biotic diversity of the earliest Ediacaran macrofossil assemblages. Such a suggestion has implications for interpretations of the 'Avalon Explosion' of macroscopic organisms (cf. Shen et al., 2008b). A regional context in which to test this claim is provided by the construction of detailed stratigraphic range charts for fossils from the Avalon terrane localities. These charts combine data from the literature with information collected by the author during fieldwork in both Newfoundland and the U.K. (see Appendix D for a comprehensive list of studied localities). Such ranges uncover important patterns and relationships, informing our views on the evolutionary history of rangeomorphs. Interesting new finds and bedding planes are discussed, and the patterns observed in these charts are examined from both regional and evolutionary perspectives.

Further images and information regarding the biota from the Drook Formation of Pigeon Cove, and a detailed map of the bedding plane on which it is preserved, can be found in Appendix A. The assemblage was discovered by Duncan McIlroy, while Jack Matthews assisted in mapping and documenting it in the field.

INTRODUCTION

The Ediacaran strata of eastern Newfoundland, dated at ~579–550 Ma (Bowring et al., 2003; Van Kranendonk et al., 2008), preserve abundant large and complex fossilised macro-organisms. Fossil assemblages are dominated by soft-bodied rangeomorphs and other frondose taxa (e.g. *Charnia*, *Bradgatia*; Brasier and Antcliffe, 2009), and discoidal forms (e.g. *Aspidella*, *Hiemalora*; Hofmann et al., 2008). These strata contain the oldest Ediacaran fossils that can be calibrated by reliable published dates, within the upper Drook Formation of Pigeon Cove, Mistaken Point Ecological Reserve (MPER; Narbonne and Gehling, 2003; Fig. 2.1), dated at 578.8 ± 0.5 Ma (Van Kranendonk et al., 2008).

The turbiditic mudstones and tuffs of the Drook Formation are interpreted to have been deposited in a deep marine basin/slope setting, near to an active volcanic island arc (Gardiner

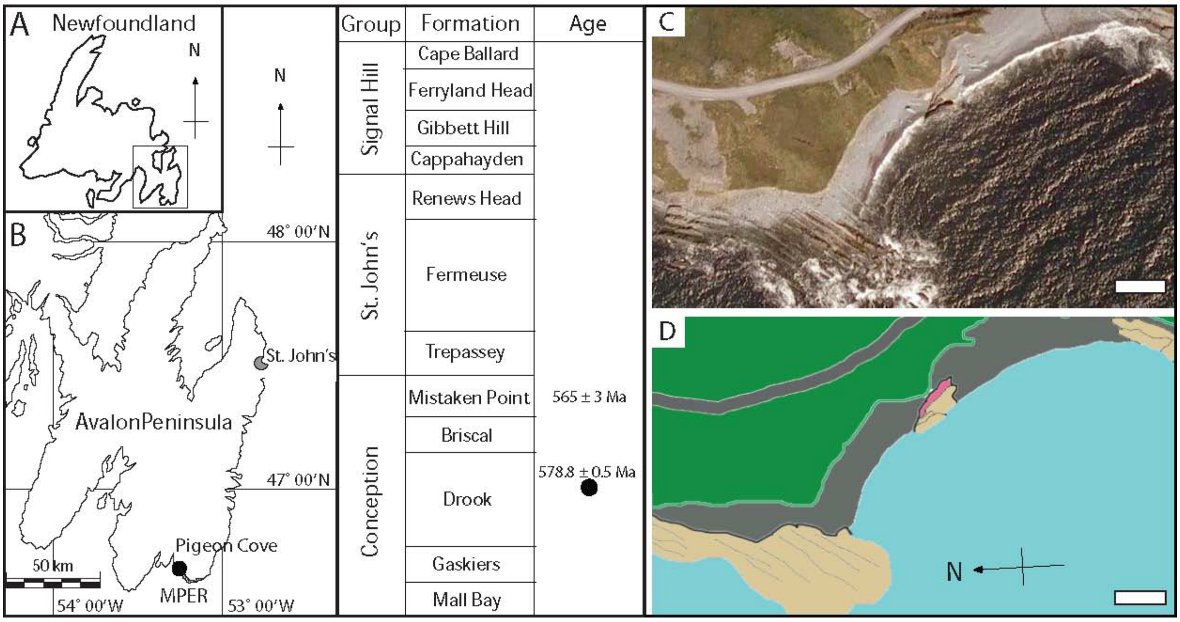

Fig. 2.1. Map and stratigraphic column showing the location and setting of the Pigeon Cove bed, Newfoundland (black circles). Dates taken from Benus, 1988 and Van Kranendonk et al., 2008. **A**: Newfoundland, eastern Canada. **B**: The Avalon Peninsula, showing Pigeon Cove on the south coast. **C**: Aerial photograph of Pigeon Cove (National Air Photo Library, Department of Energy, Mines, and Resources, Government of Canada). **D**: Digitised simplification of the Pigeon Cove aerial photograph in C, showing bedding plane exposures (sand-brown) and the mapped bed (pink). Scale bar length in C and D = 20 m.

and Hiscott, 1988; Wood et al., 2003; O'Brien and King, 2005; Ichaso et al., 2007). A low diversity assemblage of Ediacaran taxa has been documented from the Drook Formation of Newfoundland. This includes *Trepassia wardae* Narbonne et al. 2009, a rangeomorph frond up to two metres in length (Narbonne and Gehling, 2003); *Charnia antecedens* Laflamme et al. 2007; the enigmatic triangular form *Thectardis avalonensis* Clapham et al. 2004; and rare morphs of *Aspidella terranovica*, thought to be the holdfasts of unknown frondose organisms (Narbonne et al., 2007; Fig. 2.2A–C). The most commonly observed fossils on the Pigeon Cove horizon discussed herein (Figs. 2.1D, 2.3) are the ‘pizza disc’ morphs of *Ivesheadia* (Fig. 2.2D; Liu et al., 2011), which can reach up to 0.5 m in diameter.

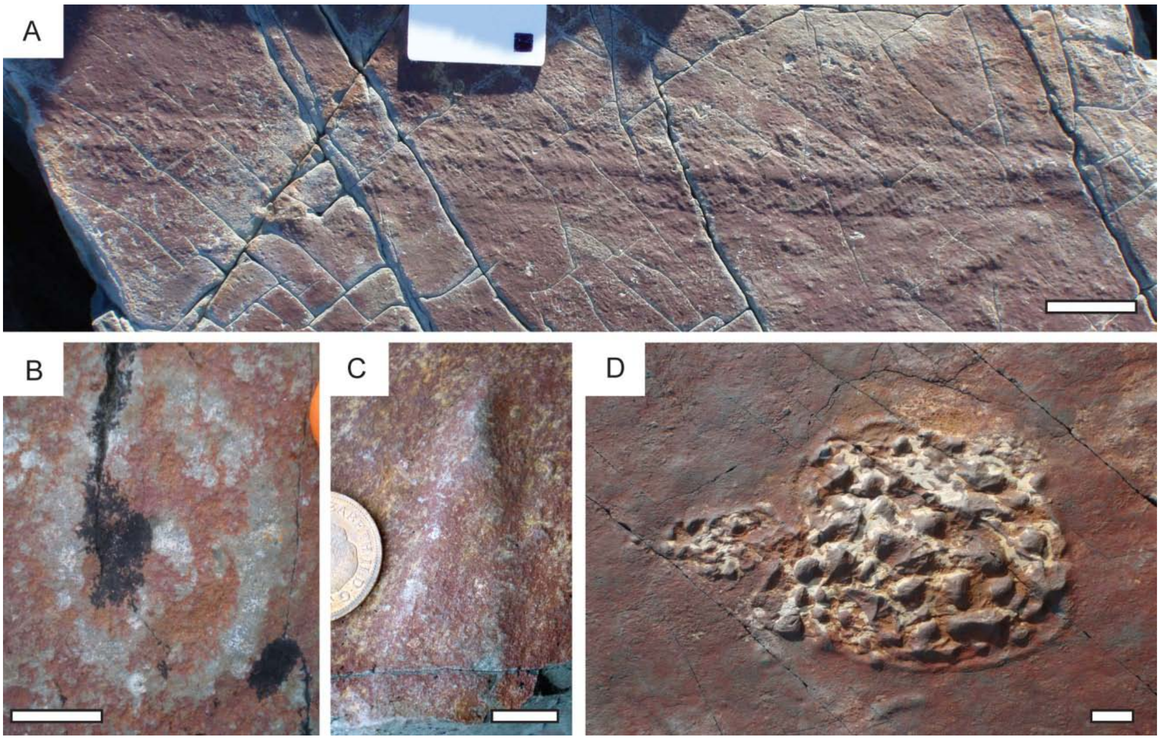

Fig. 2.2. Taxa previously reported from the upper Drook Formation of the Mistaken Point Ecological Reserve, Newfoundland. **A**: *Trepassia wardae* from Daley’s Cove, locality CW1. **B**: *Aspidella* sp. **C**: *Thectardis avalonensis*. **D**: 'Pizza disc' ivesheadiomorph. The fossils in B–D are all from the Pigeon Cove bed documented in this study, locality DRK2PC; see Figs. 2.1, 2.3 and Appendix A4 for further geographical information regarding this locality. Scale bar A, D = 50 mm, scale bar B, C = 10 mm. All figured specimens remain *in situ* in the field. All images of fossils in this chapter show the top surfaces of bedding planes.

There are no previous reports of high-fidelity fossil preservation from this particular horizon in Pigeon Cove, home to one of the oldest known Ediacaran fossil assemblages in the world. Herein, the discovery of a new assemblage of small frondose and filamentous fossils, all exhibiting fine preservation of morphological features on a scale of 1 mm or less, is reported. The bed in question (Fig. 2.3A; Appendix A4) is well documented in the scientific literature for its large ivesheadiomorph impressions (e.g. Narbonne et al., 2001, 2005; Peterson et al., 2003; Narbonne, 2007; Liu et al., 2011). Nevertheless, the remarkable diminutive fauna it preserves has previously been overlooked.

DESCRIPTION

The new fossils can be categorised within two groups, namely fronds (rangeomorph or similar Ediacaran taxa), and filaments (thin threads and strands). The Pigeon Cove bed has been extensively mapped by the writer to document all such impressions, revealing 128 fronds and 144 filaments to date (Fig. 2.3; Appendix A4). Since only those forms with undoubtedly frondose features have been recorded, these values are likely to underestimate the total population size. For example, evidence has since been found for additional partial and lower-relief preservation of both fronds and filaments from casts obtained from the bedding surface.

All fronds and filaments are preserved on the siltstone bedding plane as low positive epirelief (<1 mm) casts, their preservation consistent with the Conception-type taphonomic model, whereby organisms were preserved beneath rapidly lithifying volcanic ashes (Narbonne, 2005). Interestingly, taxa found elsewhere within the Avalon region as predominantly negative epirelief impressions (e.g. *Charnia masoni*) occur here in positive epirelief. It is possible that the unusually large thickness of tuff covering this horizon (>30 cm) is responsible for these differences, with the additional weight of this tuff compacting it sufficiently to preserve a mould of the top surface of the organisms before they decayed away. Alternatively, the small surface area of the specimens may play a part; it is noted that comparable well-preserved rangeomorph specimens from Upper Island Cove, which are only a few centimetres larger than those described here, are also capable of being preserved in positive epirelief (Narbonne, 2004). 'Effaced' preservation (Liu et al., 2011) is clearly exhibited in the numerous large 'pizza disc' ivesheadiomorphs present on the bedding plane

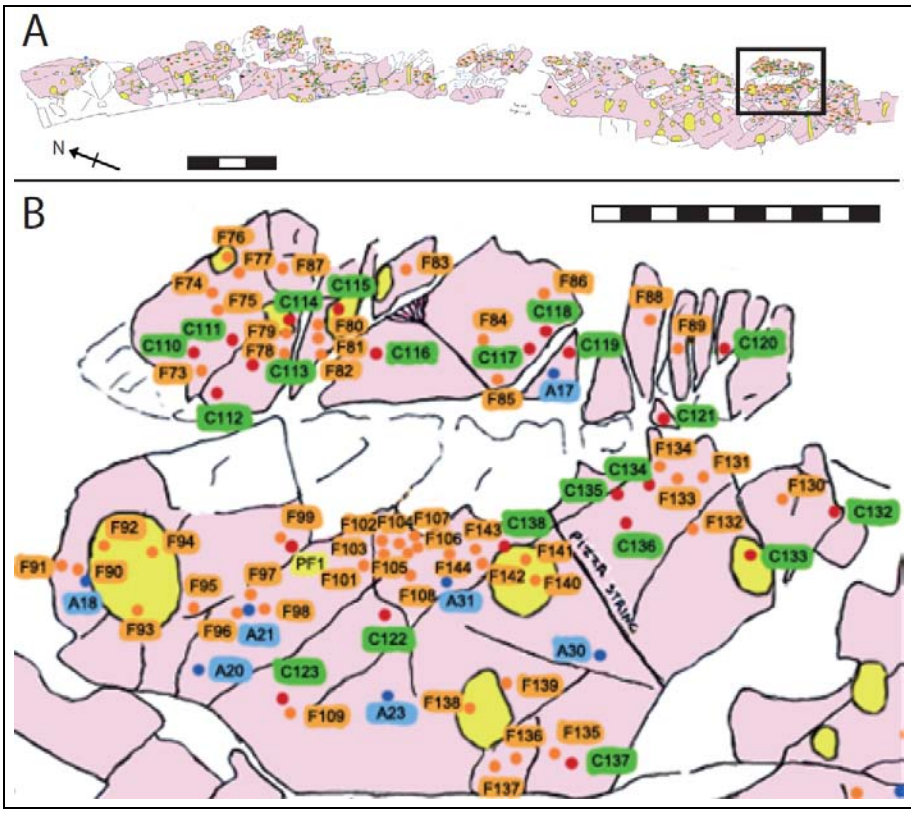

Fig. 2.3. **A**: Overview of the mapped Pigeon Cove bedding plane (as it appeared in the summer of 2008). Scale bar increments = 1 m. **B**: Small region of the Pigeon Cove surface outlined by the black box in A, which includes the ‘flower fossil’ pizza disc (see Pl. 3.1, fig. 5). Scale bar = 1 m (0.1 m increments). Note the fracturing of the surface by wave action and erosion. By 2009, all those blocks in the top half of image B (and their fossils) had been removed by the intervening winter storms; the largest block (containing C116) has been salvaged and is currently in The Rooms Provincial Museum, St John’s, NL, specimen NFM F-794. Ivesheadiomorphs are shown in yellow, frond locations by red dots (green labels), filaments are orange, biological features of uncertain affinity are blue. For a complete high-resolution fold-out map and key, refer to Appendix A4, Fig. A4.3.

(Fig. 2.2D; Chapter 3). The presence of effaced preservation within the small fronds themselves has been more difficult to determine, owing to their diminutive size, and the substantial amount of modern abrasion that has affected this surface.

The 128 fronds identified in the field range from 3–30 mm in length and 1–6 mm in width (Figs. 2.4–2.5; Appendix A1.3). Fronds are observed both with and without stems and basal holdfasts, and exhibit a broad southeasterly-trending orientation (Fig. 2.6A), suggesting that they were once tethered to the seafloor and influenced by currents flowing over the sediment-water interface (cf. Seilacher, 1992). The fronds appear to be randomly distributed across the bedding plane (Figs. 2.3, A4.2D), although localised regions of tuff cover, and damage by modern weathering, prevent objective analysis of such patterns through, for example, nearest neighbour statistical analysis.

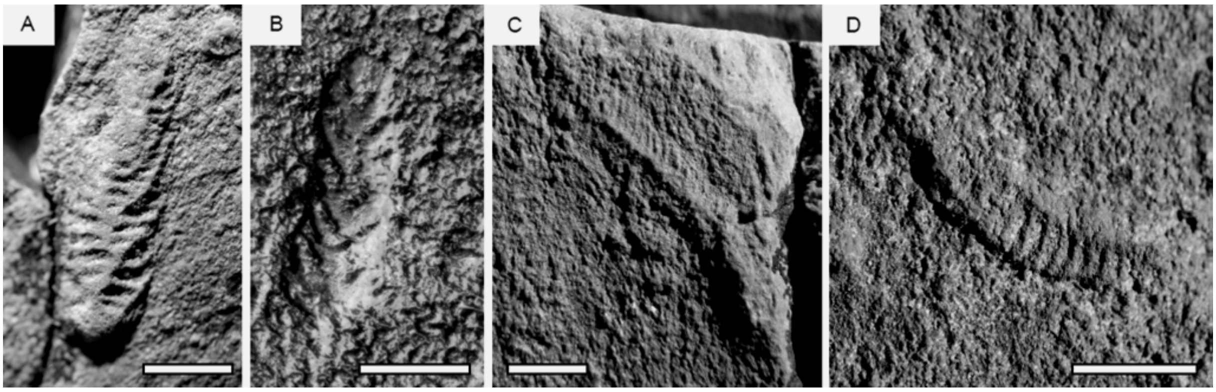

Fig. 2.4. A selection of the small frondose organisms seen at Pigeon Cove, Avalon Peninsula, Newfoundland. **A**: *Charnia* aff. *masoni*, frond C8 on the map (see Fig. 2.3; Appendix A4). A replica cast of this specimen is housed in the Oxford University Museum of Natural History, OUM ÁT.426/p. **B**: *Charnia masoni,* C1, OUM ÁT.425/p. **C**: aff. *Trepassia wardae,* C84, OUM ÁT.428/p. Note that in such specimens, primary branching angle varies substantially within the population. **D**: A specimen likely to be a partially folded aff. *Trepassia*, showing just one row of primary branches, C42, OUM ÁT.427/p. All figured specimens remain *in situ* on the bedding plane. Scale bars = 5 mm.

Several biserial taxa (i.e. rangeomorph organisms with a single frond possessing two rows of primary branches) are present within the assemblage, including some that are here interpreted to be juvenile forms of taxa commonly seen preserved in high-fidelity on younger Avalonian bedding surfaces (e.g. *Charnia masoni*; Fig. 2.4A–B). Specimens referred to *Charnia masoni* show regular parallel series of primary branches alternating along a zig-zag midline (Fig. 2.4B). Other specimens show typical furled, rotated and undisplayed *Charnia* branching patterns at first, second and third order (Fig. 2.4A; terminology of Brasier and Antcliffe, 2009), but possess higher branching angles than *C. masoni*. These angles differ enough from *C. masoni* to preclude their inclusion within that species at present. Nor can they be referred to *Charnia antecedens*, since this species typically shows a gross morphology that tapers proximally toward the frond base (a feature not seen here). Such specimens are therefore described as *C.* aff. *masoni*, though further work investigating whether the gross morphology of *Charnia* species can change through ontogentic stages would be valuable. Species of *Charnia* comprise 14 of the 60 identifiable specimens (Appendix A3, Fig. A3.3).

Specimens close to *Trepassia wardae* are the commonest frondose taxon (31 of 60 identifiable specimens), diagnosed as such by their long, narrow morphologies, central stem, and finely divided rows (Fig. 2.4C). These *Trepassia* specimens show a variety of primary branching angles within the population, consistent with the assertion that the primary branches are free to ‘pivot’ relative to one-another (Narbonne et al., 2009; Fig. 2.4C). They can also be partially folded, such that only one row of primary branches is visible (Fig. 2.4D). Rare specimens bearing a resemblance to *Charniodiscus* species, (three individuals), evidenced by a clear raised margin to the frond petalodium and a possible circular holdfast disc, also occur (Figs. 2.5B, A1.1). Further specimens do not closely resemble any frondose Ediacaran organisms yet described, and might represent a new taxon (e.g. Fig. 2.5C). These individuals possess a long stem (~70% of total organism length) and a remarkably finely

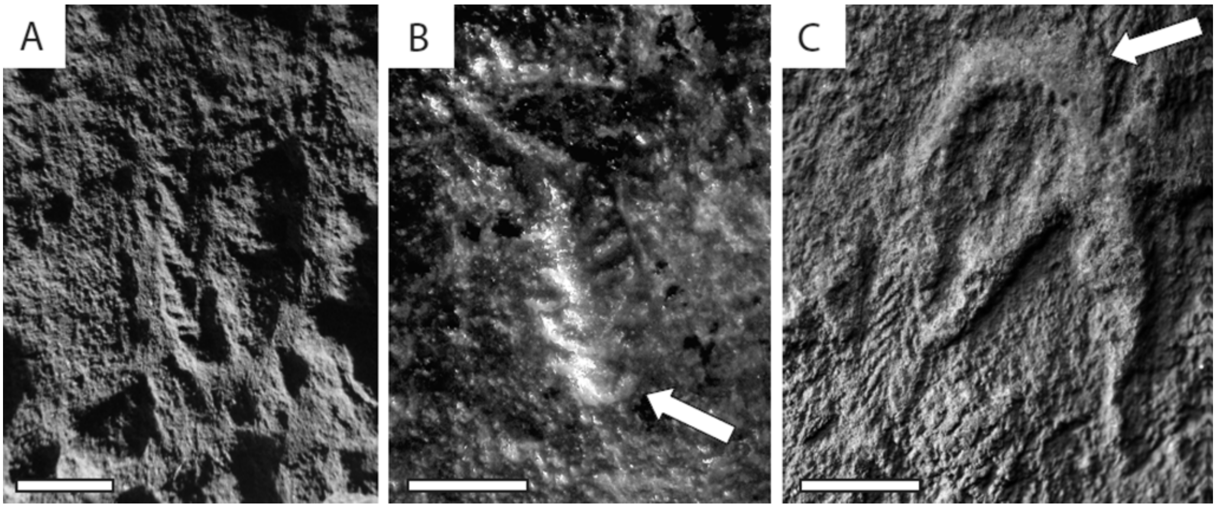

Fig. 2.5. Further examples of small fronds from the Drook Formation, Pigeon Cove, Newfoundland. **A**: *Charnia* aff. *masoni*, specimen C63. **B**: Specimen showing similarities to *Charniodiscus* sp., C16, with an apparent basal disc (arrowed), and an enclosing margin around the basal portion of the frond. **C**: A possible new form, C136, with a long curved stem (arrowed), and fine primary branching (the finest scale of preservation seen on this surface). Alternatively it is a taphomorph aff. *Trepassia*, with morphology subdued by modern erosion of the surface. Hints of branching halfway down the stem (arrowed) support the latter suggestion. The curvature of the stem implies that the original material from which the organism was constructed was relatively flexible. Replica casts of these specimens are housed in the Oxford University Museum of Natural History, OUM ÁT.429/p – OUM ÁT.431/p respectively. For further images of juvenile fronds from this surface, see Appendix A1. All figured specimens remain *in situ* on the bedding plane. Scale bars = 5 mm.

branched frond, with no visible continuation of the stem along the frond axis. Caution must be exercised, however, since the lack of observed branches along the bulk of the main stem could result from modern erosion of the surface. Potential branching at the point where the specimen bends (see arrow in Fig. 2.5C) supports this assertion, and suggests a close affinity with *Trepassia wardae*.

The small size of the fronds, coupled with the limited resolution of preservation permitted by the grain size of the casting material, mean that identification of many frondose specimens (53% of individuals on the surface), even to generic level, is not yet possible. Several of the features required by the formal diagnoses of Ediacaran rangeomorphs, and therefore necessary for objective species-level classification, are too small to have been preserved in specimens of this size. Our conservative taxonomic approach to study of the Drook Formation biota may therefore underestimate the total ecological diversity. There is also the possibility that some specimens represent taphonomically degraded individuals where only the internal supportive struts remain (Narbonne, 2004; Liu et al., 2011). The current limited knowledge of rangeomorph internal structure (though see Grazhdankin, 2004; Narbonne, 2004), combined with the incomplete suite of features preserved in many Pigeon Cove specimens, prevents critical assessment of this possibility at present.

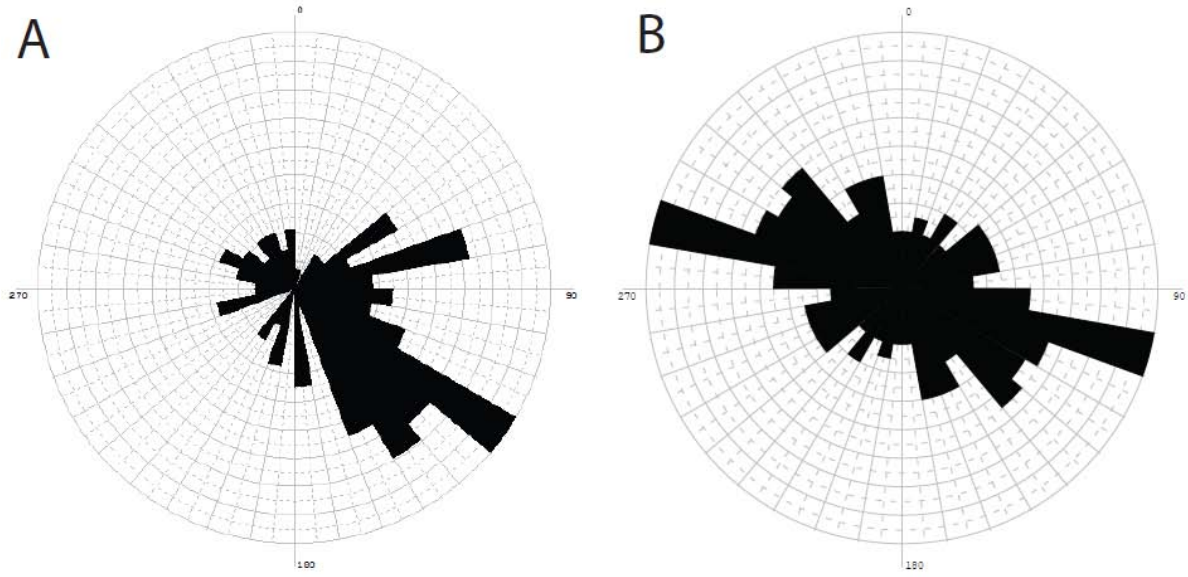

Fig. 2.6. **A**: The orientations of all small fronds on the Pigeon Cove surface, plotting the direction in which the apical tip of the frond is pointing. A broad alignment in a SE direction is clear, but nearly all orientations are seen. N = 129, maximum bin number = 19. **B**: The orientations of all ‘filamentous’ fossils on the Pigeon Cove surface. N = 134, maximum = 16. Since ‘filaments’ are tubular structures with identical ends, their orientations are plotted as a mirror image, to reflect their ESE-WNW orientation.

The ‘filamentous’ fossils are 6–130 mm in length, and commonly less than 1 mm in diameter (Fig. 2.7; Appendix A2). Filaments are generally curved, with some looping back on themselves (but never coiling), implying that the original material from which they were constructed was flexible. No primary organic material is found in association with these impressions. Some filaments appear to bifurcate (Fig. 2.7, white arrows), while other examples are superimposed rather than cutting across one another (Fig. 2.7A black arrow). These observations, combined with their positive epirelief preservation, make it highly unlikely that the filaments represent trace fossils (Jensen et al., 2005). The filamentous fossils are unevenly dispersed across the bedding plane (Appendix A4, Fig. A4.2C), and rarely come into contact with one-another. They also exhibit a strong ESE-WNW general alignment of long axes (Fig. 2.6B). This broad alignment does not necessarily suggest that the filaments were tethered to the seafloor in the same way as the fronds, but it does imply that they were influenced by bottom-water currents. Filamentous macrofossils found at other localities commonly exhibit a wide range of orientations (e.g. Fig. 2.9), but it is interesting to note that those at Pigeon Cove are broadly aligned with their neighbouring fronds.

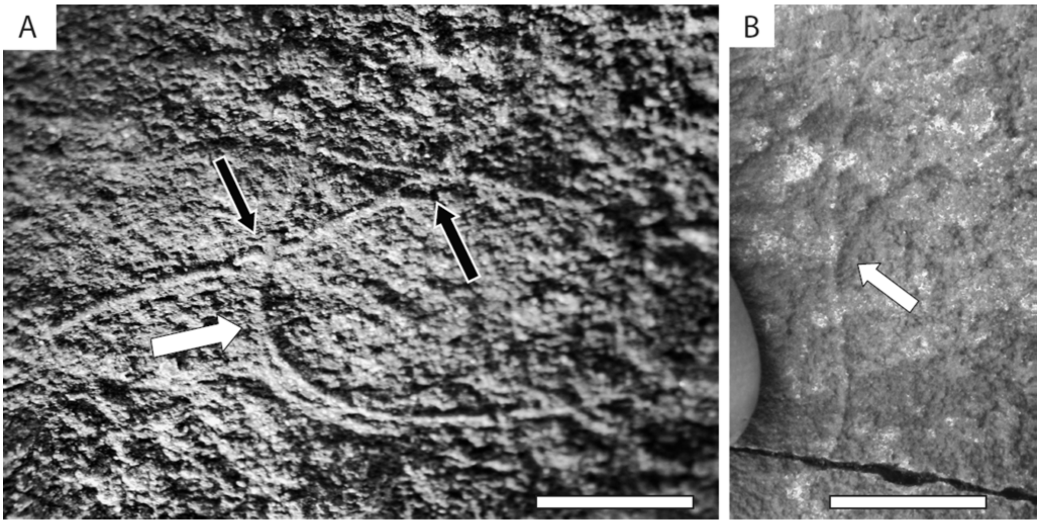

Fig. 2.7. Filamentous fossils from the Drook Formation of Pigeon Cove preserved in positive epirelief. Note the superimposition of filaments crossing over each other (black arrows), and the ‘Y’-shaped branching (white arrows). **A**: Specimen F6 showing both branching and superimposition. A cast of this specimen is held at the Oxford Museum of Natural History, OUM ÁT.432/p. **B**: Specimen F112, showing ‘Y’-shaped branching of the filament. Scale bars = 10 mm. For further images of filamentous fossils from this surface, see Appendix A2.

DISCUSSION

The diminutive Ediacaran frondose taxa at Pigeon Cove demonstrate a range of morphological diversity. While it is possible that some of the documented specimens may be incomplete second or third order branches from mature organisms, importantly, a number of specimens appear to possess holdfast discs and stems (Fig. 2.5A–B). When combined with the consistent south-easterly alignment of these fronds on the bedding plane (Fig. 2.6A), this suggests that truly juvenile forms, tethered to the seafloor, are present within the assemblage.

Prior to this study, the only reported Ediacaran macro-organisms from the Drook Formation of Newfoundland were *Trepassia wardae, Thectardis avalonensis, Charnia antecedens, Aspidella terranovica*, and the ivesheadiomorphs (see Figs. 2.2, 2.14 bed PC; Liu et al., 2011). The new small fronds represent at least two clear taxa (*Charnia masoni* and *Trepassia* sp.), while further specimens are strongly suggestive of additional species (e.g. aff. *Charniodiscus* spp., *Charnia* aff. *antecedens*). Some of these taxa (*C. masoni*, *Charniodiscus* sp.; Fig. 2.5A–B) have not been reported from rocks of this age before, and confirmation of their presence would therefore increase the diversity of this early Ediacaran macrofossil assemblage (Fig. 2.11).

Fossils of juvenile Ediacaran organisms are rare in the Avalon region, potentially due to taphonomic biases determined by the coarse grain size of the casting medium (Gehling et al., 2005). The possibility that the occurrence of juvenile forms is controlled by a temporal factor, such as a limited reproductive period, cannot yet be rejected, but the relative scarcity of such forms increases the importance of the Pigeon Cove specimens in studies of early ontogenetic development within the rangeomorph clade. Examples of immature *Dickinsonia*, *Arkarua* and *Praecambridium* are known from Ediacaran localities in South Australia (Gehling et al., 2005). Proposed juvenile rangeomorphs such as *Avalofractus, Beothukis* and *Bradgatia* sp.

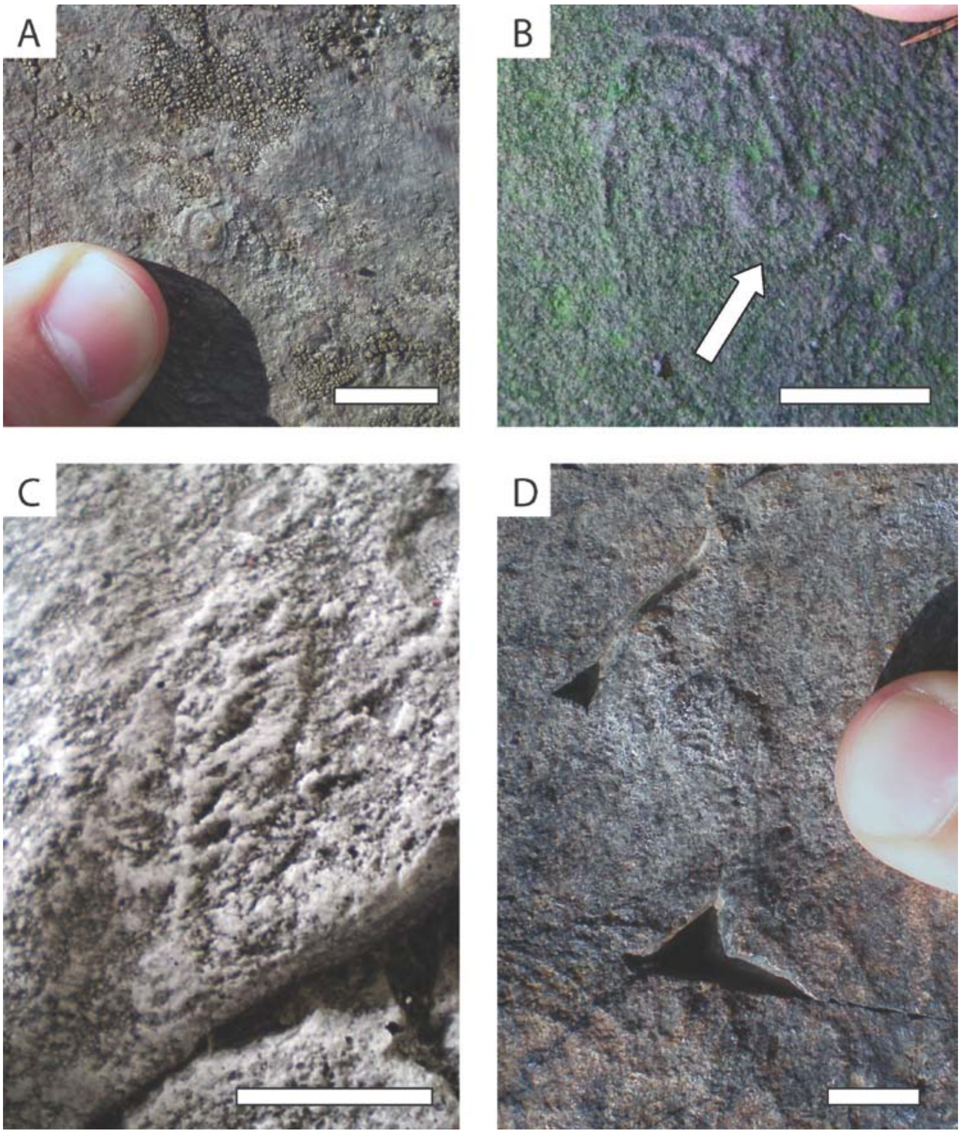

Fig. 2.8. Specimens of small Ediacaran organisms from Charnwood Forest, Leicestershire, U.K. **A**: *Aspidella*-like disc, showing concentric zoning but no attached frond or stem. Memorial Crags, Leicestershire. **B**: Apparent disc (arrowed) and stem, Outwoods, Charnwood Forest, Leicestershire. **C**: *Charniodiscus* sp. from Memorial Crags, Leicestershire. Image taken from a cast of the surface housed at the BGS, Keyworth. This specimen has previously been figured in Boynton and Ford, 1995, fig. 2. **D**: Possible juvenile rangeomorph, Memorial Crags, Leicestershire. All scale bars = 10 mm. All original specimens remain *in situ* on the bedding planes.

have also been described from Upper Island Cove, Newfoundland (Flude and Narbonne, 2008; Narbonne et al., 2009), although those examples are substantially larger and more ontogentically developed than the specimens described herein. The only other Avalonian horizons known by the author to possess fossils of this size include a bed on the Bonavista Peninsula (locality 14 in Hofmann et al., 2008), which preserves *Fractofusus andersoni* specimens smaller than 10 mm in length, and a handful of possible juvenile specimens of the Ediacara biota from Charnwood Forest in the U.K. (Fig. 2.8). Again, these Charnwood fossils are all smaller than 50 mm in length, and in some cases show clear basal holdfast discs (Fig. 2.8C), but the combination of small size, high abundance and known antiquity makes the juvenile assemblage of Pigeon Cove unique. Proposed *Dickinsonia*, *Kimberella* and *Charniodiscus* specimens from India (Maithy and Kumar, 2007) are considered by the author to represent *Aspidella*-like discs rather than true juvenile forms of more complex organisms.

The Pigeon Cove specimens have the potential to reveal valuable information regarding the ontogeny and development of Ediacaran fronds, but care should be taken to ensure that they are correctly classified before proceeding with further detailed analyses. The two best examples of *Charnia masoni* from the Pigeon Cove bed (C1 and C63; Fig. 2.4C and Fig. 2.5A) are 13 and 10 mm long respectively. Their frond rows possess 7 and 4 primary branches, with the largest and presumably oldest branches (containing the most secondary branches) at the base of the frond (see Brasier and Antcliffe, 2009 for rangeomorph terminology). This can be compared with the holotype of *Charnia masoni* from Charnwood Forest (188 mm, 18 primary branches; Antcliffe and Brasier, 2008), which also shows its largest (and developmentally earliest) primary branches at the proximal end of the frond (Antcliffe and Brasier, 2007). These simple observations alone tell us that *C. masoni* did not possess its full complement of primary branches during its early life stages. Instead, it can be inferred to have added new primary branches at its distal end throughout its frondose life cycle, confirming the findings of Antcliffe and Brasier (2007, 2008), with inflation of individual branches accompanied by distal addition during ontogeny. Juvenile specimens of aff. *Trepassia* appear to show a similar trend (compare Fig. 2.4C with Fig. 2.2A). Such information is vital if we are to fully understand and document the life cycles and ontogenetic growth patterns of the Ediacara biota, but the number of confidently identified taxa within this assemblage is not yet sufficient to take this study further.

Filaments

The role of the filaments in the ecosystems (Fig. 2.7) remains to be resolved. Similar features have been reported from nearby beds within the Drook Formation (Callow and Brasier, 2009a, fig. 6), and also from the shallow marine to fluvial Ediacaran successions of Longmynd, Shropshire U.K. (Peat, 1984; Callow and Brasier, 2009b, fig. 3), where they have been interpreted as microbial filaments (Callow and Brasier, 2009a, b). The material presented here is of comparable dimensions, but is preserved in substantially lower fossil densities, and lacks the distinctive hook-shape of the Callow and Brasier material from the Drook Formation (Callow and Brasier, 2009a). Nor are the filaments on this bed oriented exactly parallel to one-other (Fig. 2.6B; *contra* Callow and Brasier, 2009a), though they do show a strong alignment on the bedding plane. The rare branching observed in this material is generally simple with “Y” morphology, a characteristic seen in several multicellular fossil groups from pre-Ediacaran rocks (Butterfield, 2009b), as well as in extant microbial groups, such as fungi and siphonalean green algae (Brasier et al., 2010).

Abundant assemblages of filamentous fossils from the Bonavista Peninsula, Newfoundland, described for the first time here, may greatly inform our views on such enigmatic structures. These fossils are found at a number of horizons (Figs. 2.16–2.17), but those from a bedding plane on Burnt Point, near to the town of Port Union, appear the most useful for studies into their affinity. The MUN Surface (Locality PU9, named after the Memorial University of

Fig. 2.9. Filaments from the MUN Surface, locality PU9, Burnt Point, Bonavista Peninsula, Newfoundland. These filaments criss-cross the surface in all directions, forming a dense ‘mesh’ across the bedding plane. Note also the rangeomorph organism at top left. Scale bar = 10 mm.

Newfoundland; Appendix D2) is home to a diverse assemblage of spectacularly preserved Ediacaran rangeomorph fossils, made all the more attractive by the golden hue of the underlying sediment (e.g., Front Cover image). Even more remarkable is the resolution at which the fossils can be preserved on the surface. Fifth-order rangeomorph branching can be resolved in ‘*Bradgatia*’ specimens here (e.g. Fig. 1.4). This taphonomic quality provides an unprecedented view of the Ediacaran seafloor, recording not only macrofossil impressions, but also subtle linear features preserved alongside them.

Thin (<0.2–1 mm) threads and filaments criss-cross the entire surface (Fig. 2.9). Their lengths are of the order of 10s of centimetres, but terminations of individual filaments are difficult to identify, even on replica casts lit under controlled conditions. That these features lay on the seafloor beneath the macro-organisms at the time of burial, and did not sink down through the water column or get transported in with the casting tuff, is evident from the observation that frondose organisms preserved on the same surface appear to overlie the filaments (Fig. 2.10). MUN surface filaments proceed across the surface in all directions, and where they meet, are observed to be superimposed upon one another (Figs 2.9–2.10). The assemblage of filaments forms what could be termed a 'mesh' over the surface. This could theoretically be viewed as a type of biogenic 'mat' or organic surface (cf. Gehling and Droser, 2009).

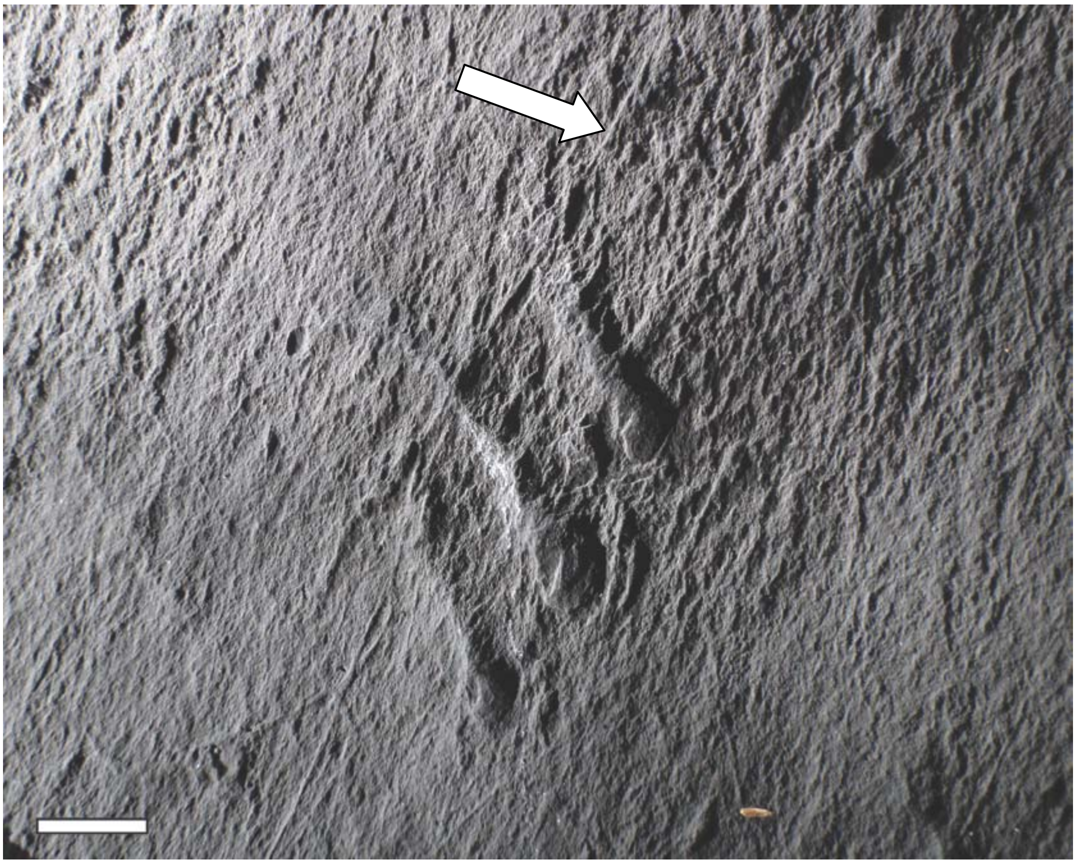

Fig. 2.10. Cast of filamentous fossils from the MUN Surface, Burnt Point, Bonavista Peninsula, Newfoundland. Note the three juvenile rangeomorph specimens, which are current aligned and apparently overlie the filaments (e.g. the arrowed filament). Scale bar = 10 mm.

Filaments are observed on several surfaces in the Avalon region, in densities of up to ten individuals per square centimetre. Their occurrence is, however, often limited to horizons directly above fine mudstones, or where the surface is smothered by an unusually fine-grained tuff. Their rarity across the region as a whole is thus likely to be explained by taphonomic processes; it seems that only particularly fine-grained substrates and casting mediums can preserve features at the scale of these filaments. Other surfaces (e.g. H26, PU6, MC2, CT4; Appendix D2) show these features reaching lengths of several metres, and in one case thicknesses of up to 10 mm (locality PU3). Although this anomalously large example could represent something different, it could be argued that many, if not all, Avalonian sediment-water interfaces may once have been covered with filamentous fabrics such as these. This supposition is made more plausible by the long stratigraphic range of such filaments in Newfoundland, from the Drook Formation all the way through to the Ferryland Head Formation (Figs. 2.16–2.17).

A lack of preserved cell walls, of distinguishable sheaths or membranes, or indeed of any preserved fine external or internal detail, negates attempts to conclusively determine the biological affinity of these filaments from macroscopic examination alone. Such attempts are hindered by the wide range of Ediacaran organisms and structures known to possess simple filamentous morphologies. Our Avalonian filamentous macrofossils seem unlikely to be cyanobacterial, since they occur in deep-water sediments deposited below the photic zone (e.g. Narbonne, 2007). The ‘H’ and ‘T’ shaped branching typical of fungal hyphal fusion (e.g. Butterfield, 2005) has not been observed in either the MUN Surface or Pigeon Cove material. Giant bacteria are one possibility, similar to the extant sulfur bacteria *Thioploca* or *Beggiatoa*, found today in huge abundances in the low oxygen environments on the Chilean continental shelf (Schulz et al., 1996 ; Teske and Nelson, 2006; Høgslund et al., 2009), though such bacteria are not known to exhibit branching (Cohen et al., 2009a). Meanwhile, larger filamentous fossils such as the potential algae *Vendotaenia* (e.g. Gnilovskaya, 1983; Cohen et al., 2009b) or *Grypania* (e.g. Butterfield, 2009b), may provide useful analogues, being of similar dimensions to the general Avalonian filament assemblages. Of these, *Vendotaenia* possesses longitudinal striations that are not observed in our material, though this absence of fine detail could have a taphonomic explanation. Some algal tubular fossils of the Miaohe biota of China also show similarities in overall morphology (e.g. *Sinocylindra yunnanensis*, Xiao et al., 2002), but do not exhibit branching, and are substantially smaller than our specimens. Filaments interpreted as lichen-like from the Doushantuo Formation of China (Yuan et al., 2005) are also two orders of magnitude smaller than the Pigeon Cove material. Unclassified tubular fossils from the Nama assemblage (Cohen et al., 2009b, fig. 4.3), are strikingly similar in general appearance to the Pigeon Cove material, but again do not branch. Meanwhile, sabelliditids, common in the youngest Avalonian rocks of Newfoundland (those of the Burin Peninsula), are of a similar thickness, but are never as long as the MUN surface specimens, and also commonly possess a transverse ornament (Urbanek and Mierzejewska, 1983; Jensen et al., 2007). Other filamentous fossils from the Ediacaran of Spain are of a similar scale, but are preserved in lower densities, and with more meandering morphologies than are seen in Newfoundland (Jensen et al., 2007). The tests of agglutinated foraminifera such as *Platysolenites*, which occur in younger Avalonian rocks from Newfoundland, would be expected to be hollow, and to possess external transverse ornament (McIlroy et al., 2001), features seen neither on the MUN surface nor at Pigeon Cove (though thin sectioning is required to confirm this). Even faecal strands (for example those from the Cambrian of China; Steiner et al., 2005) cannot yet be ruled out without microscopic study, although the apparent lack of sedimentary pellets within the Avalonian filaments reduces the plausibility of this suggestion.

Finally, it needs to be considered whether the filaments could be part of an Ediacaran frondose organism. The ‘rays’ of the discoidal fossil *Hiemalora stellaris*, recently found to be the holdfast of the frondose taxon *Primocandelabrum hiemaloranum* (Hofmann et al., 2008), bear some similarities, and can be observed to extend for tens of centimetres away from their discs at Murphy's Cove (locality MC2, Newfoundland). However, *Hiemalora* specimens are yet to be found alongside filamentous fossils at either Pigeon Cove or the MUN Surface. Ultimately, microscopic work is likely to be the only way of determining the precise biological affinities of these filamentous impressions; further research permits are required to obtain suitable specimens with which to test these possibilities. The abundance of long and thin tubular forms on the Ediacaran seafloor in many localities suggests that such structures were common and conspicuous members of the Ediacara biota. Relationships between filamentous fossils from the different Avalonian bedding planes, and with other Ediacaran macro-organisms, warrant further investigation.

The Pigeon Cove bedding plane reveals the high fidelity preservation potential of small fossils on Ediacaran bedding planes (see also Gehling, 1999; Narbonne, 2004), providing novel information on the early stages of rangeomorph growth. Appreciation of ontogeny and development is considered by some to be a pre-requisite for understanding the evolution and affinities of the Ediacara biota as a whole (cf. Thompson, 1961; Brasier and Antcliffe, 2004; Antcliffe and Brasier, 2008). In this light, the Pigeon Cove specimens will be important for future research into the rangeomorph Ediacara biota.

Ecological Succession

To find frondose fossils possessing fine preservation of small features, on a bed where much larger fossils are present but comparatively poorly preserved, is intriguing. The recently proposed model for ivesheadiomorph preservation suggests that effaced forms, such as the 'pizza discs' from this bedding plane, were organisms that were already dead and decaying prior to burial beneath an ash layer (Chapter 3; Liu et al., 2011). The Pigeon Cove surface can therefore be taken to record the co-occurrence of large ivesheadiomorphs (see Chapter 3) alongside well-preserved juvenile rangeomorphs. If the effaced preservation hypothesis is correct, this suggests that a population of mature, possibly senescent organisms was succeeded by a juvenile generation, following an event that caused the demise of the mature organisms prior to burial. The smothering ash thus records a remarkable snapshot of secondary community succession on this Pigeon Cove surface (Fig. 2.11), potentially one of the earliest examples of community succession in the fossil record. The random distribution of juvenile rangeomorphs, on a surface where there is otherwise no evidence for mature forms of those taxa alive at the moment of obrution, is consistent with the possibility of a dispersive method of reproduction for these organisms (Narbonne et al., 2009). The presence of distinct, species-specific primary branching architectures in many of the smallest fronds indicates that,

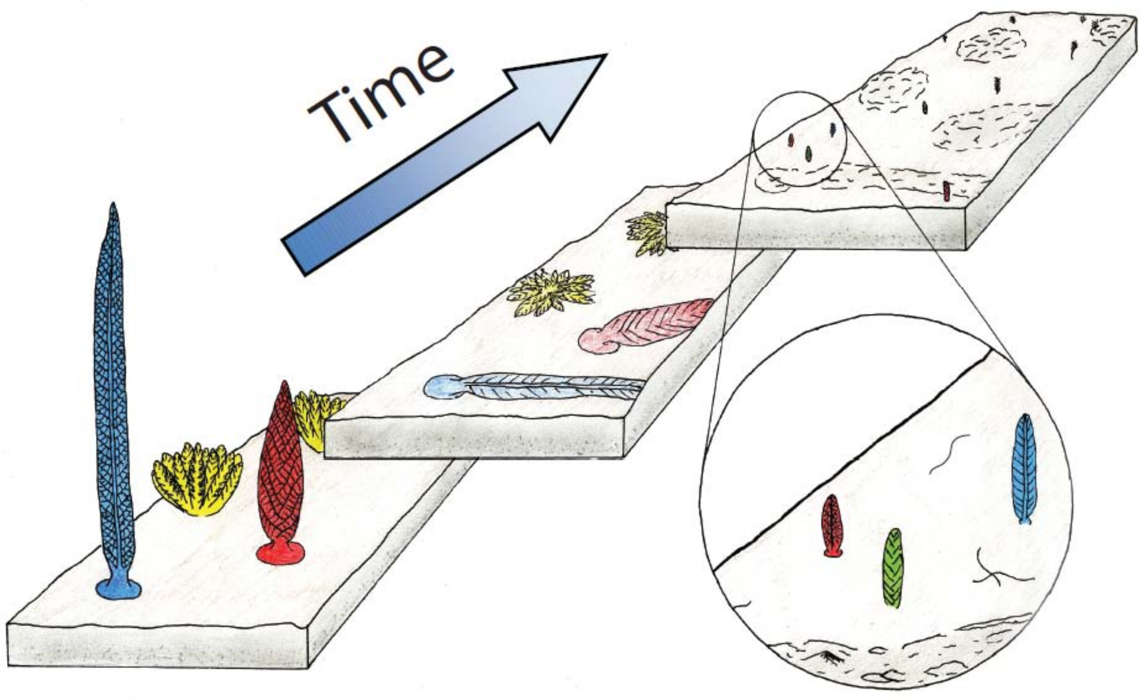

Fig. 2.11. Graphical interpretation of the ecosystem succession observed on the Pigeon Cove bed. An incumbent population of large rangeomorphs dies, and as they decay, a new population of juveniles enters and begins to grow. The bed is smothered by volcanic ash before these juveniles can grow to maturity, preserving all organisms. Note that although rangeomorphs are figured here standing upright in the water column, in truth they may have been inclined due to currents, or even reclining on the seafloor (e.g. Grazhdankin, 2004).

in at least some rangeomorph species (e.g. *Charnia masoni*, and possibly *Charniodiscus* sp.), asexual vegetative budding (*sensu* Narbonne et al., 2009) may not have been utilised. Likewise, and contrary to previous discussion of the *Charniodiscus* juvenile in Fig. 2.8C (Boynton and Ford, 1995, fig. 2, originally labelled in that publication as a *Charnia*), small size alone cannot be taken to demonstrate a 'budding mode' of reproduction. Nevertheless, material documented to date is not sufficient to completely negate the possibility of asexual budding in rangeomorphs. Further study of these specimens, the smallest rangeomorphs reported from Ediacaran beds, may yet shed light upon their reproductive strategies.

PIGEON COVE SUMMARY

The Pigeon Cove fossil assemblage arguably represents one of the earliest examples of community succession in the fossil record. Identifiable juvenile fronds can broadly be classified within well-known Avalonian taxa. Such specimens extend the stratigraphic ranges of several macroscopic taxa, including the iconic *Charnia masoni*, back to 579Ma, increasing the diversity of the earliest documented assemblages of the Ediacara biota. Juvenile Ediacaran fossil material also informs us about the evolution, taphonomy and ontogeny of Avalonian palaeocommunities, and reveals the potential for preservation of such material in these depositional settings.

Macroscopic filaments, of uncertain biological affinity, appear to be a distinct but common component of Avalonian successions, and henceforth should be considered in discussions of ecosystem dynamics in Ediacaran deep-water environments. Establishing the biological affinities of these fossils, and their relationships and interactions with the larger members of the Ediacara biota, are future research directions of considerable interest. The mapping of this bedding plane also has benefits for the management of this unique palaeontological site. Our map (Fig. 2.3; Appendix A4) allows quantitative monitoring of erosion and weathering rates on this surface, providing useful information for policy makers and researchers on how best to conserve and protect fossil-bearing sites within the MPER.

The Pigeon Cove biota is just one of several previously undocumented fossil assemblages discovered whilst undertaking fieldwork in the Avalon region. Taxonomic diversity on the Pigeon Cove surface can be combined with that of other localities to reveal broader patterns and processes governing the evolution of the Avalonian Ediacara biota over tens of millions of years. Attention will now turn to discussion of revised stratigraphic ranges for the Avalon assemblages, which arise from a combination of data from new sites and the published literature.

AVALONIAN STRATIGRAPHIC RANGES

Formal stratigraphic sub-division of the Ediacaran Period would be of enormous value, given that it spans a time interval of over 80 million years, longer than any period in the Phanerozoic (Van Kranendonk et al., 2008). Correlation of geographically widespread units is, however, hindered by difficulties in the application of many standard stratigraphic methods to Ediacaran successions. Magneto-, litho-, chemo- and chrono-stratigraphy are either unfeasible or presently not sufficiently explored to be of use on a global scale. Microfossils could be suitable biological structures on which to base a formal biostratigraphy, but their limited occurrence and diversity in sections of this age (Vidal and Moczydlowska-Vidal, 1997) diminishes their utility. Acritarch assemblages during the latest Neoproterozoic were largely confined to simple sphaeromorphic acritarchs or small acanthomorphs such as

Micrhystridium Deflandre 1937; large morphologically diverse acanthomorphs of the kind found in the Doushantuo or Pertatataka assemblages appear to have become extinct at about the time of the Gaskiers glaciations (Zhou et al., 2001, 2007). At present, only regional correlation has been achieved using microfossils (e.g. Grey and Calver, 2007). Therefore, if it could be demonstrated that certain macrofossil taxa can be of use in global biostratigraphic correlation (possessing wide geographic ranges, high abundance, independence from facies, etc.), a stratigraphic framework could potentially be developed.

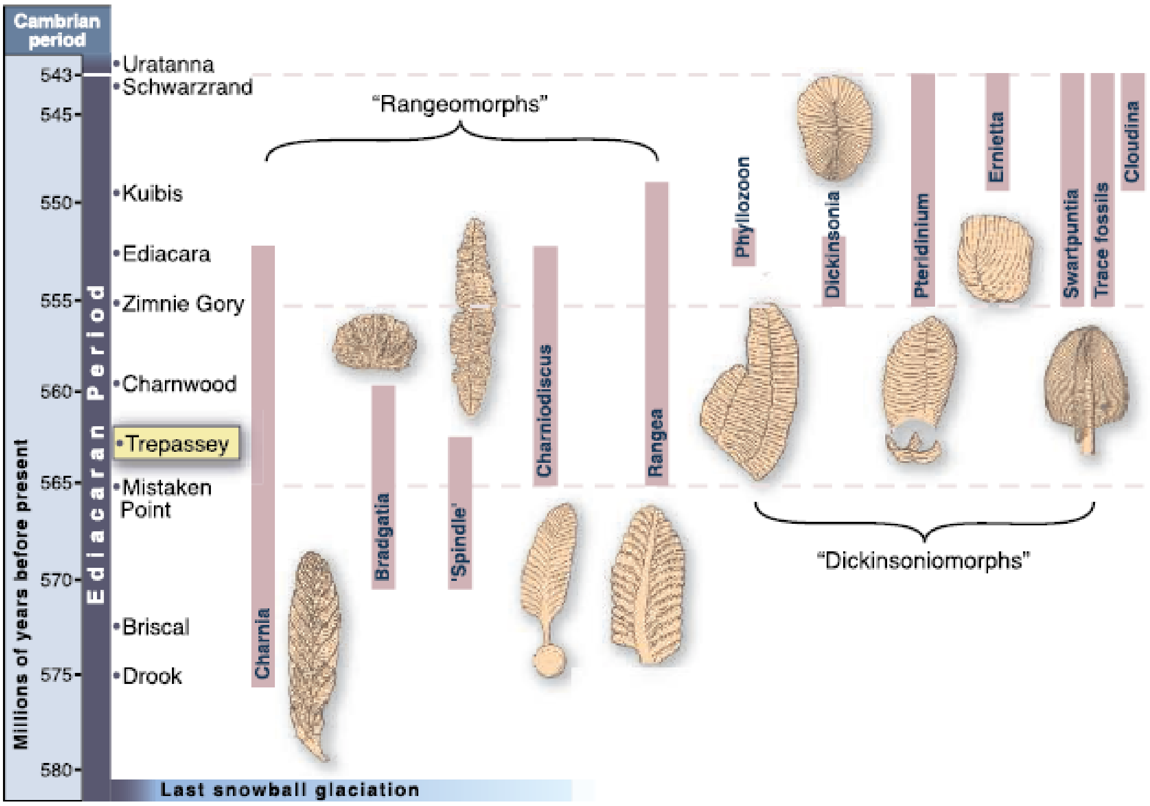

Fig. 2.12. Previous published stratigraphic ranges for members of the Ediacara biota. Image taken from Brasier and Antcliffe, 2004. The figure compares a selection of taxa from across the globe, at a regional level of resolution. Compare this to Figs. 2.13–2.17, which plot ranges for all taxa present in individual assemblages, at a Formation scale.

Biostratigraphy does suffer from notable problems in the Ediacaran, not least that many beds and even entire lithological units are devoid of fossils. Particular organisms appear to be confined to specific palaeoenvironments or facies (see Chapter 3 for discussion of taphonomic regimes). Nevertheless, taxa such as *Charnia*, observed from Canada, the U.K., Australia and Russia in siliciclastic and carbonate lithologies (Fedonkin et al., 2007a), demonstrate that some large body fossils may prove useful for global stratigraphy if their ranges can be accurately resolved. Previous published biostratigraphic ranges have been either very broad, utilising identifiable generic taxa such as *Charnia*, *Dickinsonia* and *Ernietta* in a broad review format at a regional level of resolution (Brasier and Antcliffe, 2004, and subsequent papers modifying their work; Fig. 2.12), or overly specific, focusing on just one or two taxa (e.g. *Pectinifrons abyssalis* in Bamforth et al., 2008). Only by combining data for all taxa in a region can environmental, ecological or evolutionary patterns within the biota be detected, and potential groups for global biostratigraphic correlation identified.

Detailed stratigraphic range charts are here presented for Ediacaran successions from Newfoundland, the Longmynd, and Charnwood. To construct the stratigraphic ranges, data were collated from the literature (see relevant figure captions for details), and obtained directly from a large number of field localities, many of which have not previously been documented (Appendix D). Published radiometric dates, where available, have also been incorporated. It is important to note that these revised stratigraphic columns are not presented as comprehensive, definitive ranges. As with previous work, they simply summarise current knowledge, and will be subject to revision following the discovery of new field localities. Despite this caveat, the observed patterns represent a significant advance in studies of the temporal ranges of the Ediacara biota, and enable us to formulate preliminary hypotheses regarding the evolutionary processes occurring at this point in the history of life.

THE LONGMYND, U.K.

The Ediacaran rocks of the Longmynd Hills comprise a shallow marine to fluvial siliciclastic succession, with plentiful outcrops and an abundant discoidal fossil assemblage. Previous studies have documented the fossils found in each formation, or from individual hills or valleys (e.g. Salter, 1856; McIlroy et al., 2005), but accompanying locality information is rarely provided in the published literature. It has therefore been difficult to quantify accurate stratigraphic ranges for individual taxa (see the unpublished PhD. thesis of Pauley, 1986, for the only previous information regarding this). Extensive fieldwork by the writer in the Longmyndian Supergroup, documenting fossils in each of the major valleys on the eastern flanks of the hills (Appendix D1, Fig. D1.1), has produced a stratigraphic range chart for the Longmynd biota (Fig. 2.13). Correlation of individual field sites is here based upon the geological map published by the British Geological Survey, sheet E166, and although numerous small faults are observed in the field that are not marked on the published map, the general order of outcrop occurrence in the stratigraphy is likely to be broadly correct.

Trends

Beltanelliformis minutae McIlroy et al. 2005 is the most common Longmynd taxon, but the stratigraphic ranges of both microbial mats, and the linear structure *Arumberia* Glaessner and Walter 1975, correlate with that of *B. minutae* (Fig. 2.13). However, there are no clear spatial relationships between these distinct impressions. The majority of fossil occurrences are confined to the transitional Burway, Synalds and Lightspout Formations, which document a shift from very shallow nearshore (deltaic?) deposits through to alluvial and fluvial sedimentation (McIlroy et al., 2005). Above this, the terrestrial sandstones of the Portway Formation are unfossiliferous. My own studies did not extend down into the Stretton Shales,

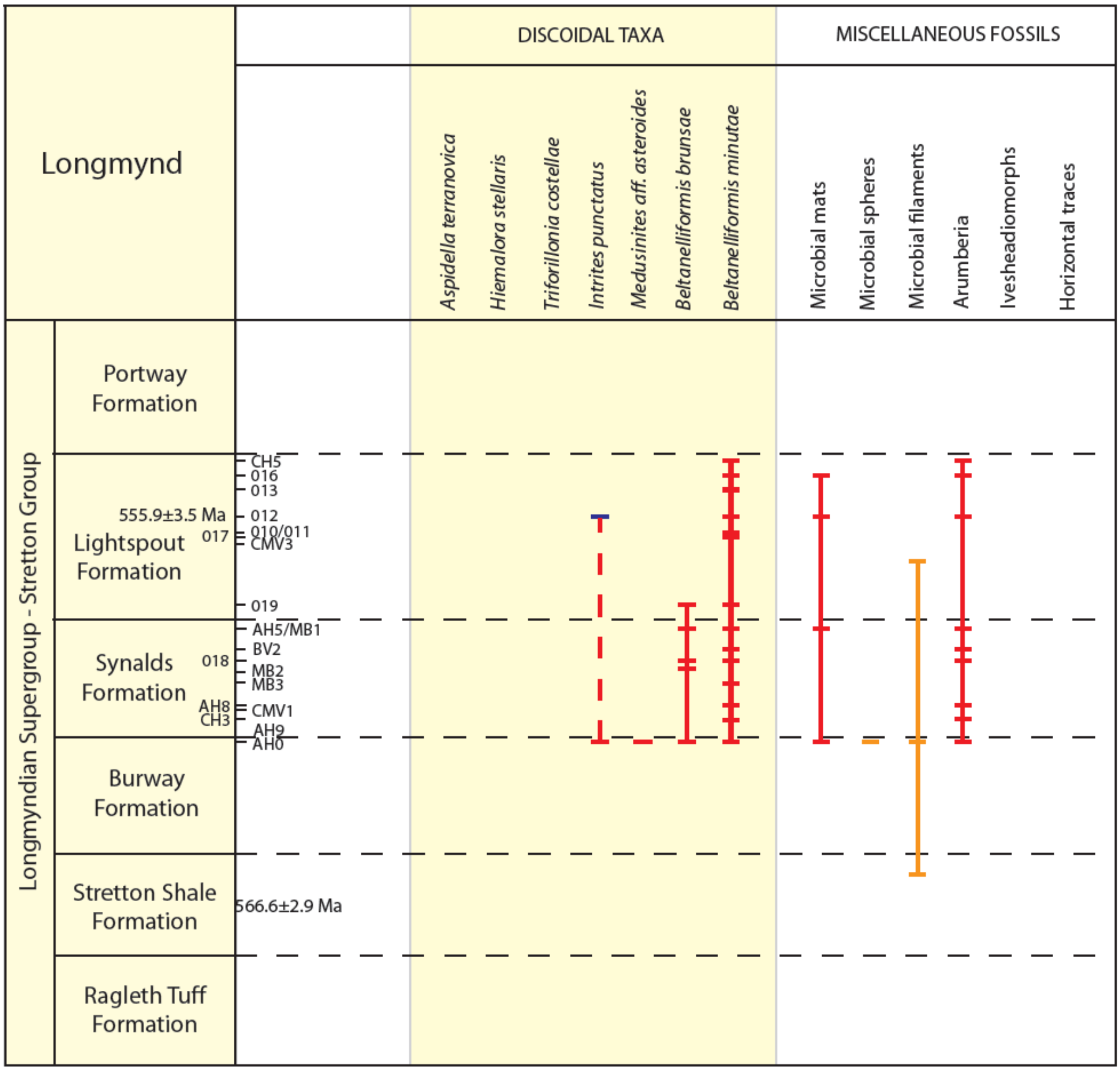

Fig. 2.13. Biostratigraphic ranges of Ediacaran taxa from the Longmynd Hills, Shropshire, U.K. Red horizontal bars indicate primary observations made by the author. Orange bars are data from Peat (1984), and Callow and Brasier (2009b). The blue bar represents a specimen that is considered doubtful. The localities on the left, adjacent to the Formation names, correspond to the locality codes and GPS co-ordinates presented in Appendix D1. Radiometric dates are taken from Compston et al., 2002.

but the discovery of filamentous microfossils within this unit (Peat, 1984), combined with an inferred turbiditic marine slope depositional environment (McIlroy et al., 2005; a similar depositional regime to Newfoundland and Charnwood), makes it a promising prospect for future palaeontological exploration. Unfortunately, its palaeontological potential may be dampened somewhat by its position directly beneath the town of Church Stretton (Fig. D1.1), and the effects of severe weathering upon the few remaining outcrops.

The Longmynd biota is very different to those of Charnwood or the Conception Group, being composed primarily of small discoidal taxa, and microbial structures. The three discoidal taxa commonly found in the Conception and St John's Groups of Newfoundland have not yet been found in the Longmynd (*Aspidella*, *Hiemalora*, *Triforillonia*; Fig. 2.13), making biostratigraphic correlation with those units difficult. New finds in the Signal Hill Group of Newfoundland (Appendix A5, Fig. A5.1), also from shallow-marine to alluvial red-bed successions, suggest a similar biota does exist in shallow water settings there. This implies that depositional environment may be the primary factor in explaining the very different biota observed in the Longmynd. As for specific controls, salinity, water depth, temperature, sedimentation rate, and nutrient supply could all be significant variables. All discoidal fossils in both regions seem to disappear once coarse-grained fluvial channel deposits begin to dominate (for example in the Portway Formation of the Longmynd, and the upper Ferryland Head Formation in Newfoundland), again suggesting that the organisms represented by the fossils were restricted to specific environments. Production of similar range charts for the shallow-water Newfoundland successions could be very revealing; a Masters project at Oxford is currently investigating this problem (Matthews, In Prep.). The relationship between these regions and the Radnor and Llangynog Inliers of the western U.K. (see Carney et al., 2000) could likewise be useful.

CHARNWOOD FOREST, U.K.

In Charnwood Forest, Leicestershire, all available sites (summarised in Carney, 1999; Appendix D1) were documented by the writer either in the field or through work on casts housed at the British Geological Survey (B.G.S.), Keyworth. Charnian outcrops occur within a geographically small area, with poor outcrop abundance, and thick vegetation and farmland covering all but a few crags. Furthermore, fossil-bearing outcrops are located on a series of faulted blocks (Appendix D1, Fig. D1.2; McIlroy et al., 1998; Carney, 1999), while pervasive

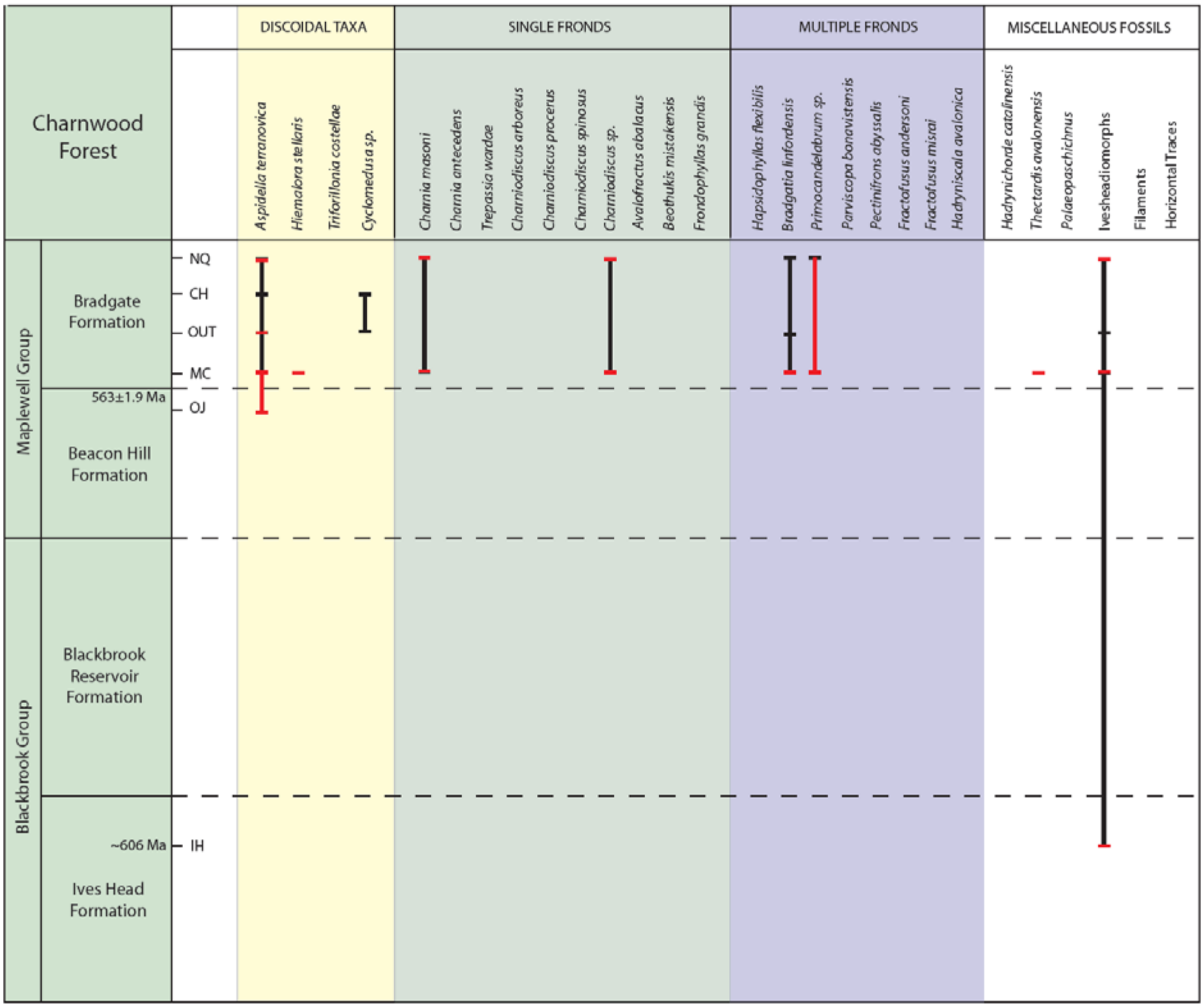

Fig. 2.14. Biostratigraphic ranges for Ediacaran taxa from Charnwood Forest, including primary data from field observations, and observations based on casts of the bedding planes (in red). Note the low taxonomic diversity, and small number of outcrops. NQ = North Quarry; CH = Cliffe Hill Quarry; OUT = The Outwoods; MC = Memorial Crags, Bradgate Park, OJ = Old John, Bradgate Park; IH = Ives Head, Lubcloud Farm. For a map showing the locations of these sites, see Appendix D1, Fig. D1.2. Dates from McIlroy et al., 1998; Carney, 2000; Wilby et al., 2011. Literature ranges compiled from Ford, 1980, 1999; Boynton and Ford, 1995; Boynton, 1999; Wilby et al., 2011.

cleavage exists on several of the critical bedding planes. When combined with logistical difficulties in accessing many Charnwood sites, these problems mean that there are relatively few published studies from which to obtain taxonomic ranges, and a limited number of recognisable Ediacaran taxa (Fig. 2.14 black bars). The B.G.S. is currently working to obtain absolute dates for the fossiliferous horizons, in order to resolve intra-regional correlation between these localities.

The Charnwood biostratigraphic range chart shows few individual localities (six), and a relatively low taxonomic diversity (Fig. 2.14), making it difficult to identify temporal or

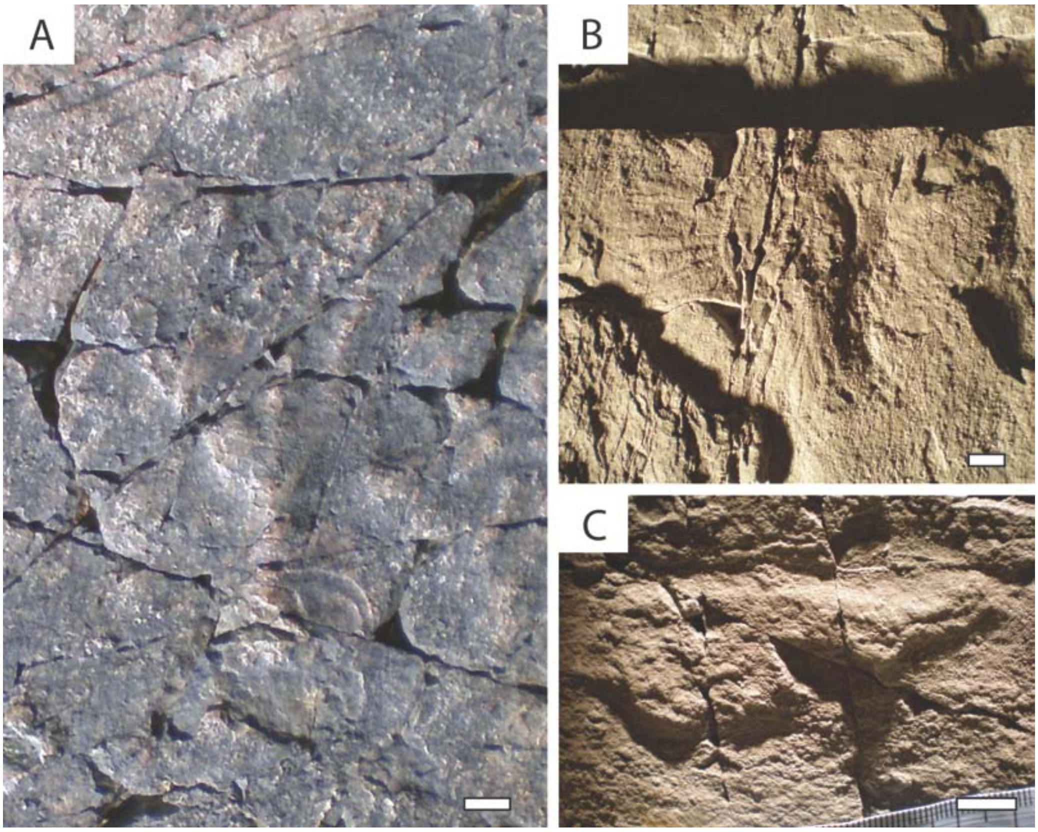

Fig. 2.15. Ediacaran fossils from Memorial Crags, Leicestershire, showing taxa not previously recorded from the Avalonian rocks of the U.K. **A**: *Primocandelabrum sp*. Note the tree-like general morphology of the fossil, and the prominent basal holdfast disc, which does not appear to possess *Hiemalora*-like rays. **B**: *Hiemalora stellaris*, a disc possessing radiating rays. **C**: The triangular fossil *Thectardis avalonensis*. Scale bars = 10 mm. Casts in B and C were taken by the British Geological Survey and are housed in Keyworth, Nottinghamshire, U.K. Figures B and C are reproduced with the permission of the British Geological Survey © NERC. All rights reserved.

other patterns within the dataset. The clearest observation is that the ivesheadiomorphs appear significantly earlier in this region than any other fossil group (discussed further in Chapter 3). My own field observations add little to the published data, largely because the published ranges are based on studies that have been made very recently on the same bedding planes as were studied by the writer (e.g. Wilby et al., 2011). My observations corroborate and confirm these previous findings, and document for the first time specimens of *Hiemalora* and *Thectardis* in rocks from the U.K. (Figs. 2.14–2.15B–C). The range of *Primocandelabrum sp.* is also extended down through the Bradgate Formation following its discovery at Memorial Crags (Fig. 2.15A). While these discoveries bring the Charnwood biota increasingly into line with that of Newfoundland in rocks of a similar age and depositional environment (Fig. 2.16), overall taxonomic diversity in Charnwood remains low. The limited abundance of exposure in this region (relative to Newfoundland) is likely to be the primary reason for this. Likewise, until further assemblages are discovered to test this hypothesis, the broadly simultaneous appearance and termination of non-ivesheadiomorph taxa in Charnwood must also be regarded as an artefact of the limited number of beds available for study (Fig. 2.14). Renewed and extensive fieldwork in this region is urgently required, in order to determine the exact components and nature of the Charnwood palaeocommunities.

NEWFOUNDLAND, CANADA

The vast majority of my fieldwork has been conducted in Newfoundland, as this province is home to both the most accessible Avalonian outcrops, and the most diverse and widespread fossil assemblages. For the Newfoundland stratigraphic ranges, data from successions on the Avalon Peninsula (Mistaken Point Ecological Reserve, Western Head, and the vicinities of Spaniard’s Bay and Ferryland), and the Bonavista Peninsula were combined. The stratigraphic levels of these sites were plotted on to a single stratigraphic column, using the correlations of

Hofmann et al. (2008) as a basis. Relative positions of individual sites were determined by assuming that the formation boundaries occurred synchronously in the various regions, and

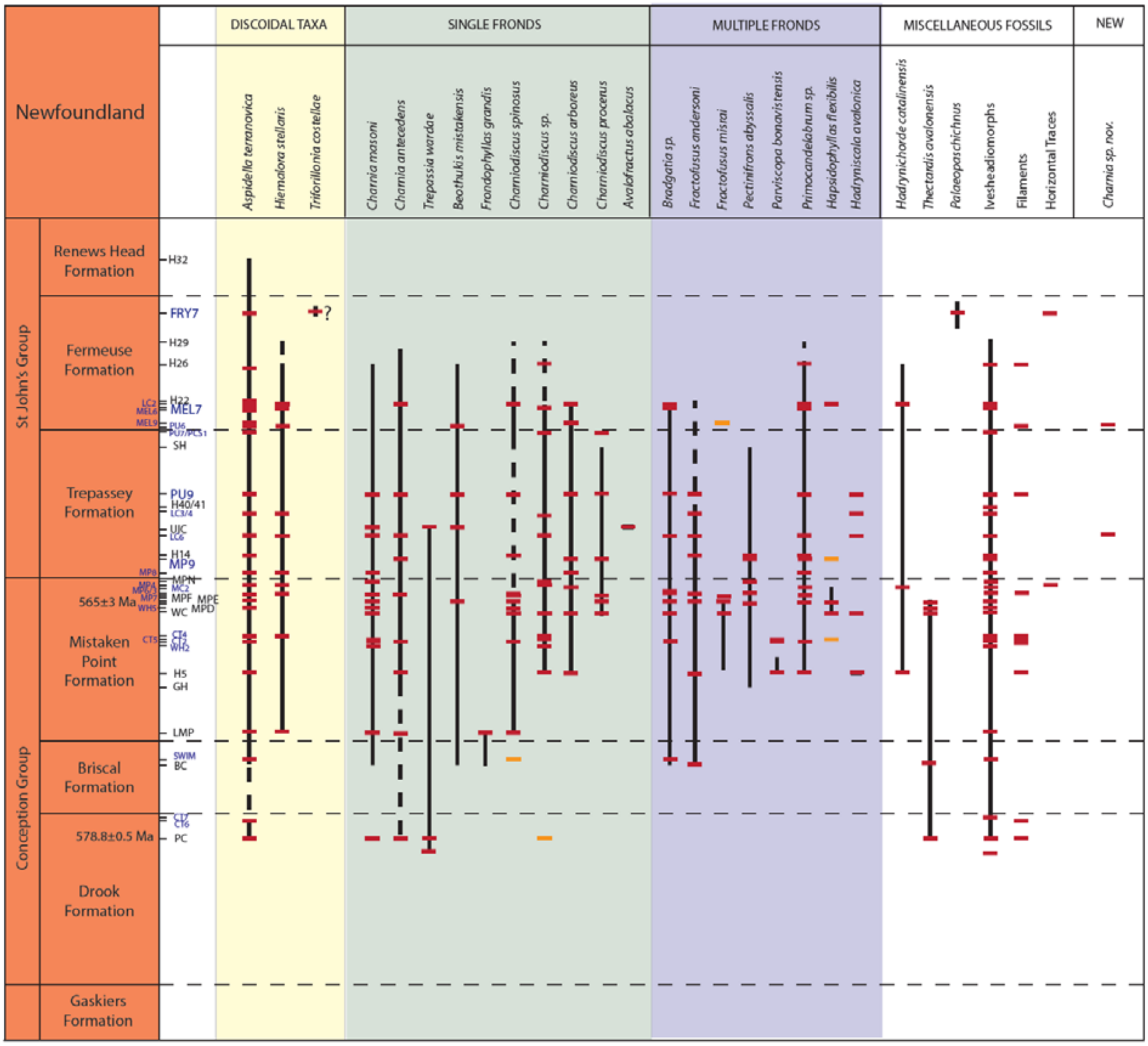

Fig. 2.16. Biostratigraphic ranges for the Avalonian macrofossil taxa of Newfoundland. The column was produced by collating data from publications documenting the Avalon and Bonavista Peninsulas. Vertical black bars represent stratigraphic ranges for individual taxa previously published in the literature. Horizontal red bars indicate definite identifications of Ediacaran taxa at particular localities made by the author. Orange bars indicate less confident observations. Data for literature ranges is collated from Gehling et al., 2000; Narbonne and Gehling, 2003; Clapham et al., 2004; Narbonne et al., 2005, 2009; Gehling and Narbonne, 2007; Bamforth et al., 2008; Hofmann et al., 2008; Bamforth and Narbonne, 2009; Brasier and Antcliffe, 2009. Radiometric dates taken from Benus, 1988, and Van Kranendonk et al., 2008.

that the relative position of individual beds within a formation in one region could be projected comparably onto the master column. This obviously introduces a degree of error due to the assumption of synchronous deposition and constant sedimentation rates, but it is the fairest and least complicated way to attempt the correlation of multiple locations spread over a geographical area of >15,000 km^2. Detailed regional sedimentological and stratigraphic studies are required to test the validity of this assumption.

The studied outcrops (Appendix D2) cover an almost complete stratigraphic section from the upper Drook Formation, >578.8 Ma (Van Kranendonk et al., 2008), through to the Ferryland Head Formation, ~555 Ma. Even on this regional scale, there is a significant degree of lithological heterogeneity (Wood et al., 2003; O'Brien and King, 2005, 2006; Ichaso et al., 2007), whilst several formations thought to be of a similar age from elsewhere on the island are seemingly devoid of fossils (e.g. the Musgravetown Group of the Bonavista and St Mary’s Peninsulas; Normore, 2010).

Data collected by the author largely confirms the stratigraphic ranges obtained from the literature (Fig. 2.16), though for several genera, stratigraphic ranges are extended, while the discovery of new species inserts additional layers of interest to the Avalonian biotic assemblage. The most striking feature of the Newfoundland stratigraphic range chart (with respect to those of Charnwood and Longmynd; Figs. 2.13–2.14) is the substantially higher taxonomic diversity exhibited in this region. This is likely to be a function of Newfoundland possessing a larger area of accessible outcrop, with more bedding planes available for study, combined with a historical sampling bias due to the greater number of researchers working on the Newfoundland successions. Further study is necessary to confirm this, since the possibility that the depleted palaeobiological diversity observed in the U.K. is real would be of great significance if correct.

Range Extensions and New Taxa

The stratigraphic ranges of several Newfoundland taxa are expanded by the new field data. Most notably, the ranges of the multifoliate taxa *Hapsidophyllas flexibilis* Bamforth and Narbonne 2009, and *Hadryniscala avalonica* Hofmann et al. 2008, are substantially extended into younger levels (Figs. 2.16–2.17). The new *Hadryniscala* specimens are particularly important, as they display the morphology of the complete organism for the first time (Pl. 2.1A). The positive epirelief primary branching rungs of *Hadryniscala* are clear in the holotype near Murphy's Cove on the Bonavista Peninsula (Hofmann et al., 2008, fig. 22.1), but study of the new material shows packages of finer, lower-relief branching 'rungs' between each of these primary units (Pl. 2.1A inset). It also appears that the two opposite sides of the 'ladder' actually join up at both ends of the specimen, giving it a long, elongate and tapering appearance (Pl. 2.1A), and suggesting a bipolar mode of growth. It is, however, not yet possible to confirm whether *Hadryniscala* belongs to the rangeomorph clade from these new specimens, since clear rangeomorph sub-units are yet to be recognised. The observations presented herein also confirm the assumed extensions to the ranges of *Aspidella terranovica*, *Charnia antecedens*, and two *Charniodiscus* species proposed by Hofmann et al., 2008 (blue

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PLATE 2.1. Important specimens and finds from the Bonavista Peninsula of Newfoundland, either representing new species, or significantly extending the stratigraphic ranges of taxa. **A**: Complete specimen of *Hadryniscala avalonica* from locality PU9 (the MUN Surface), within the Trepassey Formation. Inset (from a different specimen on the same surface) shows fine branches between the main struts. **B**: *Charnia* specimen from locality LC6, Trepassey Formation, much more slender than *C. masoni* but with similar branching structure, interpreted as a probable new species. **C**: *Hapsidophyllas flexibilis* from locality LC2, Fermeuse Formation, Little Catalina. This specimen extends the range of this taxon into the Trepassey and Fermeuse Formations. Black box on card = 10 x 10 mm. **D**: A collection of filaments from the MUN Surface, Trepassey Formation, Burnt Point. Scale bar for A = 100 mm, for B, D = 10 mm.

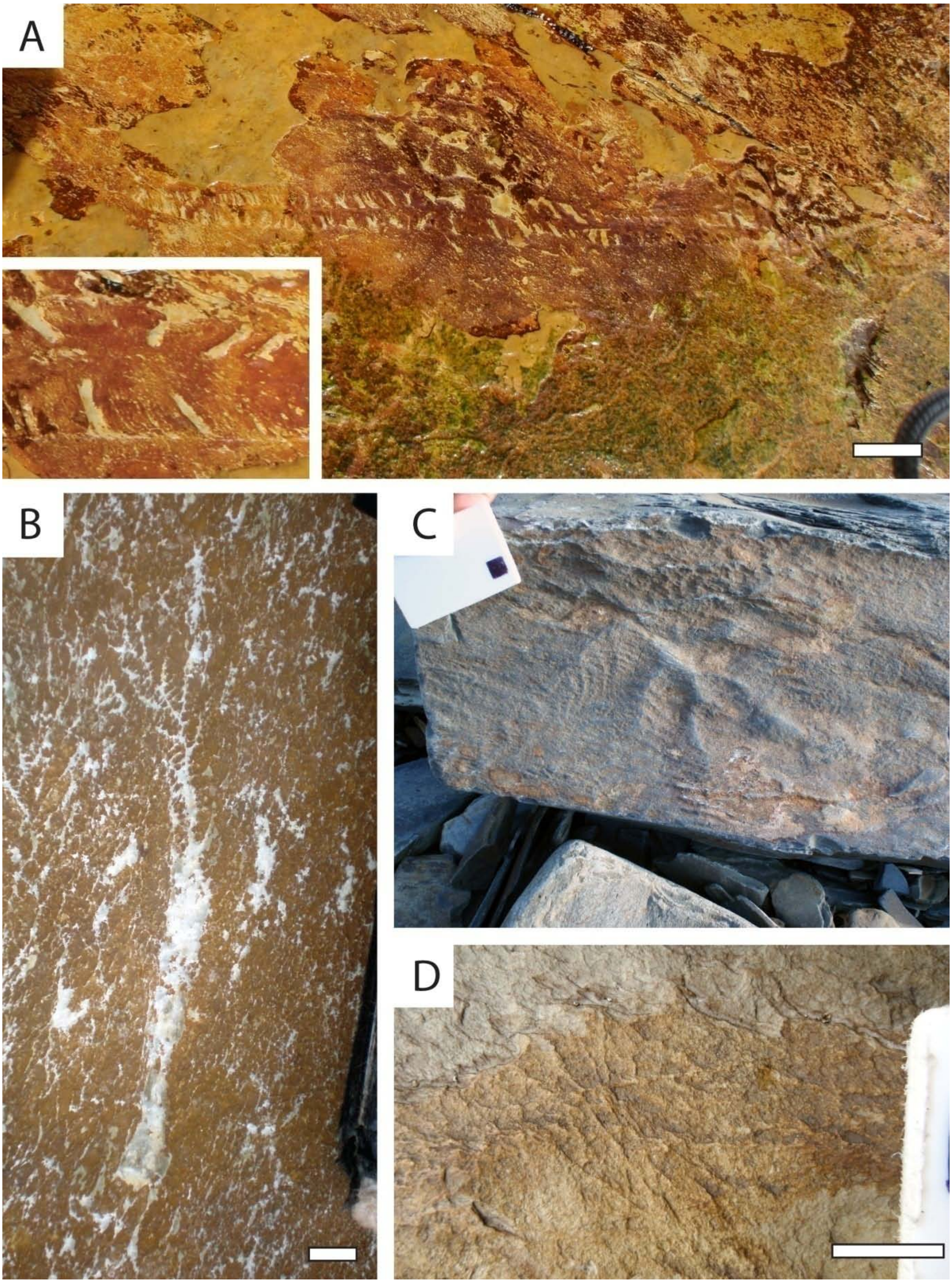

PLATE 2.1

vertical bars in Fig. 2.17). Furthermore, they add minor extensions to the known ranges of *Charniodiscus procerus* Laflamme et al. 2004, and *Parviscopa bonavistensis* Hofmann et al. 2008 (red vertical bars in Fig. 2.17).

Several notable new finds include the discovery of possible metazoan trace fossils in the Mistaken Point and Fermeuse Formations (discussed in detail in Chapter 6), and the presence of filaments on several Ediacaran bedding planes (this chapter). There is also a potential new species of *Charnia*, identified from the Bonavista Peninsula (Pl. 2.1B; Fig. 2.16). This taxon possesses a previously undocumented suite of rangeomorph morphological features, and is currently being written up for publication elsewhere.

Patterns

The discoidal taxon *Aspidella terranovica* possesses a range that encompasses those of all of the ‘single’ fronds (i.e. biserial frondose taxa with only one frond/petalodium; Fig. 2.17). This could be interpreted as consistent with *Aspidella* being an ‘organ’ taxon, and representing the basal part of a more complex frondose organism (cf. Gehling et al., 2000). Despite appearing roughly synchronously with the first rangeomorphs (*Charnia* and *Trepassia*), the upper range of *Aspidella* extends considerably past these taxa and into the Renews Head Formation. The absence of fronds from these younger levels has previously been ascribed to taphonomic processes (outlined in Gehling et al., 2000; Narbonne, 2005; Laflamme et al., 2011), whereby microbial biofilms assist in lithifying the sediment around discs (preserving them), while the fronds remain uncovered and decay away. Conversely, when the other ‘organ’ taxon *Hiemalora* is considered, its range is found to be broadly synchronous with that of the only taxon it has so far been found attached to, *Primocandelabrum*, with both disappearing from the Ediacaran of Avalonia in the upper Fermeuse Formation. This would suggest that *Hiemalora* is truly an ‘organ’ taxon, simply preserving the remains of the basal disc of the

Primocandelabrum organism. The continued range of *Aspidella* could therefore alternatively indicate that it represents a number of different taxa, which have been over-synonymised within the catchall *Aspidella* (*contra* Gehling et al., 2000). Further research into this problem is currently being undertaken by Latha Menon as part of a D.Phil. thesis at the University of Oxford. The ivesheadiomorph group (Chapter 3) has a stratigraphic range in Newfoundland that coincides precisely with that of all combined rangeomorph taxa, consistent with the hypothesis that ivesheadiomorphs represent the degraded remains of rangeomorph organisms (though note their early appearance in Charnwood, Fig. 2.14; Chapter 3; Liu et al., 2011).

In general, the first appearances of these Ediacaran macrofossil taxa appear to be staggered. It also seems that frondose taxa possessing furled and undisplayed rangeomorph branching (terminology of Brasier and Antcliffe, 2009; e.g. *Charnia*, *Trepassia*) appear first in the Drook Formation of the Avalon region (see the Pigeon Cove small fronds for example), with displayed variants (e.g. *Beothukis*, *Bradgatia*, *Fractofusus*) appearing simultaneously in both single and multifoliate rangeomorphs in the Briscal Formation. Whether this is an evolutionary pattern, an artefact of sampling biases, or in some way reflects environmental or taphonomic conditions, remains to be determined. The fine morphological detail present in displayed rangeomorph units may be simply too small to be preserved at the grain-sizes of the earliest beds. Nonetheless, the possibility that this pattern is controlled by evolutionary or ontogenetic processes remains exciting. Finds such as those at Pigeon Cove enable us to better constrain models for possible taxonomic phylogenies and evolutionary relationships at this early stage in the evolution of complex multicellular life.

A particularly striking feature is the abrupt disappearance of all taxa except *Aspidella* within the Fermeuse Formation. Multifoliate forms disappear first at the upper Trepassey/lower Fermeuse boundary, while single fronds and *Primocandelabrum* persist until the middle of the Fermeuse Formation. This may suggest that larger organisms with bigger volumes were being outcompeted by smaller, simpler forms, perhaps as a result of resources within the basin becoming restricted. Alternatively, the seemingly longer ranges of taxa possessing a stem (raising them off the seafloor), compared to reclining or low-relief taxa, may indicate that changes in conditions at the sediment-water interface were responsible for the observed declines. Rocks within the middle Fermeuse Formation arguably had the capacity to adequately preserve many members of the Ediacara biota (e.g. locality H26), but often did not. This may imply that the disappearance of certain forms at these levels requires an ecological rather than a taphonomic explanation. The disappearance of almost the entire biota (except for *Aspidella*; Fig. 2.17) within the upper Fermeuse Formation does not represent an extinction event, at least on a global scale, since several of the taxa are found in younger rocks from different terranes (e.g. *Charnia masoni* from Siberia, and *Bradgatia* from Laurentia; see Grazhdankin et al., 2008; Hofmann and Mountjoy, 2010). The loss of taxa in Newfoundland is therefore likely to reflect either a taphonomic control determined by local facies changes, or a regional extinction event.

Biases

There are obvious biases in the dataset that may have a bearing on the reliability of the described patterns. Comparison of geographically widespread localities requires that the stratigraphic correlations of O'Brien and King (2006), and Hofmann et al. (2008), be accepted as correct. This correlation skews the distribution of sampled localities within the column such that they are highly concentrated within the upper Mistaken Point and lower Trepassey Formations, with sparser coverage of the column in the earlier Drook and Briscal, and later Fermeuse Formations (Fig. 2.16). The Briscal Formation is reportedly entirely absent on the Bonavista Peninsula, while the Fermeuse Formation displays very different lithological characteristics there (Hofmann et al., 2008), making accurate correlations difficult. This

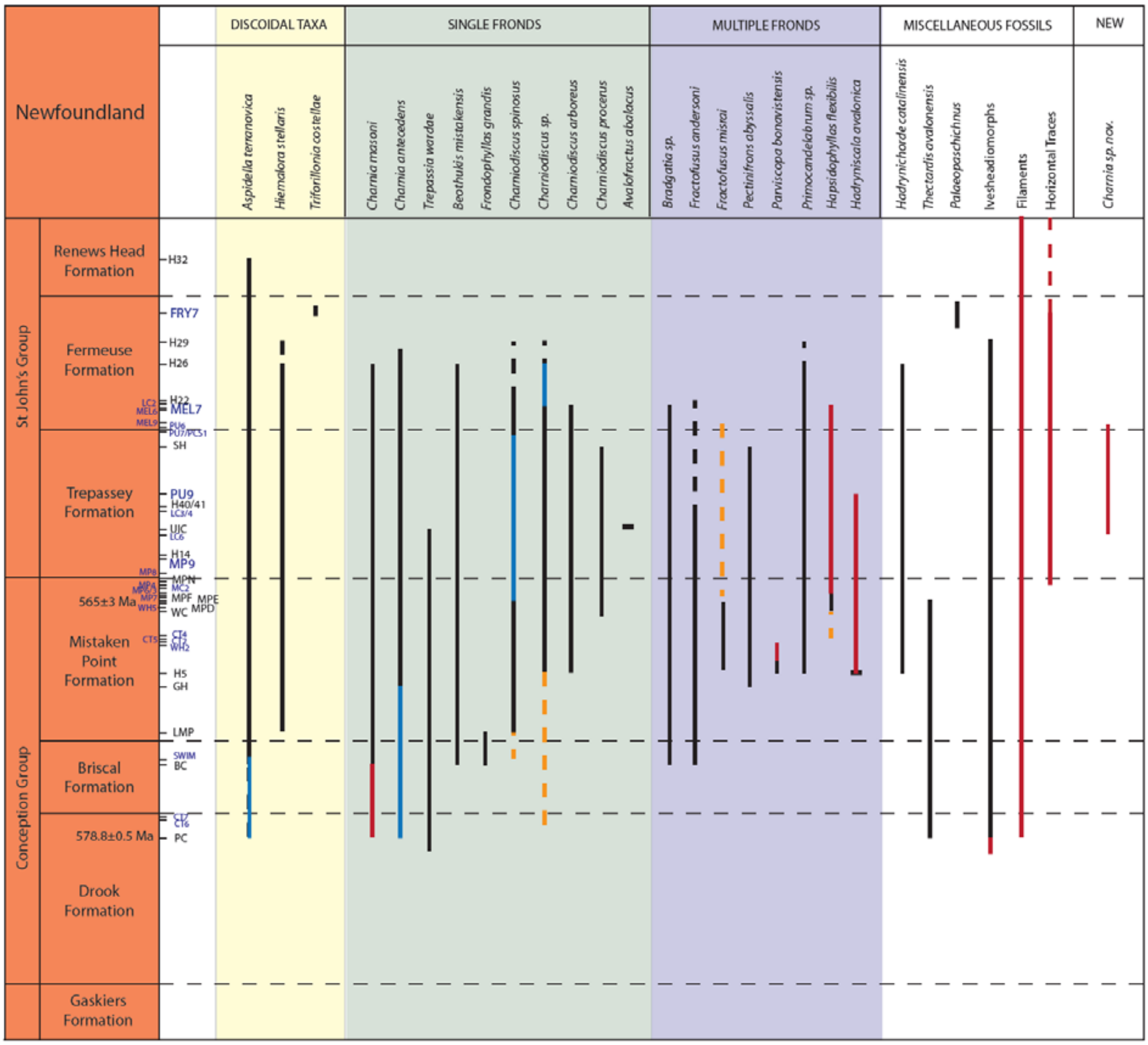

Fig. 2.17. Summary biostratigraphic chart for the Ediacaran rocks of the Avalon terrane, Newfoundland. In addition to the legend in Fig. 2.16, blue vertical bars indicate confirmation of stratigraphic ranges determined as ‘possible’ from the published literature. Orange represents possible extended ranges for individual taxa obtained during this study. Red indicates definite extended stratigraphic ranges of Ediacaran taxa, based on data obtained during this D.Phil. The range of filaments is extended up past the Renews Head Formation due to the discovery of individual filaments within the Ferryland Head Formation, at locality FRY 4.

scarcity of outcrop, at exactly the times when lineages appear to have been diversifying or locally dying out, exposes serious limitations in our ability to critically compare, at fine resolution, the ranges of Ediacaran taxa. It also needs to be noted, as mentioned previously, that several taxa are defined by morphological features that are often too small or fine to be preserved on ‘typical’ Avalonian bedding planes. It is therefore entirely possible that some taxa may have been overlooked or misidentified due to the poor quality of preservation. Despite these issues, this first attempt at plotting stratigraphic ranges for the Avalonian Ediacara biota raises some interesting questions and possibilities, and provides abundant avenues for future research. Construction of such charts may be hindered by a scarcity of accurate radiometric dates, and variation in facies between basins, but it is hoped that as our knowledge of the Ediacaran Period improves, the robustness of the observed trends will increase.

SUMMARY

Compilation of the stratigraphic ranges of Ediacaran macrofossil taxa can reveal interesting insights into the evolution and relationships of these organisms. These ranges can also be used to compare localities, and potentially even for regional or global biostratigraphic correlation, though it is premature to suggest suitable taxa for such a purpose at present. Although it is evident that various species have specific ranges in Newfoundland, many of which extend for considerable lengths of time in multiple locations, the extensions to the taxonomic ranges revealed by just three field seasons of discoveries suggest that these ranges are far from being finalised. Further investigation and exploration is necessary to refine them. It is clear that Charnwood and Newfoundland contain similar taxonomic assemblages, and theoretically could be correlated on the basis of their biota. Unfortunately, Charnwood possesses so few taxa and localities that such a correlation would be speculative based upon current knowledge. Longmynd cannot yet be correlated with either Charnwood or Newfoundland on the basis of the macrofossil assemblage thus far described, despite an age range that likely overlaps with that of Charnwood and Newfoundland. This finding is consistent with the suggestion that its distinctive biota has been shaped by environmental factors. Utilising stratigraphic ranges of macro-organisms for the purposes of correlation is therefore considered to be a ‘work in progress’; macrofossil stratigraphic ranges show considerable promise for regional correlation, but extensive fieldwork and taxonomic study is required to determine whether true biostratigraphy can be usefully applied to the Ediacaran Period as a whole.

The increased diversity documented at Pigeon Cove demonstrates that several rangeomorph structural architectures, including the majority of those exhibiting undisplayed branching architecture (*sensu* Brasier and Antcliffe, 2009), were present only three million years after the deposition of the Gaskiers tillite. This morphological diversity, when combined with data from other beds in the Avalon terrane, raises questions concerning the timing of the evolutionary events that led to the explosion of multicellular life. These questions resonate with those concerning the timing and nature of the Cambrian Explosion of metazoan diversity (e.g. Darwin, 1859; Brasier, 2009). The Ediacaran diversification of body plans can similarly be considered to be a result of either: 1) taphonomic biases hiding an earlier phase of evolutionary diversification, with evolution of the Ediacara biota being contemporaneous with or perhaps even prior to the Gaskiers glacial event, or; 2) genuine explosive rates of evolution, which given our discoveries would require evolution of this morphological diversity within three million years of the end of the Gaskiers glacial (cf. Shen et al., 2008b). Determining which of these possibilities is correct, and exploring the stepwise appearance of rangeomorph taxa implied by the stratigraphic ranges of the Newfoundland biota, will reveal much about the patterns and processes governing the initial diversification of macroscopic life during the Ediacaran Period. Furthermore, the extended stratigraphic ranges for several Ediacaran taxa documented by these finds indicate a substantial degree of evolutionary stasis amongst some members of the Ediacara biota. Specific relationships between particular taxa and facies types (see also Grazhdankin, 2004) can also be extracted from biostratigraphic range charts such as those presented here, and all of these topics warrant further consideration.

Consolidating our understanding of the Ediacara biota is vital if we are to determine its true place in the evolution of life. Continued field exploration, and the construction of stratigraphic range charts, both provide enormous potential for uncovering and resolving critical questions about the nature of evolution during the Ediacaran Period.

ACKNOWLEDGEMENTS

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CHAPTER 3
THE 'EFFACED PRESERVATION' HYPOTHESIS

PREFACE

One major obstacle to determining the biological composition of Ediacaran ecosystems, and the true diversity of the Ediacara biota as a whole, has been the problem of taxonomy. Largely due to the cosmopolitan nature of Ediacaran research, several taxa have been assigned multiple names by different researchers, while others have been classified under a host of higher level taxonomic groupings (see the taxonomic inventory in Fedonkin et al., 2007a for numerous examples). Unfortunately these problems show no sign of abating, with the new field of research into tubular Ediacaran body fossils already beset by taxonomic confusion and disagreement (e.g. *Gaojiashania* from China and Siberia, see Zhuravlev et al., 2009; Cai et al., 2011). The ancient nature of the Ediacara biota, coupled with the views of earlier researchers that the Ediacaran organisms were ancestors of modern groups (e.g. Glaessner, 1984), has also encouraged the over-interpretation of features (e.g. the Australian ‘echinoderm’ *Arkarua*, Gehling 1987; the ‘arthropods’ *Pseudovendia*, Boynton and Ford 1979 and *Parvancorina*, Glaessner 1980; and even a chordate; Gehling in Fedonkin et al., 2007a). Meaningful research into Ediacaran biotic diversity or palaeoecology should be based upon precise and consistent taxonomic foundations, which hopefully reflect the true biotic diversity and biology of the preserved ecosystem. The problems outlined above, however, suggest that a certain degree of taxonomic revision is required before this can be attempted.

In Chapter 2, the writer has discussed how taxonomic concepts have the potential to be undermined by descriptions and diagnoses that are often too specific to be applied to many preserved specimens. Although there are numerous candidates for taxa requiring attention, the research in this chapter focuses upon the fossil *Ivesheadia* Boynton & Ford, 1996. Once described as a medusoid from Leicestershire, U.K., in the regional journal *Mercian Geologist*, *Ivesheadia* has defied higher classification for years. It is reported from the Avalonian assemblages of Newfoundland and the U.K., and has the distinction of appearing to be one of the oldest fossils in both regions. Reinterpretation of *Ivesheadia* and several similar forms as taphomorphs, formed by the processes of decay on the seafloor prior to burial, is the focus of this chapter. The bulk of this section has now been published by Liu et al. (2011) in the journal *Palaeontology* under the title *'Effaced Preservation in the Ediacara Biota and its Implications for the Early Macrofossil Record'*. The general concept was originally conceived, but never published, by Duncan McIlroy, Jonathan Antcliffe and Martin Brasier in the period up to 2007, before I joined the project. My contribution was to test this hypothesis in the rocks, by obtaining and analysing detailed field, laboratory and palaeoecological evidence. I also named and developed the concept of effaced preservation, and moved the original field hypothesis into the realm of experimental taphonomy (Chapter 4).

This chapter outlines the effaced preservation hypothesis, and describes the field evidence obtained to test and support it. A discussion of the methods used by Ediacaran researchers to faithfully remove tectonic deformation from fossils is also included. Later chapters will describe the experimental support for effaced preservation (Chapter 4), and its implications for Ediacaran palaeoecology (Chapter 5). One new figure has been added to the published version (Fig. 3.14), while only minor edits have been made to the original text, mostly to discuss interesting specimens that have come to my attention since acceptance of the *Palaeontology* manuscript.

ABSTRACT

Ediacaran structures known as 'pizza discs' or *Ivesheadia* have long been considered enigmatic. They are amongst the oldest known members of the Ediacara biota, seemingly restricted to the Avalonian successions of Newfoundland, and the United Kingdom, *c*. 579–560 Ma. Biological interpretations of these impressions have included jellyfish and fungi. Here it is suggested that they are taphomorphs, resulting from the post-mortem decay of the frondose Ediacaran biota. Fossils range from well-preserved, high fidelity variants to almost completely effaced specimens. The effaced specimens are inferred to have undergone modification of their original morphology by post-mortem microbial decay on the sea-floor, combined with sediment trapping and binding. In this style of preservation, morphological details within the organism became variously subdued as a function of the extent of organic decay prior to casting by overlying sediments. Decay and effacement were progressive in nature, producing a continuum of grades of preservation on Ediacaran bedding planes. Fossils that have suffered these processes to the extent that only their gross form can be determined are preserved by 'effaced preservation'. The lack of detailed morphology preserved in effaced specimens renders such fossils unsuitable for use as type material, since it is possible that several taxa may, upon degradation and burial, result in similar morphological taphomorphs. Here the genus *Ivesheadia* is reinterpreted as a taphomorph resulting from extensive post-mortem decay of frondose organisms. *Blackbrookia*, *Pseudovendia* and *Shepshedia* from beds of comparable age in England are likewise regarded as taphomorphs broadly related to *Charnia* or *Charniodiscus* spp. To reflect the suggestion that such impressions are likely to be taphomorphs, and not taxonomically discrete, the term ‘ivesheadiomorphs’ is proposed to incorporate all such effaced taphonomic expressions of Ediacaran macrofossil taxa in the Avalonian assemblages. The existence of effaced preservation has serious implications for Ediacaran taxonomy, and consequently for measures of Ediacaran diversity and disparity

before the rapid evolution of animals during the Cambrian Explosion. It is implied that Ediacaran assemblages preserve both organisms that were alive and the remains of organisms that were dead at the time of burial. As such, the fossil assemblages cannot be taken to represent census populations of living organisms, as in prior interpretations.

INTRODUCTION

The Ediacara biota is of critical importance to our understanding of the origin of animals, since it immediately precedes the Cambrian fauna from which all subsequent animal life evolved (e.g. Brasier, 2009). The biota is also justly famous for its exceptional quality of preservation of soft-bodied organisms. The initial study of any palaeontological biota naturally focuses on the best preserved and most eye-catching fossils. However, to only focus on these may lead researchers to miss valid and interesting information from relatively poorly preserved specimens. Study of the full spectrum of Ediacaran fossil preservation is starting to show that we may have some surprising and interesting things to learn about the Ediacara biota and the Ediacaran Period. These new observations and insights are the focus of this chapter.

The earliest diverse communities of Ediacaran macro-organisms appear in the fossil record of south-eastern Newfoundland, and the United Kingdom. It seems highly likely, given the suite of comparable taphonomic features, shared taxa and geology, and palaeogeographic proximity, that these two regions form a coherent assemblage to the exclusion of other Ediacaran-age localities. Cluster analysis of the Ediacara biota supports this assertion (Waggoner, 2003). Since the earliest fossil discoveries (Salter, 1856; Billings, 1872; Ford, 1958), these two regions have yielded a rich, well-preserved, Ediacara biota, principally composed of *Charnia* spp. and other closely related frondose taxa such as *Charniodiscus,* *Bradgatia*, *Beothukis*, *Fractofusus* and *Primocandelabrum*, and related discoidal forms such as *Hiemalora* and *Aspidella* (Narbonne, 2005; Hofmann et al., 2008). Rangeomorph organisms (a term used herein to describe gross-scale morphological elements *sensu* Narbonne, 2004, but without any phylogenetic implications) often contain sub-unit detail visible at resolutions of tenths of a millimetre (Brasier and Antcliffe, 2009; Fig. 1.4), and are often preserved in high fidelity.

The biotic assemblages of the Avalon province also include poorly defined ovate fossils, reaching up to 0.8 m in diameter (Hofmann et al., 2008). In Newfoundland these fossils, which are usually considered to be morphs of *Ivesheadia* Boynton and Ford, 1996 (Narbonne et al., 2001; Brasier, 2009; Brasier and Antcliffe, 2009), range from the upper beds of the Drook Formation (dated at 578.8 ± 0.5 Ma; Van Kranendonk et al., 2008), through to the

PLATE 3.1. Variation in ivesheadiomorph morphologies in the Ediacaran beds of Newfoundland.

Fig. 1. 'Pizza disc' morph of *Ivesheadia* (*sensu* Narbonne et al., 2001). Drook Formation, Pigeon Cove, Avalon Peninsula, Newfoundland. Scale bar = 50 mm.

Fig. 2. 'Lobate' morph of *Ivesheadia* (*sensu* Narbonne et al., 2001). E Surface, Mistaken Point, Avalon Peninsula, Newfoundland. Scale bar = 50 mm.

Fig. 3. Bubble mat morph of *Ivesheadia* (*sensu* Narbonne et al., 2001). E Surface, Mistaken Point, Avalon Peninsula, Newfoundland. Scale bar = 50 mm.

Fig. 4. Elongate bi-lobed 'Pizza disc'. Drook Formation, Pigeon Cove, Avalon Peninsula, Newfoundland. Scale bar = 100 mm.

Fig. 5. A 'tethered' individual, seemingly attached to a filament. Drook Formation, Pigeon Cove, Avalon Peninsula, Newfoundland. Scale bar = 50 mm.

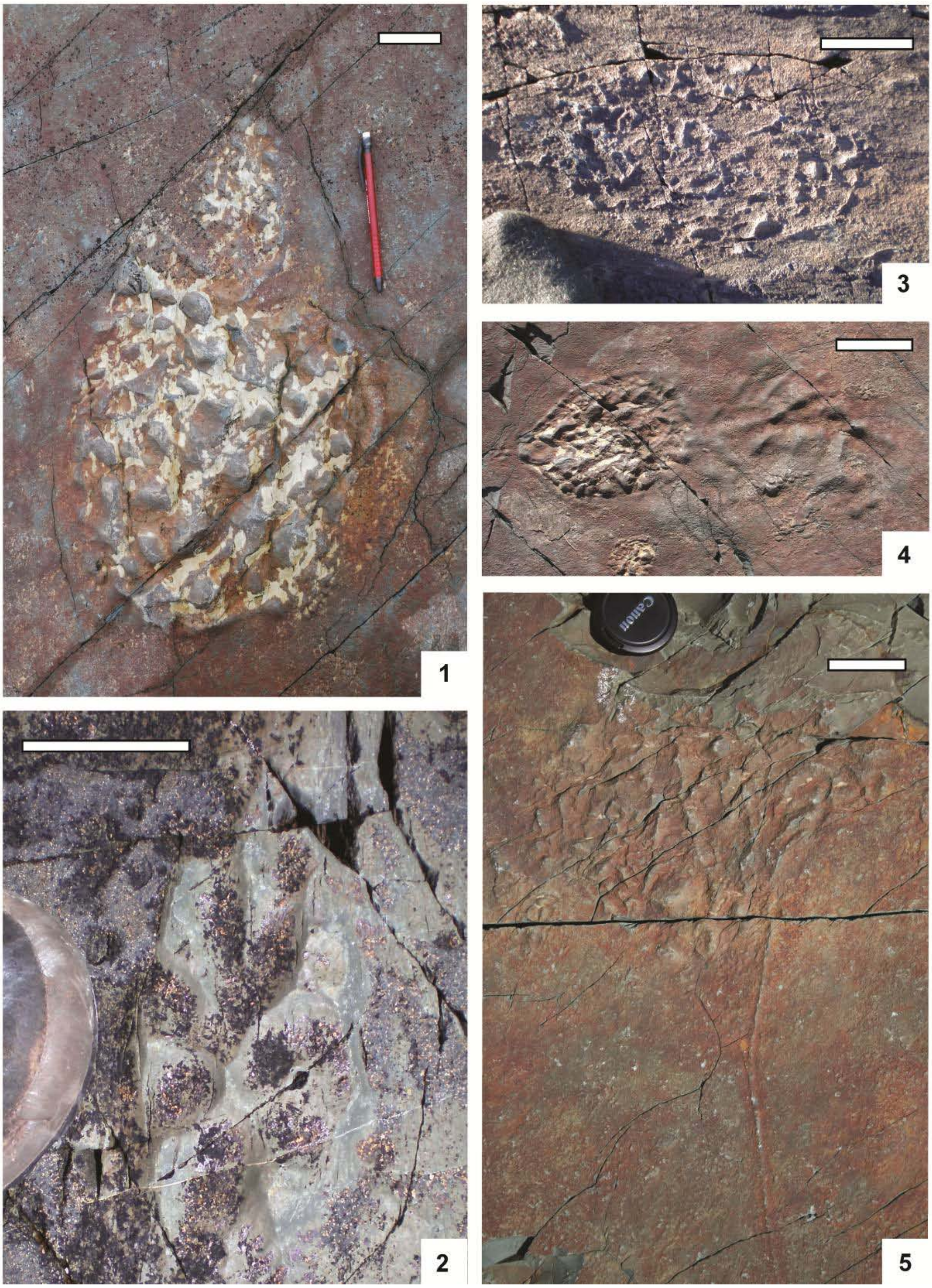

PLATE 3.1

Fermeuse Formation (Hofmann et al., 2008), *c*. 560 Ma (Pls. 3.1–3.2). In Charnwood Forest, U.K., *Ivesheadia* likewise appears in the lowest fossil-bearing levels, within the Blackbrook Formation, which in part may be older than 600 Ma (see McIlroy et al., 1998; Carney, 2000).

Most specimens attributed to *Ivesheadia* exhibit little to no fine-scale internal detail. Morphology within *Ivesheadia* discs is highly variable, and usually comprises a collection of smooth irregular ridges, some 10–20 mm wide (Pls. 3.1–3.2). These ridges are typically preserved in high positive epirelief, rising up to 10 mm above the modern bedding surface. Interestingly, *Ivesheadia* represents one of the largest elements of the Ediacara biota in terms of surface area, with diameters ranging from 30 mm–0.8 m (Hofmann et al., 2008), and they are commonly observed distributed randomly on the bedding planes (Clapham et al., 2003). Although the majority of *Ivesheadia* specimens are circular or oval in outline (Pl. 3.1), several elongate or irregular examples have been documented both in Newfoundland and the U.K. (Pl. 3.1, fig. 4; Pl. 3.2, figs. 3–4).

The term ivesheadiomorph is used herein as a catch-all to encompass Ediacaran fossil taxa with low preservational fidelity, of the kind seen in the holotype of *Ivesheadia lobata* Boynton and Ford, 1995 (Pl. 3.2, fig. 2). Such ivesheadiomorphs include *Ivesheadia sensu stricto,* the 'pizza discs', 'lobate discs', and 'bubble discs' reported by Narbonne et al. (2001) from Mistaken Point (Pl. 3.1), and the problematic taxa *Blackbrookia, Pseudovendia,* and *Shepshedia* (Pl. 3.2 figs. 1,3–4; see Boynton and Ford, 1979, 1995), which also lack internal detail and are composed of irregularly arranged, high-relief lobes. Ivesheadiomorphs are generally found on bedding planes in conjunction with other Ediacaran fossil taxa characteristic of the Avalon assemblage (see Clapham et al., 2003; Hofmann et al., 2008). The latter typically show substantially more internal detail and structure than associated ivesheadiomorphs, an observation that has been widely interpreted to suggest ivesheadiomorph taxa differed fundamentally from coeval frondose and discoidal taxa in morphological construction or ecology (e.g. Narbonne et al., 2001; Peterson et al., 2003).

The biological affinity of *Ivesheadia* and other ivesheadiomorphs is problematic, with previous discussion of this subject limited by a lack of internal morphological detail. The genus *Ivesheadia* (formerly *Ivesia* Boynton and Ford, 1995; revised in Boynton and Ford, 1996), was described first as a medusoid of possible cnidarian affinity from the Ediacaran rocks of Leicestershire, U.K. (Pl. 3.2, fig. 2; Boynton and Ford, 1995, 1996; Ford, 1999). Recent descriptions of *Ivesheadia* from the Bonavista Peninsula of Newfoundland have suggested that such fossils represent the 'collapsed compartmentalised bodies' of organisms (Hofmann et al., 2008, pg. 33). A single 'pizza disc' specimen seen attached to a >3 m long

PLATE 3.2. The range of ivesheadiomorph morphology in the Ediacaran successions of the U.K. Specimens in figures 1–3, 5 from the Blackbrook Group, Ives Head, Leicestershire. Specimen in figure 4 is from a loose block within the Woodhouse Beds, Outwoods, Leicestershire. For a geological map of Charnwood Forest and its outcrops, see Appendix D1, Fig. D1.2.

Fig. 1. Cast of the holotype of *Shepshedia palmata* Boynton and Ford, 1995. Scale bar = 50 mm.

Fig. 2. Cast of the holotype of *Ivesheadia lobata* Boynton and Ford, 1996. Scale bar = 50 mm.

Fig. 3. Cast of the holotype of *Blackbrookia oaksi* Boynton and Ford 1995. Scale bar = 50 mm.

Fig. 4. Cast of the holotype of *Pseudovendia charnwoodensis* Boynton and Ford 1979. Cast P.78, University of Oxford Palaeontological Collection. Scale bar = 10 mm.

Fig. 5. Elongate form, which may represent the effaced remains of a disc and stem. Scale bar = 50 mm.

Casts in Figs 1–3 were taken by the British Geological Survey, and are housed in Keyworth, Nottinghamshire, U.K. Figs. 1–2 reproduced with the permission of the British Geological Survey © NERC. All rights reserved.

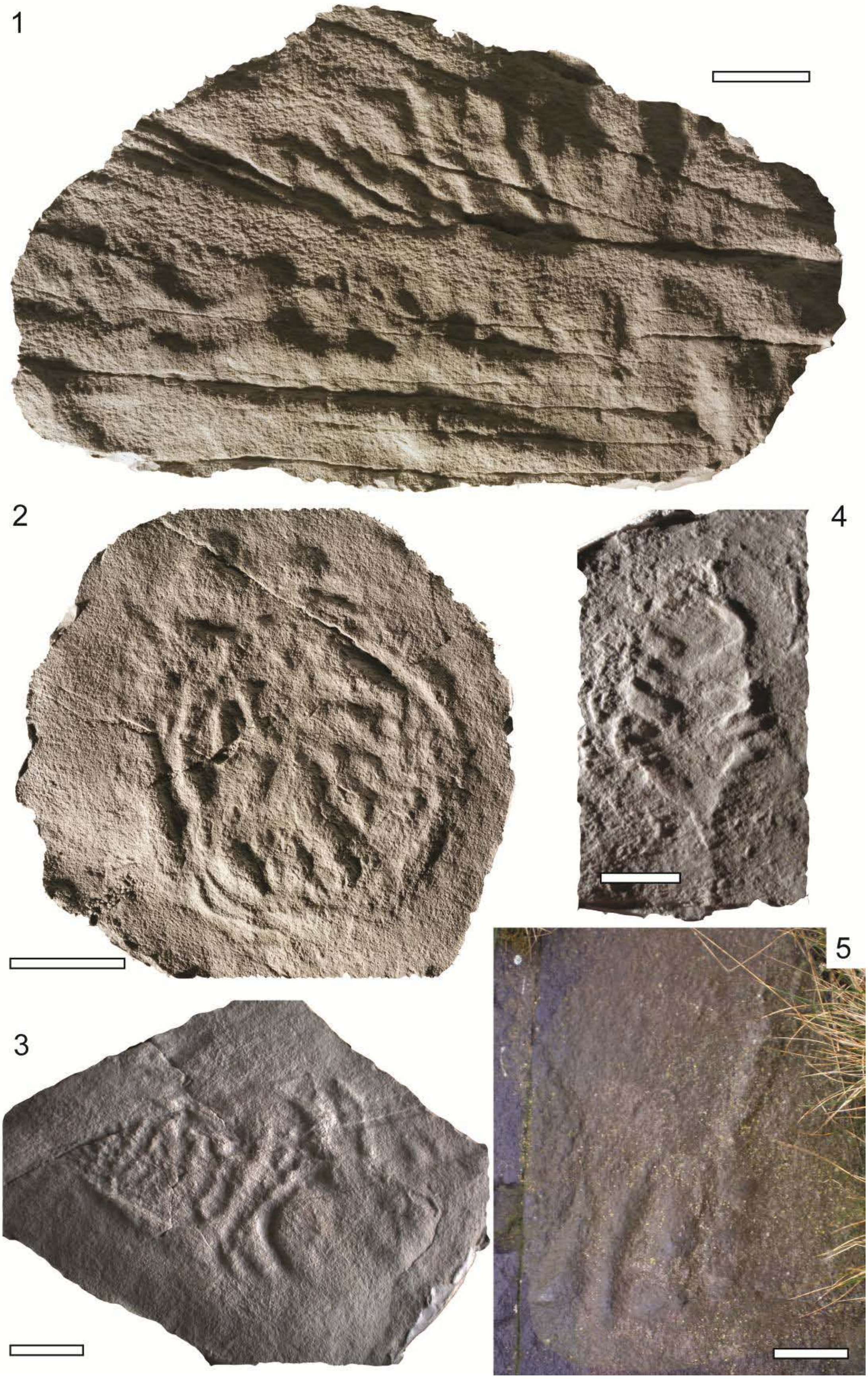

PLATE 3.2

filament in the Drook Formation of Newfoundland (Pl. 3.1, fig. 5), has been interpreted as a 'tether' stretching from the organism down to the seafloor below (Narbonne et al., 2001), or alternatively as a respiratory organ for an organism living beneath the sediment-water interface (Peterson et al., 2003; Gehling and Narbonne, 2007). However, this form is highly atypical in the Avalonian assemblages, and is not representative of the majority of ivesheadiomorphs (Pl. 3.1, figs. 1–4; Pl. 3.2, figs. 1–5). Importantly, no two ivesheadiomorph fossils have been observed to be identical.

Below, we use a series of observations to propose a new hypothesis to explain the wide range of ivesheadiomorph structures and morphologies. Ivesheadiomorphs are interpreted here as the remains of poorly preserved Ediacaran macro-organisms that had undergone slow decomposition on the seafloor prior to rapid burial and preservation. We then consider whether *Ivesheadia* and similar forms represent a morphologically disparate grouping of fossils, linked by their having experienced similar taphonomic processes rather than by true biological relationships.

FIELD EVIDENCE FOR A SPECTRUM OF EDIACARAN PRESERVATION

Field studies in Newfoundland and the U.K. indicate that while both well-preserved rangeomorphs and poorly-preserved ivesheadiomorphs can be found on Avalonian bedding planes, there is also a preservational continuum between these end members. Forms showing both high-relief, irregular *Ivesheadia*-like morphology, and regions of high fidelity branching frondlets, are present, albeit rare. Below, Avalonian fossils are described whose preservation grades from very well-preserved material in both positive and negative epirelief, through progressively more effaced examples, to poorly preserved variants classified as *Ivesheadia sensu lato*. Many different elements of the Avalonian Ediacaran biota are observed as effaced ivesheadiomorph variants. Here, the common Avalonian genus *Charniodiscus* Ford 1958, and the multi-foliate *Bradgatia* Boynton and Ford 1995, from the Conception and St John's Groups of Newfoundland, Canada, have been chosen to demonstrate this preservational continuum.

The Charniodiscus spectrum

Specimens attributed to the genus *Charniodiscus* provide a case study for the existence of a preservational spectrum between pristine and effaced fossil preservation. The following

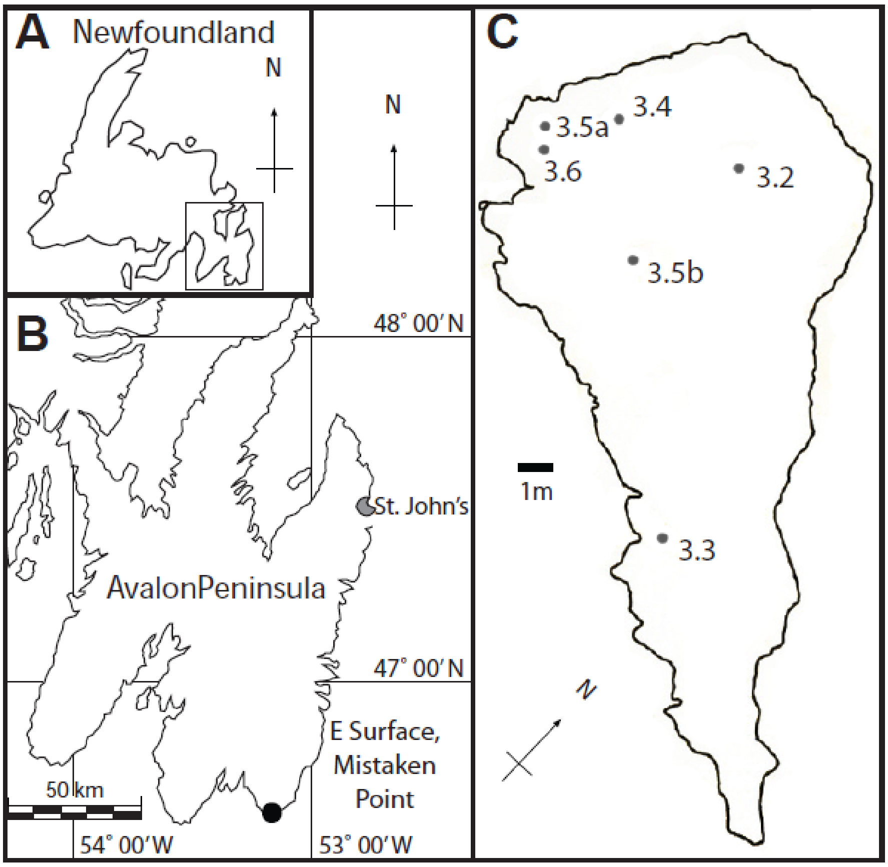

Fig 3.1. Locality map for figured *Charniodiscus* specimens from Mistaken Point. **A**: The island of Newfoundland, Eastern Canada. **B**: The Avalon Peninsula, showing the location of the Mistaken Point E Surface (black spot). **C**: Map of the E Surface bedding plane at Mistaken Point, illustrating the locations of *Charniodiscus* specimens figured herein. Numbers correspond to the relevant parts of Figs. 3.2–3.6. All figured *Charniodiscus* specimens remain *in situ*.

specimens, all from the E Surface of Mistaken Point (Fig. 3.1; Appendix D2; *sensu* Landing et al., 1988), document a clear spectrum of preservation within *Charniodiscus s.l.* specimens (Figs. 3.2–3.6). The fact that all figured specimens are found on the same bed within an area of 6 m x 13 m (Fig. 3.1C) suggests erosional or tectonic processes are not responsible for the differences in preservation between specimens.

The distinctive elongate shape and basal disc of *Charniodiscus* (Fig. 3.2) contrast strongly with the circular or oval outlines of *Ivesheadia lobata s.s.* (Pl. 3.2, fig. 2). Although the majority of ivesheadiomorph specimens observed in the Avalon region are approximately circular in outline, a substantial number of elongate forms also exist (e.g. Pl. 3.1, fig. 4). That

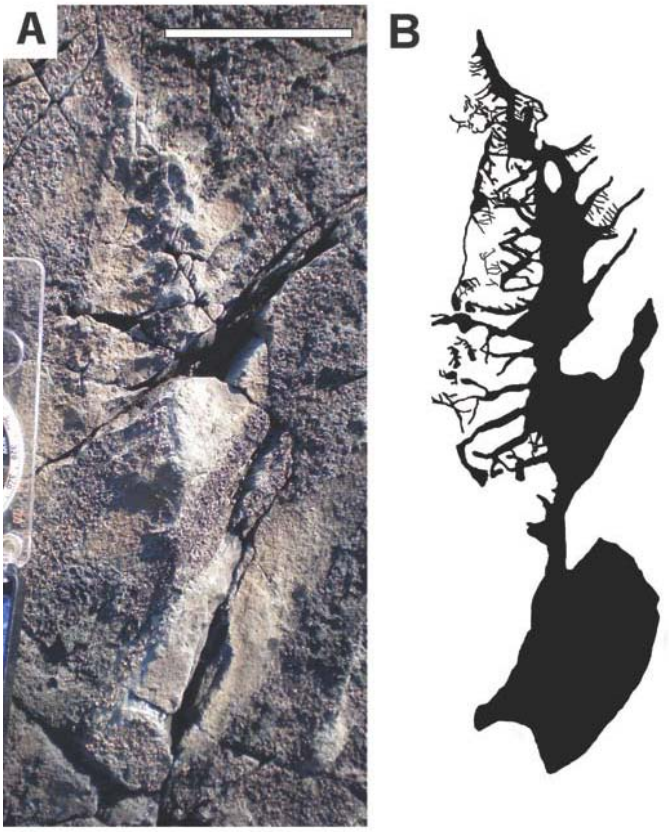

Fig. 3.2. A well preserved specimen of *Charniodiscus spinosus* Laflamme et al., 2004 from the E Surface at Mistaken Point, Avalon Peninsula, Newfoundland (position indicated in Fig. 3.1C). **A**: Digital image from the outcrop. **B**: Digital interpretive drawing of the fossil, emphasising the features preserved in positive relief (in black). Scale bar represents 50 mm.

this elongation is original in many cases, and not tectonic, is evident from simple documentation of the orientations of ivesheadiomorph long-axes. These elongate forms have a stratigraphic range from the Drook to Trepassey Formations in Newfoundland.

Charniodiscus specimens are normally seen preserved on these beds in positive epirelief, with a clearly visible disc, stem, and spatulate, leaf-shaped frond (Figs. 3.2–3.4; terminology following Laflamme et al., 2004). However, we have observed a number of ivesheadiomorphs that appear to have originally been *Charniodiscus* specimens (e.g. Figs. 3.5–3.6). While many frondose Ediacaran organisms show good preservation along their whole length, in others the apical regions are often less well preserved than basal regions, even in high-fidelity specimens

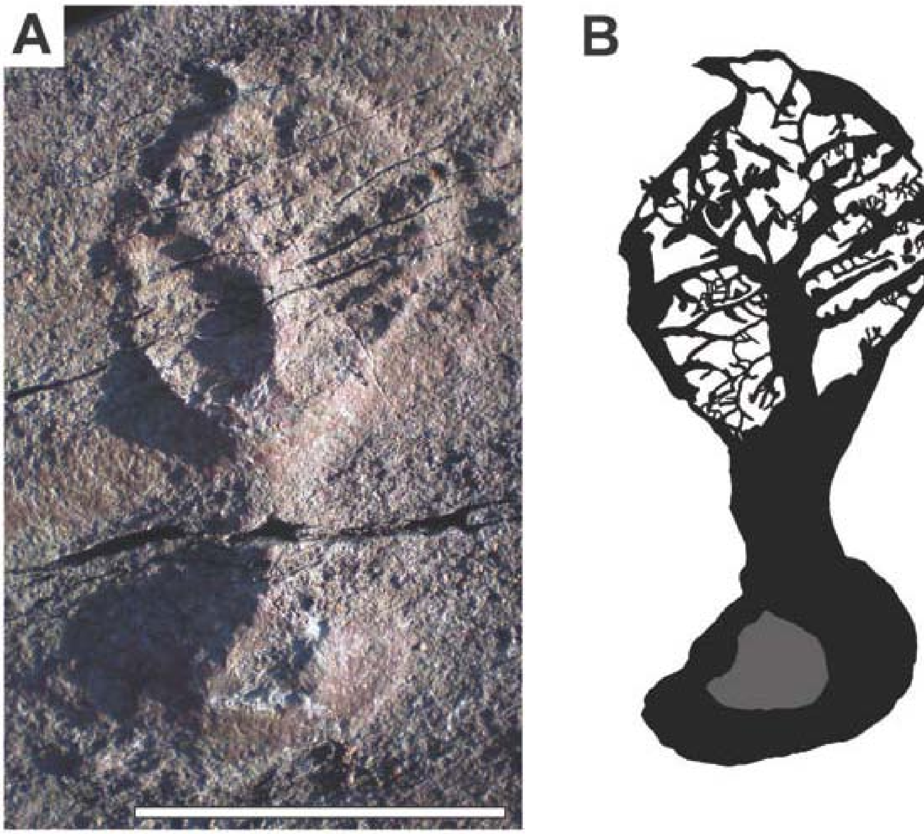

Fig. 3.3. A *Charniodiscus* preserved by Conception-type preservation from the E Surface at Mistaken Point, Avalon Peninsula, Newfoundland (position indicated in Fig. 3.1C). **A**: Digital field photograph, lit from the top right. Scale bar represents 50 mm. **B**: Digital interpretive drawing outlining the raised features (in black) within the fossil.

(e.g. Seilacher, 1992; Wood et al., 2003; Clapham et al., 2004; Laflamme et al., 2007).

It has therefore been suggested that the preservation potential of the fronds and their apical portions was less than that of basal stems and holdfasts, either because (1) the thickness of ash trapped between the organism and the seafloor at the time of burial is greater further away from the base of the organism (Laflamme et al., 2007); (2) the disc and stem were made of a more refractory organic material than the frond; or (3) the stem and base were thicker, possibly due to their function as supporting structures (Laflamme and Narbonne, 2008). None of these explanations account, however, for effaced preservation along the entire length of the organism (e.g. Figs. 3.5–3.6).

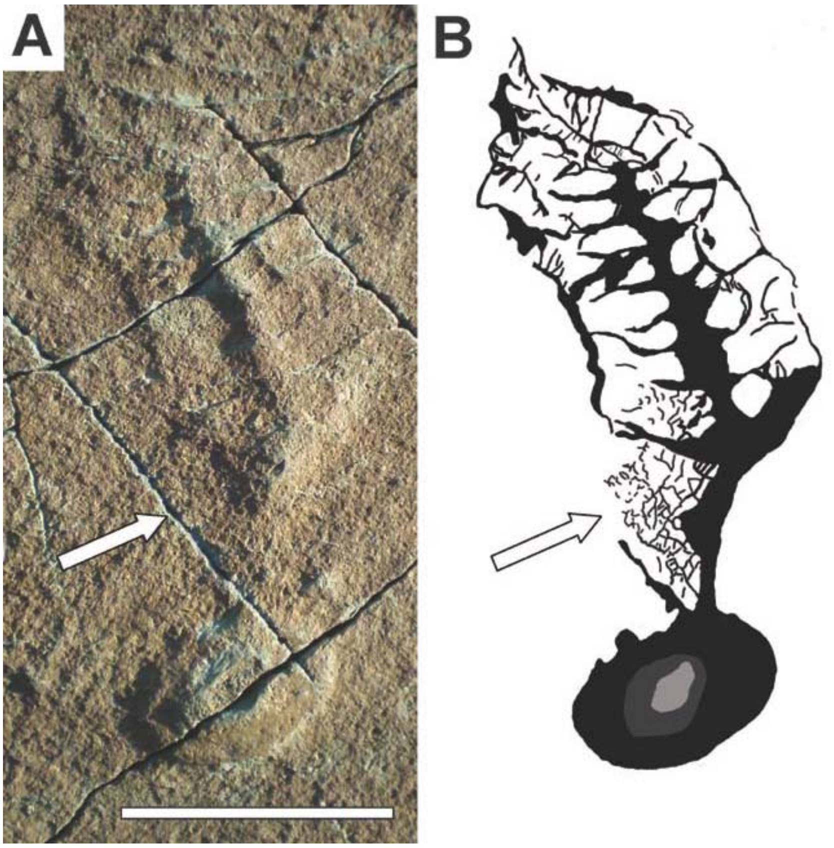

Fig. 3.4. A moderately pristine *Charniodiscus* specimen from the E Surface at Mistaken Point (position indicated in Fig. 3.1C). **A**: Digital photograph from the outcrop, lit from the top right. Note the region of fine filamentous structure along the length of the stem (arrowed), which may represent localised microbial growth. **B**: Digital interpretive drawing emphasising the positive relief features of the fossil (in black). Scale bar represents 50 mm.

Specimens of well-preserved *Charniodiscus s.l.* (Figs. 3.2–3.3) commonly exhibit a rounded basal holdfast, a prominent stem, and a leaf-shaped frond divided by branches at a high angle to the stem axis. The second and third order branching expected between these branches is not evident along the entirety of the frond in many specimens. Instead, detailed preservation is present only locally. This contrasts with the extensive preservation of fine details in associated organisms reconstructed as lying flat on the seafloor (e.g. *Fractofusus*; Gehling and Narbonne, 2007; Pl. 1.1B).

Also present on the bedding surface are specimens attributed to *Charniodiscus* that not only display clear primary branching, but also include regions with filamentous and net-like structures that lie both within and adjacent to the fossil (Fig. 3.4, arrowed). These structures

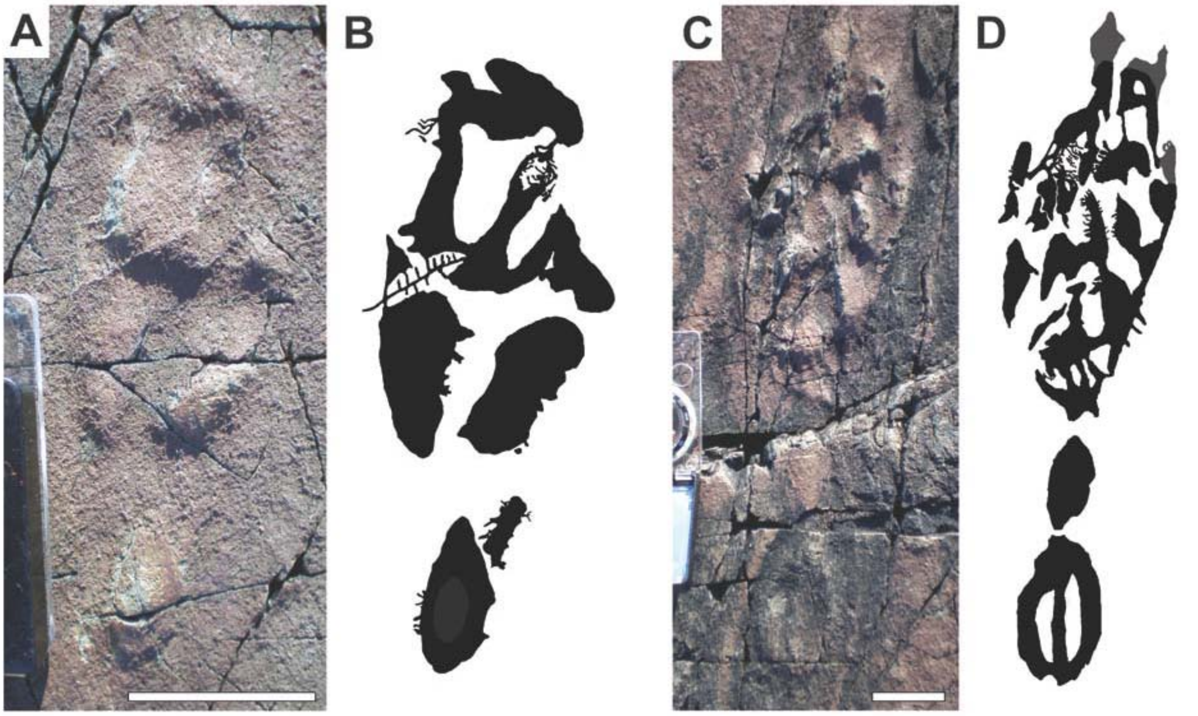

Fig. 3.5. Two effaced *Charniodiscus* specimens from the E Surface at Mistaken Point, Newfoundland (position indicated in Fig. 3.1C). **A**: Digital photograph from the field, lit from the top. Note the *Fractofusus misrai* specimen overlying the *Charniodiscus*. **B**: Digital interpretive drawing of specimen figured in Fig. 3.5A. **C**: Digital image of a probable *Charniodiscus spinosus*, lit from the top. **D**: Digital interpretive drawing of specimen figured in Fig. 3.5C. Note the irregular and high relief preservation of raised lobes, and the sharp outer margin of the impressions. In the absence of the discs at the bottom of the images, these specimens would be considered ivesheadiomorphs. Scale bars represents 50 mm.

are closely associated with the fossil, and strongly resemble structures from the Ediacaran of China interpreted as prokaryotic colonies (Steiner and Reitner, 2001). They therefore may record evidence for breakdown of the organic material by microbes, and/or the presence of a microbial mat growing around the organism.

Several other specimens on the E Surface appear to possess the characteristic ivesheadiomorph features of irregularly-spaced lobes preserved in high positive epirelief, within a circular to oval raised rim. Taken in isolation, these would almost certainly be interpreted as morphs of *Ivesheadia lobata*, but the presence of an adjacent disc (Fig. 3.5A–B), and even the remnants of an attached stem (Fig. 3.5C–D) reveal their true affinities. It appears that the frondose portion of the *Charniodiscus* organism has been preserved in the same way as a 'pizza disc', while the relief of the stem and disc has become subdued. Some small areas of detail are present within the frondose region in both figured specimens. It is likely that these represent filamentous growth of a microbial colony rather than preservation of original branching, due to the lack of an organised structure, and small scale of the features.

Finally, we have observed specimens that consist entirely of irregular, rounded bumps with high positive epirelief, and show no evidence for internal branching (Fig. 3.6). These resemble the ivesheadiomorph features of so-called 'pizza disc' or 'lobate disc' morphs (*sensu* Narbonne et al., 2001) of *Ivesheadia lobata*. Despite the absence of a clear stem or basal disc, the overall morphology of the impression is elongate and bilobed, resembling the outline of the disc and frond of *Charniodiscus s.l.* This raises the possibility that such ivesheadiomorph impressions are simply effaced taphomorphs of vendobionts rather than biologically distinct organisms, with all original internal branching obscured prior to preservation. However, care must be taken when attempting to interpret such specimens, since the possibility that they are neighbouring circular ivesheadiomorphs cannot easily be discounted. The orientations of both

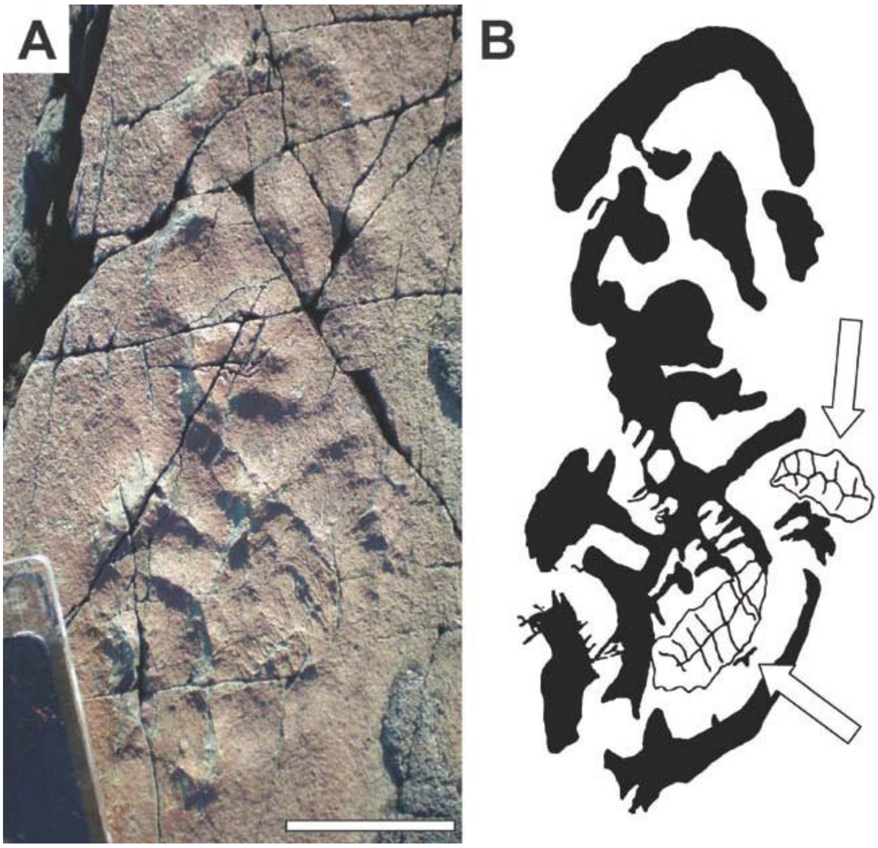

Fig. 3.6. Bi-lobate fossil from the E Surface at Mistaken Point, Avalon Peninsula, Newfoundland (position indicated in Fig. 3.1C), preserved by 'effaced preservation'. **A**: Digital photograph from the outcrop, lit from the top right. **B**: Digital interpretive drawing of the specimen figured in Fig. 3.6A, indicating the positive relief features of the fossil (black). Note two specimens of *Fractofusus* (arrowed in Fig. 3.6B) overlying the ivesheadiomorph. Scale bar represents 50 mm.

effaced and well-preserved specimens of *Charniodiscus* on the E Surface were collated and compared to determine whether there was any distinct difference (Fig. 3.7). It is clear from these figures that those specimens judged (albeit qualitatively) to be pristine share an orientation distribution with effaced forms. This adds further support to the suggestion that the effaced specimens are likely to have originally been *Charniodiscus*, since the common felling orientation is likely to have resulted from alignment by contourite currents.

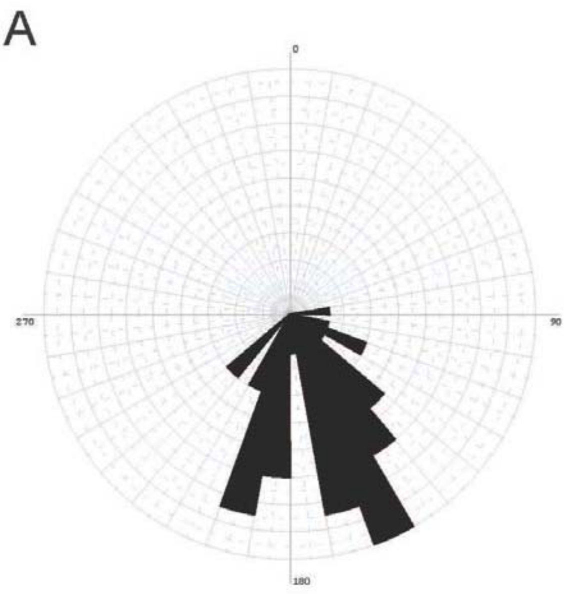

Fig. 3.7. Rose diagrams showing the orientations of *Charniodiscus* specimens on the E Surface of Mistaken Point. **A**: Pristine specimens of *Charniodiscus*, n = 37. **B**: Effaced presumed specimens of *Charniodiscus*, n = 30.

The individuals discussed above demonstrate the existence of a gradational spectrum running from well-preserved, high fidelity preservation of *Charniodiscus* specimens, through intermediate stages where much of the detail has been lost and the surface topography has become raised and less regular, towards ivesheadiomorphs in which all characteristics other than the overall general shape have been lost, and the organism is preserved entirely in the manner of *Ivesheadia lobata*. Images of additional *Charniodiscus* specimens from the E Surface are presented in Appendix B to further substantiate this claim.

The Multi-foliate Spectrum

If elongate ivesheadiomorphs are simply taphonomic, effaced variants of forms such as *Charniodiscus* sp. as outlined above, this raises the possibility that the more common rounded ivesheadiomorphs could also represent taphonomic variants of known rangeomorph or similar taxa. *Ivesheadia lobata*-like forms (e.g. Pl. 3.1, figs. 1–3; Pl. 3.2, fig. 2) are extremely common in the Avalon successions, and compare closely in overall outline with the bushy ‘V’-shaped top of *Primocandelabrum* (Fig. 3.8A; Hofmann et al., 2008), the 'network' *Hapsidophyllas* (Fig. 3.8B; Bamforth and Narbonne, 2009), and the 'U' or 'O'-shaped morphs of mature *Bradgatia* (Fig. 3.8C; Boynton and Ford, 1995; Flude and Narbonne, 2008). Fieldwork in Newfoundland has revealed rare intermediate forms that may provide clues as to the original organism represented by the rounded ivesheadiomorphs (Figs. 3.9–3.10).

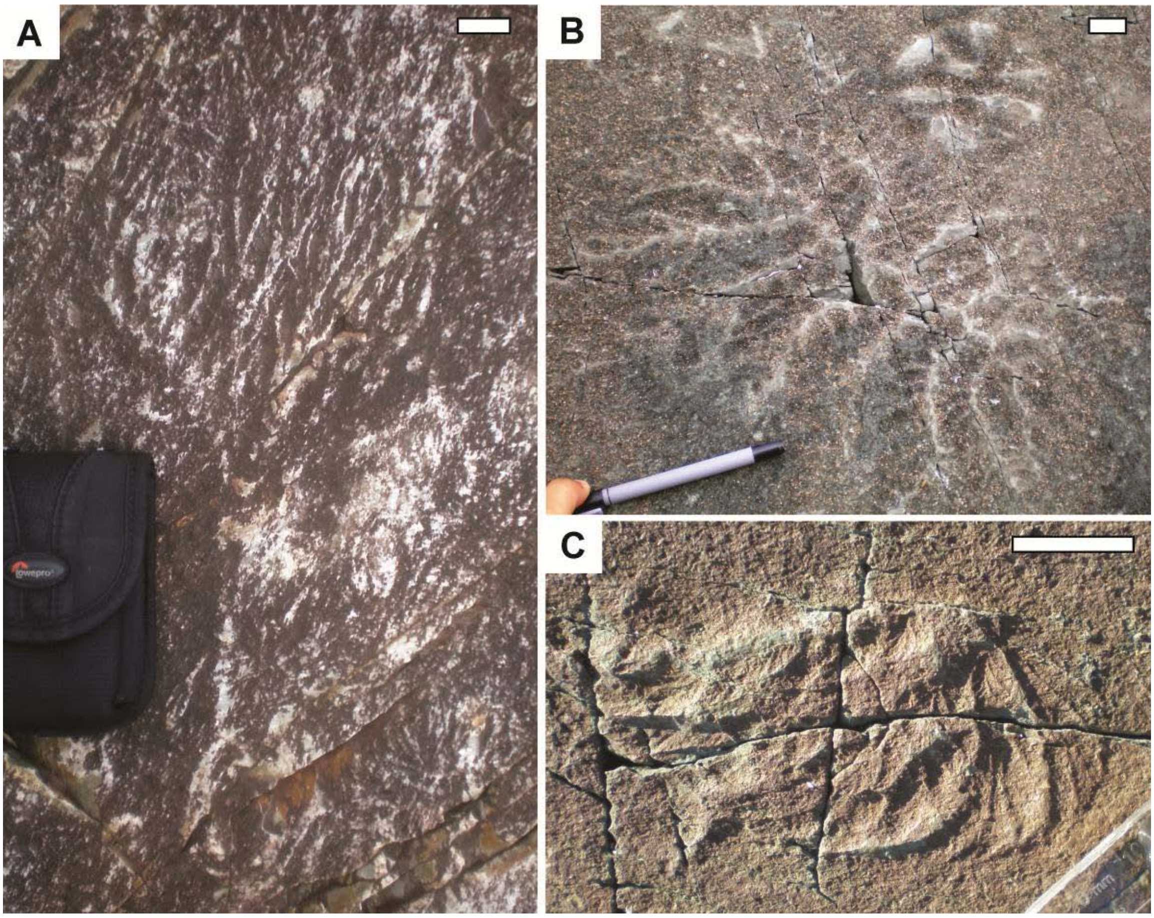

Fig. 3.8. Avalonian taxa which could potentially be effaced to produce rounded ivesheadiomorphs. **A**: *Primocandelabrum* sp., Catalina Member of the Trepassey Formation, Locality LC6, Little Catalina, Bonavista Peninsula, Newfoundland. **B**: *Hapsidophyllas flexibilis*, Mistaken Point Formation, Watern Cove (MP1), Avalon Peninsula, Newfoundland (disc at top right is not associated). **C**: *Bradgatia* sp. from the Mistaken Point Formation, Mistaken Point (near MP1), Avalon Peninsula, Newfoundland. Note the high positive epirelief of the edges of individual *Bradgatia* frondlets. Scale bars = 20 mm.

Unlike the *Charniodiscus* taphonomic morphs outlined above, in which the original affinities of ivesheadiomorphs can be determined simply from the overall shape of the impression and/or the presence of a basal disc or stem, multifoliate fronds are more complex to directly associate with their correlative ivesheadiomorphs. Firstly, *Bradgatia* and *Hapsidophyllas* do not possess either large basal holdfast discs or stems proximal of the frondose units; therefore, for these taxa such a criterion does not exist. Secondly, for *Bradgatia* at least, the broad preserved morphology of the organism is variable and reflects in part the strength of the current in which the organism was located. Individuals residing in strong currents will have their constituent fronds more strongly aligned than those inhabiting regions with weak currents. Therefore a spectrum of overall morphology will exist for *Bradgatia*, from 'V' through 'U' to 'O'-shaped morphs (*sensu* Flude and Narbonne, 2008) in plan view, and any resultant ivesheadiomorphs may retain this original morphology.

Fig. 3.9. A partially effaced *Hapsidophyllas* specimen from the D Surface of Mistaken Point. Note the presence within the specimen of both raised, rounded and irregularly spaced lobes, and frondose branching radiating from the centre of the specimen. Scale bar represents 50 mm.

What instead identifies some rounded ivesheadiomorphs as taphomorphic products of multifoliate organisms is the presence of frondose branching within the lobate irregular structure of the impressions (Fig. 3.9). Obviously, care must be taken to ensure that such perceived structures are actually part of the ivesheadiomorph, rather than for example a second organism superimposed either above or below the specimen in question. However, in some cases there is little doubt that the branching is a primary feature, with the presence of such branching within these ivesheadiomorphs clearly indicating that they belong to the same group of organisms as Ediacaran fronds. In some specimens, pockets of frondose branching remain visible within the collection of effaced lobes and troughs of the ivesheadiomorph (Fig. 3.9). In such specimens, the original radial branching can be followed in the raised and smoothed positive ridges for some distance, suggesting both that the high-fidelity branching is related to the rest of the structure, and that these ridges mark the location of (1st order) branches of a frondose organism. Other specimens (e.g. Fig. 3.10) are far more effaced and closely resemble classic *Ivesheadia* specimens. Nevertheless, the fan-shaped arrangement of ridges, and the occasional cluster of rangeomorph-like branches (arrowed), suggests an original affinity with an organism more akin to *Bradgatia*.

It is suggested that effacement of the surfaces of Ediacaran organisms prior to their burial, combined with sediment trapping and binding, generated the variation now observed amongst the fossils. It is evident that this effacement was a gradual process that could vary both laterally across an organism (as in Fig. 3.10), and temporally (see Figs. 3.2–3.6). The fact that we do not see otherwise well-preserved portions of *Charniodiscus* or other taxa emerging randomly from beneath/above *Ivesheadia* impressions leads us to reject any interpretation that sees these as accidental composite impressions of one organism over another.

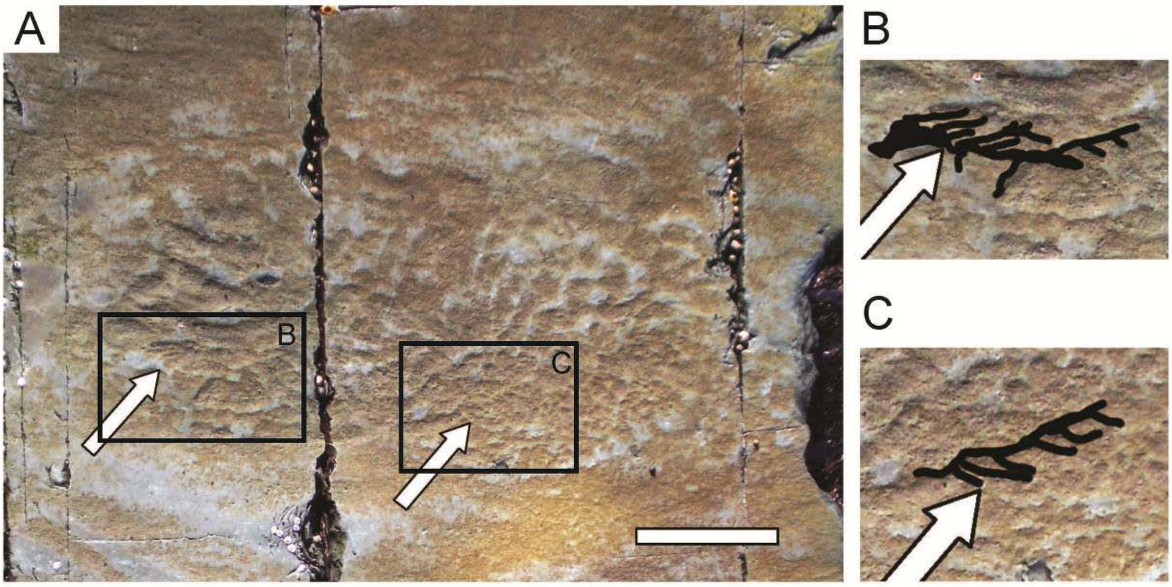

Fig. 3.10. A: *Ivesheadia* from the Trepassey Formation near Burnt Point, Port Union, Bonavista Peninsula, Newfoundland. Although the majority of the impression comprises irregularly positioned lobes, small regions that exhibit rangeomorph branching are present (arrowed; Fig. 3.10B–C). The lobes also seem to radiate. **B–C**: Close up images of areas indicated in A, showing, in black, the frondose branching visible within the ivesheadiomorph. Scale bar represents 0.1 m.

To test the possibility that some of the specimens may not have originally resembled *Charniodiscus* etc. in overall morphology prior to tectonic deformation, the technique of retrodeformation could be employed (see Wood et al., 2003). Although tectonic deformation has undoubtedly distorted fossils on many Avalonian bedding planes, and while such distortion can in theory be removed, there are good reasons for being cautious. Hitherto in publications from the Oxford group, (e.g. Brasier and Antcliffe, 2004, 2008, 2009; Antcliffe and Brasier, 2007b, 2008) the use of retrodeformation techniques (e.g. Wood et al., 2003) has been avoided. First, we question the logic of basing strain estimates upon measurement of ‘disc’ shaped fossils (including basal holdfasts, or *Aspidella*, or even problematic *Ivesheadia*, cf. Bamforth et al., 2008), and then of using these strain estimates for retrodeformation of the fossils themselves. Such a procedure is arguably a form of circular reasoning because it involves the assumption that a discoidal fossil was truly circular itself. This assumption can be challenged using the data from many undeformed bedding planes, where we find that varying degrees of ellipticity can be seen in discoidal fossils on the same bed (Fig. 3.11). Therefore either some discs clearly were not originally circular, and the question then becomes which disc should be used for our strain estimate; or the degree of tectonic shortening experienced by Avalonian bedding planes was not uniform (e.g. Gehling and

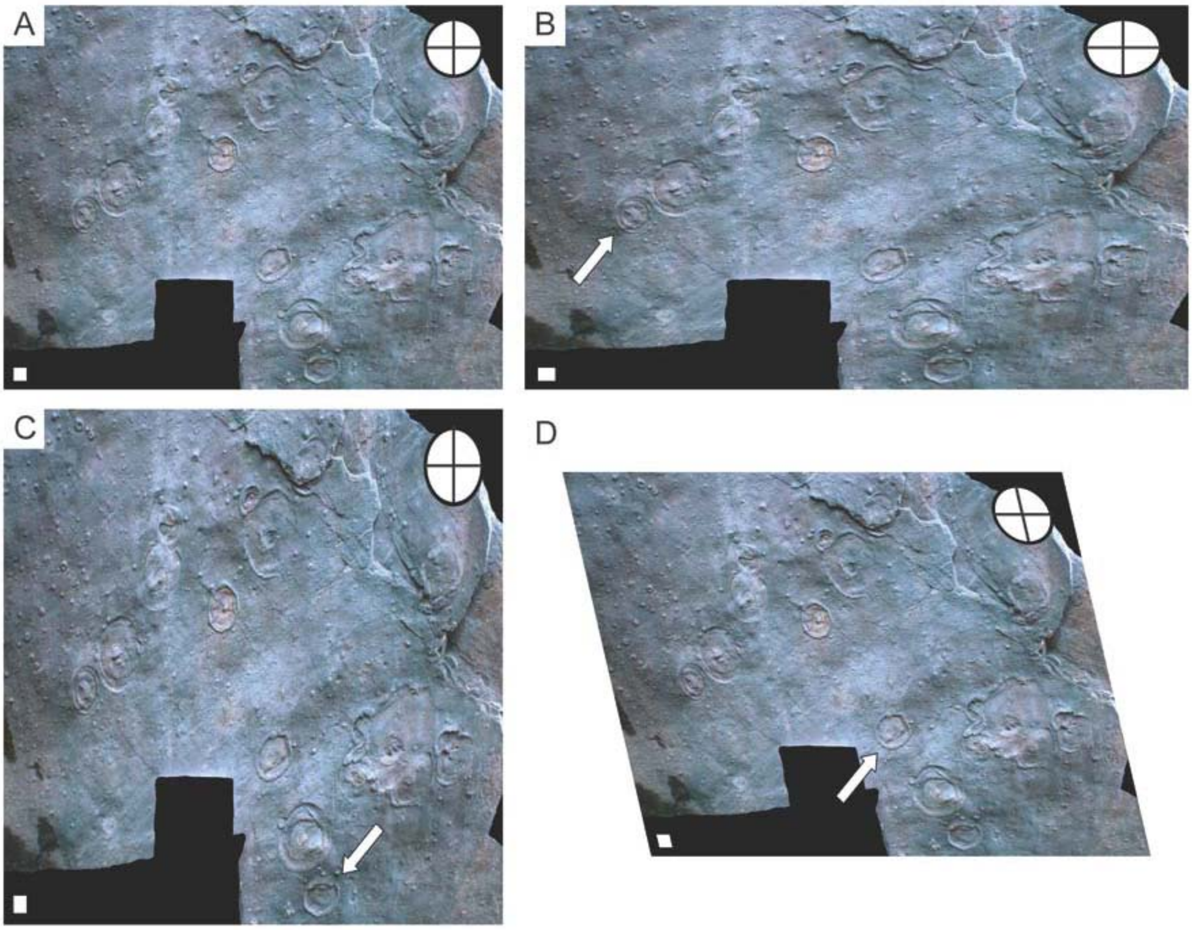

Fig. 3.11. Illustration of the problems encountered when using discoidal fossils to estimate strain rates on Ediacaran bedding planes. Fig. 3.11A is the original image. Figs. 11B–D are retrodeformed images each correcting a different disc (arrowed) on that surface to a perfect circle. Note the different effects of applying these corrections on the circle at top right, and on the dimensions of the scale box (bottom left). **A**: Original photograph of a bedding plane covered in *Aspidella terranovica* (considered to be a frond holdfast by Gehling et al., 2000), Fermeuse Formation, Newfoundland. Scale box is 10 x 10 mm. The white circle at top right is undeformed. **B**: Image has been elongated along the x-axis by a factor of 1.329. **C**: Image has been elongated along the y-axis by a factor of 1.343. **D**: Image has been subjected to an anticlockwise horizontal shear of 13 °. Each of the corrections in Figs. 3.11B–D reverts an *Aspidella* specimen in Fig. 3.11A to a circular disc, but no single correction factor can correct all of the discs on the surface. Note the effects of the varying degrees of alteration on the scale box.

Narbonne, 2007). This means that a single value for retrodeformation cannot be applied (e.g. in the manner of Bamforth et al., 2008) without error. In our view, key specimens should be portrayed without hidden bias by illustrating them exactly as they appear on the bedding plane.

Furthermore, retrodeformation of holotypes and paratypes leads to taxonomic problems. It is essential that all such specimens be imaged faithfully, as they actually appear in the rocks. We would argue that where independent estimates of strain are lacking, retrodeformed images of holotypes can be regarded as subjectively defined. The issue of scale bars utilised in retrodeformed images (there is more than one way to produce an observed strain - e.g. simple elongation/compression versus simple shear, both of which will have different effects on the dimensions of specimens), also means that such holotypes cannot be accurately compared to other specimens (Fig. 3.11). We therefore find that the description of the following holotypes, which have been figured in the literature using only retrodeformed images, is open to question: *Pectinifrons abyssalis* Bamforth et al., 2008; *Primocandelabrum hiemaloranum* Hofmann et al., 2008; *Parviscopa bonavistensis* Hofmann et al., 2008; *Hapsidophyllas flexibilis* Bamforth and Narbonne, 2009; *Frondophyllas grandis* Bamforth and Narbonne, 2009.

In future, we consider that retrodeformation should either be avoided for holotype descriptions, or non-retrodeformed images also included; that strain estimates for fossil deformation should be independent of the fossil structures themselves; that the dataset on which they are based be presented; and that all retrodeformed images clearly display the degree of strain that has been removed (as in Seilacher, 1999, fig. 3).

An important point deserves emphasis here. Although the Ediacara biota can be well-preserved in high fidelity in the Avalon assemblages (e.g. Figs. 3.2–3.3), this is not always the case. Instead, we find a mixture of both well-preserved and effaced variants preserved together on a single bedding surface (Figs. 5.1–5.3). This being so, there is clearly a need to distinguish those features and morphology that were present at the time of burial from those that have arisen from taphonomic, microbial, diagenetic, structural and even erosional processes. The possible nature of these processes is now examined.

TAPHONOMIC MODELS

The original interpretation of *Ivesheadia* and related forms as part of a valid and distinct biological grouping requires that specimens around the world should exhibit a similar morphology and structure, with a series of characteristic and defining features. Likewise, on individual bedding planes, there should be no forms that are intermediate or gradational between taxa. The evidence described herein indicates, however, that these criteria are not met. A wide variety of ivesheadiomorph shapes, sizes, and internal structures are observed both within and between bedding planes (Pls. 1–2; Figs. 3.5–3.6, 3.9–3.10). Furthermore, intermediate and gradational morphologies occur on single bedding planes, which can be explained as part of a continuous spectrum of preservation between rangeomorph and ivesheadiomorph end members (Figs. 3.2–3.6, 3.9–3.10). Below, the taphonomic processes that could explain these observations are explored.

Recent erosion and weathering of many of the bedding surfaces, by wind, wave, and even human activity on the most popular sites, has had a noticeable effect on the relief and resolution of the fossils. Most such erosion abrades the surfaces of the fossils and lowers the surface topography. Importantly, it usually affects all fossils with comparable relief on a given surface in a similar way, and is clearly insufficient to explain the observed scenario, where effaced variants can be seen randomly distributed on bedding planes alongside well-preserved specimens. The observation that effacement is highly localised raises the possibility that pre-burial taphonomic processes may be a primary control on ivesheadiomorph morphology.

Taphonomic processes in the Avalon assemblages have been widely addressed (Gehling, 1999; Grazhdankin, 2004; Narbonne, 2005; Callow and Brasier, 2009a; McIlroy et al., 2009), although discussion has mainly focused upon comparisons between Avalonian taphonomy and that seen in other Ediacaran successions. These studies have given rise to the concept of 'death mask' (Flinders-type) preservation, typically seen in South Australia and the White Sea region of Russia (e.g. Gehling, 1999; Dzik, 2003; Narbonne, 2005; Brasier and Antcliffe, 2008), and Conception-type preservation, as seen at Mistaken Point in Newfoundland (Narbonne, 2005; McIlroy et al., 2009). Both styles are capable of producing high quality preservation of soft-bodied organisms. The style of preservation seen in the younger Nama assemblage (Waggoner, 2003), where fossils are preserved in three-dimensions within sandstone beds (Narbonne, 2005), is not considered here. It is noted that the Spaniard's Bay locality in Newfoundland (BC1, Appendix D2) is reported to preserve frondose taxa in three-dimensions within turbidites, arguably exhibiting evidence of post-burial decomposition (Narbonne, 2004). However, that bed may document an extreme variation of Conception-style preservation, rather than true 3-D taphonomy (personal observation).

The 'Death Mask' and Conception taphonomic models

The 'death mask' model of Ediacaran fossil preservation requires that the late Neoproterozoic seafloor was covered by microbial mats, which then colonised the upper or lower surfaces of organisms after their burial beneath event beds (see Gehling, 1999; Mapstone and McIlroy, 2006; Callow and Brasier, 2009a). These microbial mats are inferred to have caused rapid lithification of the soles of overlying beds, preserving with high-fidelity the upper surface (usually) or lower surface (more rarely) morphology of the underlying organisms prior to soft tissue degradation (Gehling, 1999; McIlroy et al., 2009). This mechanism can therefore explain the preservation of Ediacaran organisms in positive or negative hyporelief in siliciclastic Ediacaran successions (Wade, 1968). It has been demonstrated subsequently that microbially-mediated pyritization of this 'death mask', and the overlying sediment, could have been responsible for retaining the 3-D surface geometry of the organism, thereby preserving a mould of the organism during early diagenesis (Mapstone and McIlroy, 2006). This mode of preservation is also termed Flinders-style preservation, after the Flinders Ranges of South Australia where it is particularly dominant (Narbonne, 2005). Early lithification of the casting medium allowed the space created by decomposition of the body tissues to be in-filled later by unlithified sediment moving upwards from immediately below the organism (Fig. 3.12; Gehling, 1999; Gehling et al., 2005).

In the Conception Group of Newfoundland, and the Charnian Supergroup of Leicestershire, U.K., the Ediacara biota is preserved by smothering beneath volcanic ash or volcaniclastic distal turbidite flows (the 'Conception-type' preservation of Narbonne, 2005). The tuffaceous casting medium itself may have been integral to the preservational processes in these assemblages, but this has yet to be demonstrated by studies of the diagenesis of fossil material (cf. Gehling and Narbonne, 2007). Until the precise preservational role, if any, of the tuffaceous material is demonstrated, it can therefore be argued that the processes involved in the 'death mask' model are equally applicable to the Avalonian localities (Gehling, 1999). This possibility is supported by the fact that many of the fossil-bearing beds in the Conception Group also show iron staining and the local presence of pyrite (Gehling et al., 2005). Seen in this light, the primary difference between Flinders and Conception-type preservation (*sensu* Narbonne, 2005) is lithological.

'Lower Surface' preservation

Of special interest to studies of Avalonian Ediacaran organisms is the phenomenon of negative epirelief moulds, here termed 'lower surface' preservation (Fig. 3.12). Moulds of *Charnia* and *Fractofusus* are typically preserved as impressions of body tissues that formed negative troughs separated by intervening positive ridges (Narbonne, 2005; Pl. 1.1A–B). Such preservation is believed to result from downward collapse of an unlithified volcanic tuff on to the underlying mudstone, following rapid decay of the organism after burial by the casting medium (Fig. 3.12; Narbonne, 2005; Gehling and Narbonne, 2007). This mode of preservation commonly exhibits very finely detailed (sub-mm) internal structure, and has been taken by some to suggest that organisms preserved in this way were reclining on the seafloor during life (Gehling and Narbonne, 2007), and perhaps directly interacting with the substrate for support or nutrition. Both microbes, and the early lithification of the substrate beneath the organisms, may also be implicated in this process (Brasier, 2009; Callow and Brasier, 2009a, 2009b; McIlroy et al., 2009).

While 'death mask' and 'lower surface' preservational processes, both arguably components of Conception-type preservation (Narbonne, 2005), can explain many occurrences of Avalon-assemblage fossils, we do not believe that they adequately explain the taphonomic processes involved in the preservation of ivesheadiomorphs.

Effaced preservation in the Ediacara biota

The famed high-fidelity preservation of the Ediacara biota is not always present in the Charnian Supergroup and the Late Precambrian Conception–St John's Groups. Our field observations demonstrate that many fossils show little to no fine detail, preserving only the

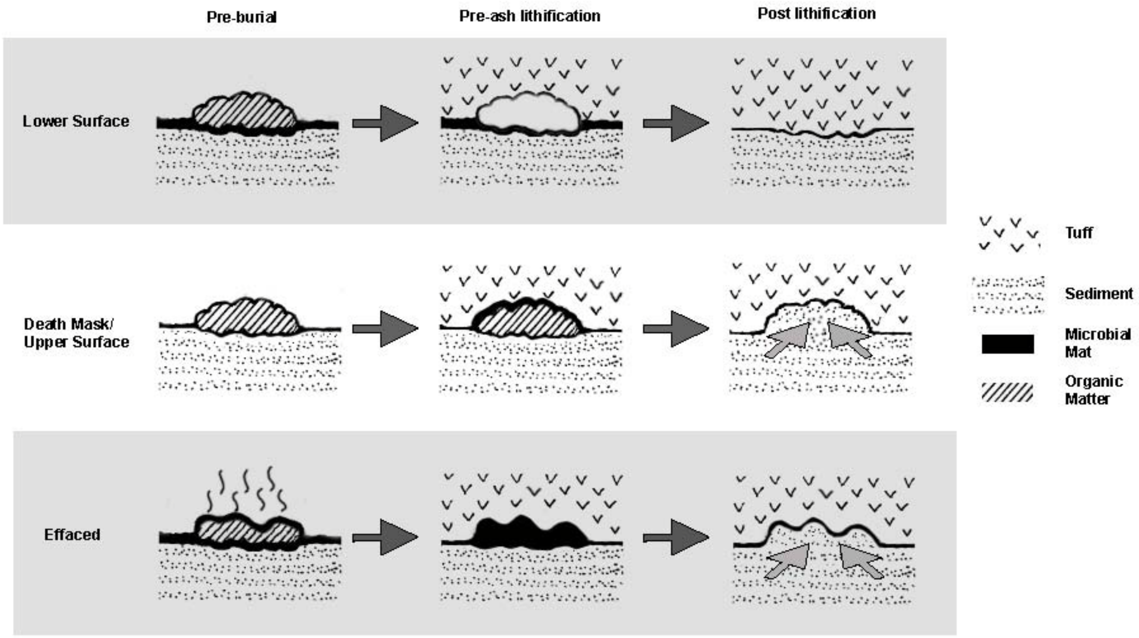

Fig. 3.12. Cartoon displaying the preservational styles observed in Ediacaran organisms from Avalonia. **Lower surface preservation** *sensu* Narbonne (2005): The basal surface of the organism is preserved in high fidelity by downward collapse of ash into the space created by decay of the organism before lithification of the tuff or turbidite. **Death Mask/Upper Surface preservation** *sensu* Gehling (1999): The upper surface of the organism is colonised by a microbial mat and cast by the overlying tuff or turbidite at or following the time of burial. The presence of the mat leads to retention of the cast upper surface upon decay of organic material. After decay, sediment loading then forces underlying unlithified sediment upwards into the void to form a positive epirelief cast. **Effaced Preservation herein**: The deceased organism is decaying on the seafloor, with the upper surface becoming progressively more irregular and smoothed (effaced) owing to microbial colonization and degradation of the organic matter. Following tuff or turbidite deposition, the upper surface of the effaced organism is preserved.

rough outline of an organism, often in high surface relief (e.g. Fig. 3.6). These morphotaxa, with poor preservation of surface detail, could constitute different taphonomic expressions of both well known taxa and currently undocumented organisms, the detailed morphology of which remains to be resolved.

The effaced preservation we propose includes fossils where only the gross morphology of the original organism remains, as is typical of the highly enigmatic Ediacaran fossils *Ivesheadia, Shepshedia* and *Blackbrookia* (Boynton and Ford, 1995, 1996), and 'pizza discs', lobate discs and bubble mats (Narbonne et al., 2001). These structures differ from other Ediacaran taxa in having irregular, high relief morphologies that lack a consistent pattern of internal detail. We consider that effaced preservation is caused by the decay of deceased organisms on the seafloor prior to burial, with the resulting corpses then being preserved by standard 'death mask'/Conception-type preservation. Smoothing of the surface is here suggested to result from colonization of the dead carcass by microbial mats (see for example Costerton and Stoodley, 2003). In the absence of both bioturbation (e.g. Sepkoski, 1979; McIlroy and Logan, 1999; Seilacher, 1999; Bottjer et al., 2000; Droser et al., 2002; Jensen et al., 2005; Liu et al., 2010a) and predation/scavenging (Sokolov, 1976; Seilacher, 1999; Bottjer et al., 2000), microbes including fungi and protozoans would probably have been the

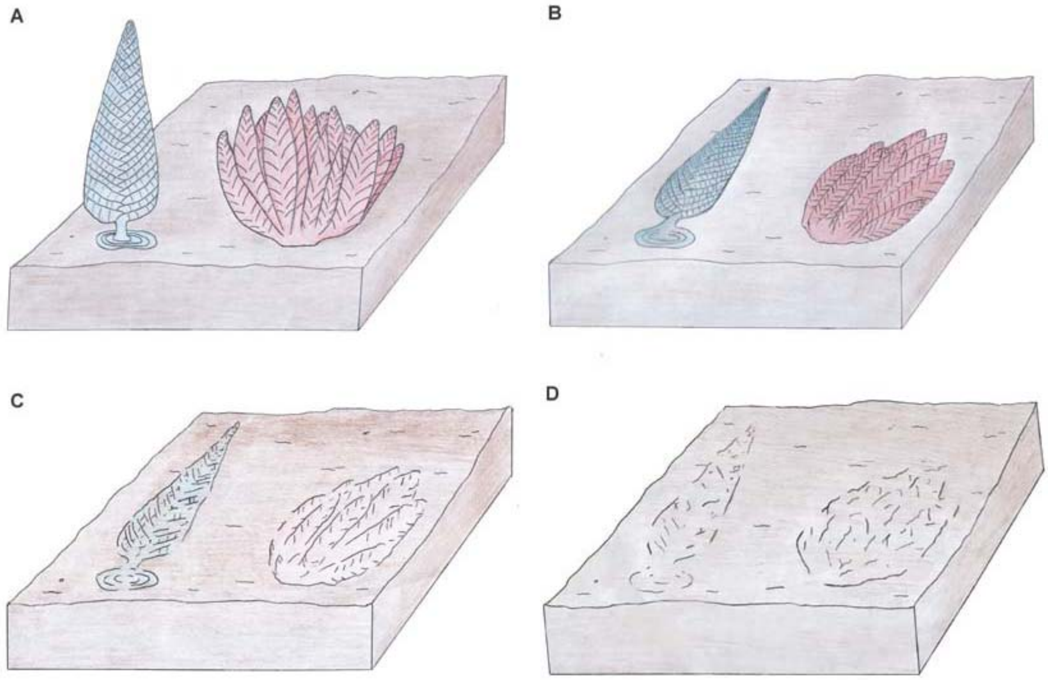

Fig. 3.13. Explanation for the preservational spectrum observed in specimens from Avalonia. **A**: Organisms in life position. **B**: Recently deceased organisms now parallel to, and lying on, the bedding plane. **C**: Gradual loss of morphological detail as the exposed organism decays. **D**: Effaced specimens that have lost all but their gross morphology following a long period of microbial decay. Burial below an event bed can occur at any stage of this decay process, such that variants B, C and D can all be preserved, often together, on a single Ediacaran bedding plane.

dominant agents of removal and breakdown of organic matter on the Ediacaran seafloor (see also Glaessner, 1984).

Microbially induced sedimentary structures (Noffke et al., 2001) are known to be a common feature of Proterozoic marine bedding surfaces (e.g. Seilacher and Pflüger, 1994; Schieber et al., 2007). Indeed, 'wrinkle mats' on Ediacaran bedding planes worldwide were probably an important part of both shallow and deep water Ediacaran ecosystems (Gehling, 1999; Noffke et al., 2002; Callow and Brasier, 2009a; Gehling and Droser, 2009). Such micro-organisms are likely to have had various effects upon decaying Ediacaran organisms (see McIlroy et al., 2009). Sediment trapping and binding (Black, 1933; Noffke, 2003) could take place across the surface topography of the degrading organism. This binding effect could both help to reduce breakdown of the carcass by current erosion, and help maintain its position on the seafloor (Krumbein et al., 1994; Seilacher and Pflüger, 1994; Gehling, 1999). Osmotrophs and other saprophytes among the microbial community (Brasier et al., 2010) could then have decomposed the organic material into more labile organic matter. Prokaryotic bacteria (including methanogenic, sulphate reducing, and nitrogen-fixing saprophytes) are abundant at all levels of the modern marine water column (Gast and Gocke, 1988), and the highly abundant wrinkle mats suggest that such prokaryotes were also widespread during the Ediacaran Period. Eukaryotic fungi are also prominent in modern deep marine ecosystems (Sparrow Jr., 1936; Vishniac, 1956; Gast and Gocke, 1988; Hyde et al., 1998; Stolz, 2003), and while the Precambrian fossil record of fungi is not convincing, possible Ediacaran fungal fossils have been identified (Butterfield, 2005; Callow and Brasier, 2009b). It has even been suggested that some Ediacaran macrofossils may have been fungal in organization (Retallack, 1994; Peterson et al., 2003). Microbial communities are therefore considered to have been firmly established within Avalonian Ediacaran ecosystems, and were available to remove organic matter from the seafloor.

Seen in this way, the gradational spectrum of preservation described above may be regarded as a function of time. Organisms that were buried alive or very soon after death were preserved by Conception-type preservation, as seen with well-preserved *Charnia* specimens. Organisms that were not rapidly buried and had been decomposing on the seafloor for a period of time before burial experienced loss of morphological detail owing to microbial colonization and growth, and the degradation of the carcass beneath (Figs. 3.12–3.13). It is likely that autolysis also contributed as a means of degradation. In the Avalonian assemblages, effaced preservation is therefore interpreted to represent an end member of Conception-type preservation, in which all the fine detail of the original organism (such as rangeomorph frondlets) has become subdued prior to burial, leaving only the gross outline of the original form to be preserved.

DISCUSSION

Observations of ivesheadiomorphs from the Charnian Supergroup and Conception Group show that few ivesheadiomorphs are ever identical, even on the same bedding plane. This variability in fossil morphology can be explained in the effaced preservation hypothesis by different combinations of microbes or original organisms, changing environmental conditions, and different lengths of time for pre-burial exposure at the sediment-water interface, all of which could potentially produce greatly different taphomorphs, even from the same object.

If we are correct in attributing the phenomenon of effacement in the Ediacara biota to taphonomic processes capable of transforming rangeomorphs and other frondose Avalonian biota into ivesheadiomorphs, this has important implications for understanding the nature of late Neoproterozoic fossil preservation. Hitherto, it has been argued that the presence of abundant soft-bodied fossils on the Ediacaran seafloor was an outcome of less effective decay processes acting at that time (Seilacher, 1989). We argue, however, that microbial decay on the seafloor was no less effective during the Ediacaran Period than in the Phanerozoic (Glaessner, 1984). Rather, it was the lack of competition or interference from metazoans that afforded a higher preservation potential for soft bodied organisms. For example, the absence of a through-gut, bioturbation and macro-scavenging would have led to conditions very different from those on the Phanerozoic seafloor (e.g. Brasier, 2009; Callow and Brasier, 2009a). Under such transitional conditions, with large body masses but no large consumers, corpses could remain unconsumed for long periods on the seafloor, where they would decay by means of bacterial, protozoan and fungal activity.

Effaced preservation should occur widely throughout the Ediacara biota, as the processes of its formation are arguably universal, acting upon all deceased organisms that were not rapidly smothered by event beds. Ivesheadiomorphs are found throughout both the Newfoundland and U.K. sections, and have a stratigraphic range encompassing almost the entire fossil-bearing Avalonian succession (Fig. 2.17; Hofmann et al., 2008). The question then arises as to why ivesheadiomorphs have not been described from other Ediacaran biotic assemblages. The Avalon assemblages underwent rapid episodic deposition of sediment in deep marine environments, beneath infrequently deposited ash beds. In contrast, both the Ediacara and Nama palaeoenvironments were considerably shallower than those of the Avalon (Grazhdankin, 2004). These environments are likely to have undergone higher mean rates of sedimentation, being frequently buried beneath storm sands. Ediacaran organisms in such environments would have less time to grow to maturity and then perish on the seafloor from natural causes. There is also evidence to suggest simple but widespread bioturbation in these younger assemblages (Jensen et al., 2006), which would disrupt the activities of microbes (McIlroy and Logan, 1999), and destroy microbial mat fabrics in normal marine siliciclastic facies. Such bioturbators may also have been actively involved in the removal and breakdown of organic matter. It is considered that the shallower, presumably warmer, waters in which the White Sea and Nama assemblages were deposited would also accelerate the process of microbial decay, restricting the taphonomic window in which effaced forms could be produced. However, Gehling has mentioned '*sculptured surfaces, with irregular ridges and pustules'*, in the S. Australian successions (Gehling, 1999, pg. 52), and has even hinted at the presence of irregular impressions that may represent organic matter that had decomposed prior to burial (Gehling et al., 2005). Indeed, variability in the thickness of *Dickinsonia* specimens from Australia has been taken as evidence to suggest decay prior to burial (Retallack, 2007), though this variation may be caused by mat smothering or compaction rather than decay (Gehling et al., 2005; Gehling, 2007; McIlroy et al., 2009). These observations strongly suggest the operation and preservation of pre-burial decay processes in Australia, though more work is required to document this. Potential *Ivesheadia* specimens from Australia (Gehling et al., 2005) remain in need of verification (Gehling pers. comm. 2009). It is therefore possible that effaced preservation extends to the White Sea biotic assemblage. Further, features interpreted as internal anatomical structures in dickinsoniids from the White Sea (Dzik, 2003) could instead represent preservation of these organisms as effaced taphomorphs, with turgor pressure within the organism lost at death (Gehling et al., 2005; Brasier and Antcliffe, 2008). As yet there are no reports of ivesheadiomorphs from the youngest, Nama, assemblage, though this could simply reflect a sampling bias. Alternatively, the increase in bioturbation in the latest Ediacaran to Cambrian, and the ecological changes that resulted, may have led to the disappearance of not only ivesheadiomorphs, but all Ediacaran organisms from the fossil record (Gehling, 1999; McIlroy and Logan, 1999; Brasier, 2009).

Our hypothesis is not consistent with the traditional view that every fossil on the bedding planes was alive at the time of burial. It readily explains several key observations, including the preservational spectrum seen on many bedding planes, and the fact that poorly preserved ivesheadiomorphs are commonly seen lying adjacent to well-preserved frondose organisms. The presence of *Fractofusus* specimens, thought to be flat-recliners on the seafloor, overlying some of the more effaced variants of *Charniodiscus* on the E Surface (Figs. 3.5A, 3.6; see Gehling and Narbonne, 2007), supports the hypothesis that some *Charniodiscus*' were already dead and lying flat on the seafloor in various stages of decay prior to burial by the tuffs. Acceptance of the effaced preservation hypothesis leads to several important implications for Ediacaran palaeontology and palaeoecology, which will be discussed in more detail in Chapter 5.

The importance of distinguishing between taphonomic and palaeobiological components of the Ediacaran fossil record has been discussed previously (Gehling et al., 2005). Palaeoecological studies on the Ediacara biota have commonly incorporated ivesheadiomorphs as component organisms in census populations across bedding planes (Clapham and Narbonne, 2002; Clapham et al., 2003). We argue, however, that ivesheadiomorphs were not alive at the time of burial. Therefore, conclusions drawn from such data, along with studies of species diversity, disparity, and palaeoecology (e.g. Droser et al., 2006) may need considerable revision. It should also be noted that ivesheadiomorphs are unsuitable for use in retrodeformation (e.g. Bamforth et al., 2008), since they likely represent a variety of different organisms, some of which may not have originally been circular. The 'poor' preservation of Ediacaran fossils is capable of telling us a great deal about the taphonomic and ecological processes acting during the Ediacaran Period. However, effaced variants alone should never be used to infer the presence of certain organisms in an ecosystem.

THE TAXONOMIC IMPLICATIONS OF EFFACED PRESERVATION

Although effaced fossils can be distinctive and common in the Ediacaran fossil record, it is considered unwise to define taxa based upon poorly preserved material. Such morphotypes may nevertheless remain useful in describing morphological diversity. Our study of 'pizza discs', *Blackbrookia*, *Ivesheadia* and *Shepshedia*, among others, has demonstrated that there is considerable potential for these poorly defined taphomorphs to represent more than one biological taxon. Given the potential for a dual taxonomy dependant on taphonomic state, it would seem logical for effaced preservational variants without significant morphological detail to be considered tapho-taxa until these problems can be resolved. The names for these tapho-taxa can then be used in parallel with formally named fossil taxa of similar gross form, but with an appropriate range of taxobases. This does not require substantial change in the common parlance of the subject, but it does resolve the difficulty of taxonomic duality.

Systematic Palaeontology

The taxa considered herein are reviewed and refigured to incorporate the hypotheses and evidence presented above. The existing, very short taxonomic descriptions for *Blackbrookia*, *Ivesheadia* and *Shepshedia* are of little practical use in distinguishing their morphologies. We consider that the three genera show little discernable difference in morphology, and that variation in overall shape is the result of microbial degradation; they are united by common taphonomic processes, rather than by original biological/morphological features. *Blackbrookia*, *Shepshedia*, and *Ivesheadia*, along with the various morphs of the latter, are therefore considered as tapho-taxa with no validity under the ICZN. *Pseudovendia charnwoodensis* Boynton and Ford 1979, which strongly resembles an effaced *Charniodiscus* frond (Pl. 3.2, fig. 4), is likewise considered a tapho-taxon. The term ivesheadiomorphs is suggested as an umbrella term for these Ediacaran impressions to communicate the distinctive effaced morphology of all of these former taxa, while simultaneously acknowledging that they are not distinct taxonomic entities. In this way, the taphonomic processes fundamental to the formation of these structures are officially recognised. Usage of ivesheadiomorphs also recognises the taxonomic priority of *Ivesheadia* from the Charnian Supergroup of Leicestershire, U.K.

IVESHEADIOMORPHA

1978 *Medusae* (?) BOYNTON, p. 293, pl. 22, figs 2, 3.

1979 *Pseudovendia charnwoodensis* BOYNTON & FORD, pl. 20.

1995 *Ivesia lobata* BOYNTON & FORD, p. 176, figs 12, 13.

1995 *Shepshedia palmata* BOYNTON & FORD, p. 177, fig. 16.

1995 *Blackbrookia oaksi* BOYNTON & FORD, p. 178, fig. 17.

1996 *Ivesheadia lobata* BOYNTON & FORD, p. 3.

1999 *Ivesheadia lobata* FORD, p. 232, fig. 7.

1999 *Pseudovendia charnwoodensis* FORD, p. 233, fig. 10.

1999 *Shepshedia* aff. *palmata* BOYNTON, p. 198, fig. 1.

2001 *Ivesia* morphs NARBONNE, DALRYMPLE & GEHLING, pp. 30–31, pl. 1,I, J.

2003 ‘Pizza disc’ PETERSON, WAGGONER & HAGADORN, p. 129, fig. 1C.

2004 *Ivesia* CLAPHAM, NARBONNE, GEHLING, GREENTREE & ANDERSON, p. 1033, fig. 2.4.

2005 Pizza disc NARBONNE, DALRYMPLE, LAFLAMME, GEHLING & BOYCE, p. 28, pl. 1G.

2007 *Ivesheadia* CANFIELD, POULTON & NARBONNE, p. 93, fig. 2A.

2007 *Ivesheadia* GEHLING & NARBONNE, p. 373, fig. 5.

2007 *Blackbrookia oaksi* FEDONKIN, GEHLING, GREY, NARBONNE & VICKERS-RICH, figured on p. 264.

2007 *Ivesheadia lobata* FEDONKIN, GEHLING, GREY, NARBONNE & VICKERS-RICH, figured on p. 274.

2007 *Pseudovendia charnwoodensis* FEDONKIN, GEHLING, GREY, NARBONNE & VICKERS-RICH, figured on p. 284.

2007 *Shepshedia palmata* FEDONKIN, GEHLING, GREY, NARBONNE & VICKERS-RICH, figured on p. 286.

2007 *Ivesheadia* NARBONNE in FEDONKIN, GEHLING, GREY, NARBONNE & VICKERS-RICH, p. 56, figs 72, 73.

2007 'Pizza disc' form of *Ivesheadia* NARBONNE in FEDONKIN, GEHLING, GREY, NARBONNE & VICKERS-RICH, p. 59, fig. 80.9.

2007 Lobate morph of *Ivesheadia* NARBONNE in FEDONKIN, GEHLING, GREY, NARBONNE & VICKERS-RICH, p. 59, fig. 80.10.

2007 Pizza disc NARBONNE in FEDONKIN, GEHLING, GREY, NARBONNE & VICKERS-RICH, p. 63, fig. 89.

2007 Pizza-disc with stem NARBONNE in FEDONKIN, GEHLING, GREY, NARBONNE & VICKERS-RICH, p. 67, fig. 96.

2007 *Pseudovendia charnwoodensis* VICKERS-RICH & FEDONKIN in FEDONKIN, GEHLING, GREY, NARBONNE & VICKERS-RICH, p. 187, fig. 355.

2008 *Ivesheadia lobata* HOFMANN, O'BRIEN & KING, p. 31, fig. 24.1–24.6.

2008 *Blackbrookia* sp. HOFMANN, O'BRIEN & KING, p. 32, fig. 25.1–25.5.

2009 *Ivesheadia lobata* BRASIER & ANTCLIFFE, p. 373, fig. 10.

2009 *Ivesheadia* aff. *lobata* BRASIER & ANTCLIFFE, p. 374, fig. 11.

2009 *Ivesheadia* BRASIER, p. 154, fig. 15.

2009 'Bubble mat' CALLOW & BRASIER 2009a, p. 211, fig. 2B.

2010 *Ivesheadia* BRASIER, CALLOW, MENON & LIU, p. 143, fig. 6b.

Description: In the absence of a consistent morphology for these impressions, we provide a broad definition to incorporate the whole range of ivesheadiomorph morphologies. Ivesheadiomorph fossils share an internal morphology consisting of sub-rounded to sub-angular raised lobes and depressions, both of variable shape. These are arranged irregularly, such that the overall impression lacks symmetry, with lobes reaching up to 120 mm in length. The external margins of the fossils are often strongly defined, occasionally with a raised rim or a trough. Specimens can vary from 30 mm to 0.8 m in diameter, but their gross outline is variable; the impressions can be circular, ovate, bi-lobed, broadly triangular, rectangular or elongate. In rare specimens, branching frondlets or remnants of a disc or stem are visible within the irregular internal structure, providing hints as to the original affinity of the fossil. It cannot be assumed that these impressions were all originally circular, because ivesheadiomorph morphology is considered to result from a combination of the morphology of the original organism, microbial processes, and diagenesis.

Discussion: Ivesheadia, Shepshedia and *Blackbrookia* have been formally described only from Avalonian biotic assemblages of the Ediacaran Period, although similar discs have been reported from carbonate-hosted beds from the Khatyspyt region of Russia (Grazhdankin et al., 2008). Consideration of these impressions as taphomorphic expressions of fossils that already possess valid taxonomic descriptions means that their classification here as tapho-taxa (similar to the concept of taphoseries in ichnology; MacNaughton and Pickerill, 1995), is valid. All three genera were named after forms from Leicestershire, U.K. (Pl. 3.2, figs. 1–3; Boynton and Ford, 1995, 1996), and represent some of the oldest Ediacaran fossils known, occurring in the Upper Drook Formation of the Avalon Peninsula in Newfoundland (Gehling et al., 2000), dated at 578.8 ± 0.5 Ma (Van Kranendonk et al., 2008), and in the Blackbrook Group of England (Boynton and Ford, 1995, 1996; McCall, 2006), potentially older than 600 Ma (Boynton and Ford, 1995; McIlroy and Horak, 1996; McIlroy et al., 1998; Carney, 2000). Such ages reveal a potential problem. Although the oldest U.K. beds contain ivesheadiomorphs, there is currently no evidence for contemporary high fidelity Ediacaran organisms that could have decayed to form these taphomorphs. This remains a valid argument against the effaced preservation hypothesis, but it is expected that such specimens will be unearthed in time. *Ivesheadia* and *Blackbrookia* are also described from the Bonavista Peninsula (O'Brien and King, 2006) in Newfoundland.

Originally named *Ivesia lobata*, the genus *Ivesheadia* was initially interpreted as a medusoid impression (Boynton and Ford, 1995); a scyphozoan or chondrophore affinity was proposed by Ford (1999). However, with rare exceptions (e.g. Waggoner, 2003), the medusoid interpretation has given way to the consensus that *Ivesheadia* is an enigmatic taxon, with no objective evidence to suggest a jellyfish affinity (Fedonkin et al., 2007a; Narbonne, 2007). Narbonne et al. (2001) suggested that it may represent a holdfast, or a 'tethered floating body' due to the presence in one specimen of a 'string' attached to the disc. This same specimen also gave rise to the alternative idea that the string may be the respiratory organ of an organism living beneath the microbial mats (Peterson et al., 2003). We have noted the existence of such threads in abundance without associated *Ivesheadia* on the Bonavista Peninsula, reaching up to 5 m in length, and we suspect these new specimens may have a bearing on the affinity of the 'tethered' specimen. Clapham et al. described *Ivesheadia* only as an “*enigmatic lobate form*” (Clapham et al., 2003, pg. 533), while more recently, it was regarded as being of uncertain phylum, perhaps representing “*collapsed compartmentalised bodies*” (Hofmann et al., 2008, pg. 33). A review of Ediacaran biota proposed that there were in fact three morphs of *Ivesheadia* – namely a 'lobate disc', a 'bubble disc' form, and the 'pizza disc' form – based on the general appearance of the impressions (Pl. 3.1, figs. 1–4; Narbonne et al., 2001; Fedonkin et al., 2007a). The view that *Ivesheadia* is preserved beneath microbial mats continues to endure within some working groups (Gehling and Narbonne, 2007), and is consistent with our suggestion that *Ivesheadia* represents decayed forms that have been covered by mats post-mortem. Ivesheadiomorphs are commonly found in the Conception Group of Newfoundland with other Avalonian taxa (such as *Fractofusus* sp. or *Charniodiscus* sp.) superimposed on top of them (Figs. 3.5A, 3.6; Gehling and Narbonne, 2007), providing further evidence that they represent organisms lying flat on the seafloor (see also McIlroy et al., 2009). One of the most recent papers on the subject described a form *Ivesheadia* aff. *lobata*, which displays *Fractofusus*-like rangeomorph units radiating from a central point, thus interpreted as the remains of a colonial rangeomorph organism, with "*multiaxial, multipolar and indeterminate*" growth (Brasier and Antcliffe, 2009, pg. 371). The personal opinion of this author is that that particular specimen instead represents a coincidental occurrence of *Fractofusus* specimens overlying *Ivesheadia*.

Shepshedia palmata is known only from the type specimens from one bedding plane at Ives Head, Leicestershire. A monospecific genus, it was originally discussed as a dubiofossil (Boynton, 1978), and later as 'problematica' (Ford, 1999). A possible hint of a stem (Boynton and Ford, 1995; Ford, 1999), suggests an interpretation as a frond holdfast, but internal detail is lacking. The original description suggested a classification within the Phylum Cnidaria (Boynton and Ford, 1995). A second specimen exhibiting a stem and 'palmate fingers', found associated with discs (Boynton, 1999), is also considered herein to resemble a poorly preserved frond. The presence of a stem would be consistent with *Shepshedia* being a taphomorph of a decayed frond. As the two known specimens of *Shepshedia* are not significantly distinct from other ivesheadiomorphs, we feel that the genus should be synonymised within the ivesheadiomorph suite.

Blackbrookia has been described from both Leicestershire (as *Blackbrookia oaksi*; Boynton and Ford, 1995), and the Bonavista Peninsula of Newfoundland (O'Brien and King, 2006). Originally reported as a pseudo-fossil (Boynton, 1978), *Blackbrookia* has since been described as a possible medusoid (Boynton and Ford, 1995), although it was later expressed by Ford (1999, pg. 231) to be simply a "*group of three discs*". The most thorough review of the taxon, based on the Bonavista specimens of Newfoundland, suggested that *Blackbrookia* represents localised microbial mat growth (Hofmann et al., 2008). Our interpretation elaborates on this by explaining the mat growth as occurring on and around the rotting carcasses of Ediacaran macro-organisms, both on and within the sediment. We propose that the holotype *Blackbrookia oaksi,* with its array of bars perpendicular to its length, likely represents the decayed remnants of a large (mature) rangeomorph frond, and we include *Blackbrookia s.s.* within the ivesheadiomorphs. Figured specimens assigned to *Blackbrookia*

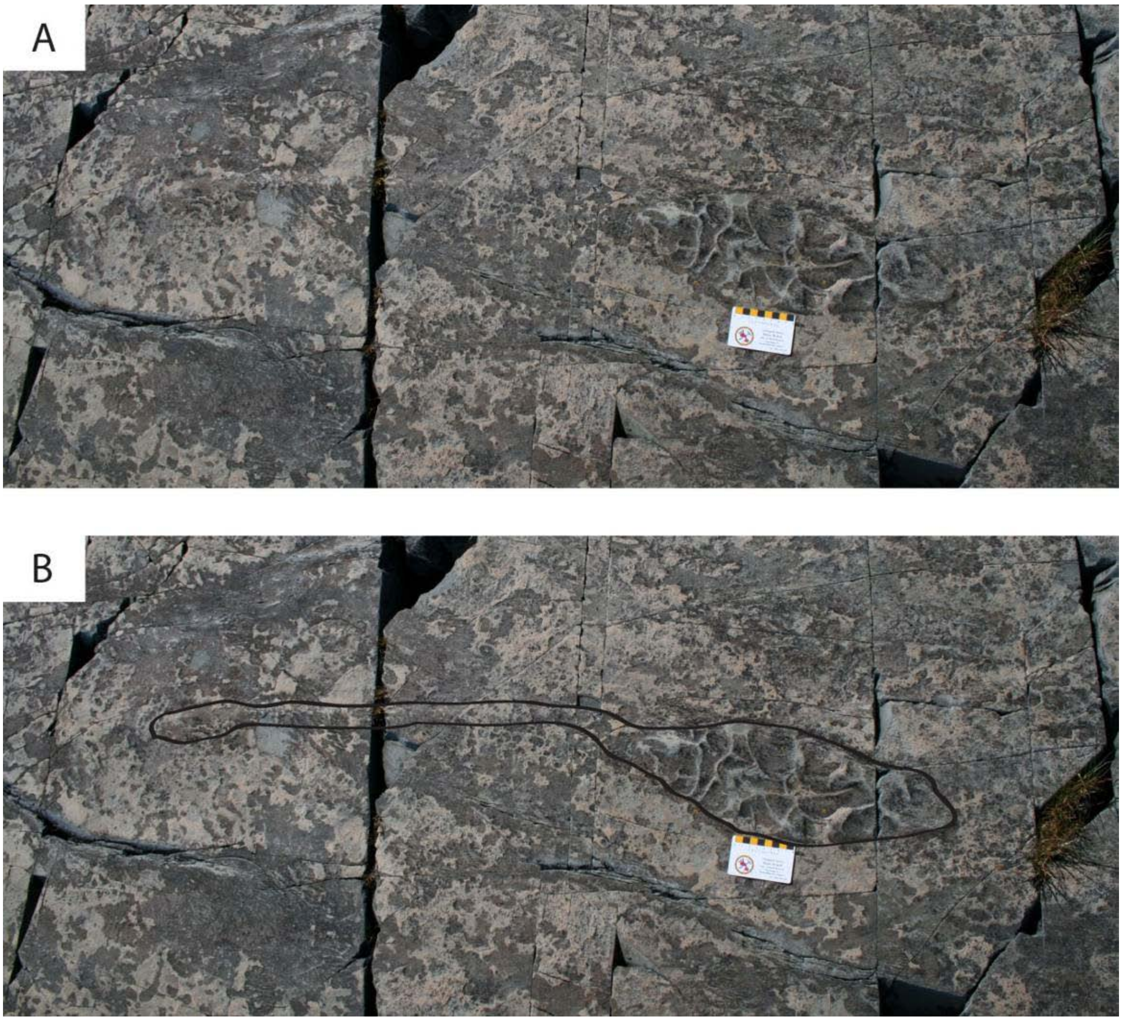

Fig. 3.14. *Blackbrookia* specimen from locality 14 of Hofmann et al., 2008 (locality LC 5, Appendix D2). **A**: Original image. **B**: Specimen with the possible frondose structure outlined digitally. Note that the oval *Blackbrookia* seems to continue from its apex on the left, into a possible remnant of a stem, which crosses the crack and appears to bulge out into a larger 'disc'-like appendage. This suggests that the ovate *Blackbrookia* may actually preserve the effaced remains of a large rangeomorph frond. Divisions on the scale bar are at 10 mm increments. Photograph courtesy of Leon Normore, Geological Survey of Newfoundland and Labrador.

that include pimples and 'reticulate structure' (see Hofmann et al., 2008, fig. 25.4-5) do not readily conform to the type material. However, recent evidence suggests that some of these specimens may extend past the high-relief oval shape, possessing a stem and even a possible disc (Fig. 3.14). This implies that despite their different morphology, the Bonavista *Blackbrookia* specimens may also represent taphomorphs of Ediacaran rangeomorphs. Work is required to determine whether such a stem is present in all specimens on the surface, but this observation is consistent with the effaced preservation hypothesis. It is worth noting that the White Sea taxon *Vaveliksia vana* Ivantsov et al. 2004 shares the bulbous gross morphology of *Blackbrookia* specimens from the Bonavista Peninsula of Newfoundland, and a possible relationship between these specimens warrants further attention.

Pseudovendia charnwoodensis Boynton and Ford, 1979 was originally classified under the Family Vendomiidae (Keller and Fedonkin, 1976) within the Phylum Arthropoda. Although the original authors briefly discussed the possibility of a frondose affinity, they opted to classify the impression as a primitive arthropod based on similarities between it and the fossil *Vendia sokolovi* Keller 1969 from the White Sea of Russia. It has since been suggested to be a possible fragment of a frond (Boynton and Ford, 1995), an interpretation supported by our research, while others have suggested it may be a dickinsoniomorph (Fedonkin et al., 2007a). At present only the holotype is known from the Avalon Assemblage, but based on the findings of this study, and comparison with other material from the Bradgate Formation from which *Pseudovendia* likely originates, it is suggested that *Pseudovendia* actually represents a partially decayed frond, aff. *Charniodiscus*, with the 'lobes' of the original description actually being primary branches (Pl. 3.2, fig. 4).

The Ediacaran taxa *Blackbrookia oaksi*, *Shepshedia palmata*, *Pseudovendia charnwoodensis* and *Ivesheadia lobata*, along with various morphs of the latter, are therefore synonymised as ivesheadiomorphs and designated as tapho-taxa. This move lowers the standing taxonomic diversity of Avalonian bedding planes, and has significant implications for prior interpretations of Ediacaran palaeoecology.

CONCLUSION

Ediacaran organisms within the Avalon assemblages show a gradational spectrum of preservation on individual bedding planes. This gradation is attributed to taphonomic processes related to the rate of decay of deceased Ediacaran organisms on the seafloor, prior to the influx of the event beds that preserved the ecosystems. The suggestion that Ediacaran assemblages are not snapshots of living communities on the seafloor at the time of smothering, but complex assemblages incorporating both living and deceased organisms, resolves the status of many enigmatic fossils.

Forms such as *Ivesheadia*, *Blackbrookia*, *Shepshedia* and *Pseudovendia* are considered to represent taphomorphs, and they have been synonymised within the ivesheadiomorpha to reflect this. Their effaced preservation is thought to result from their having decayed on the seafloor prior to burial by event beds. Further, the Ediacaran Period, as opposed to the Phanerozoic, lacked the usual organism processing (i.e. bioturbation and scavenging) that would normally prevent routine fossilization of semi-decayed organisms. Study of the Avalonian Ediacara biota demonstrates that complex taphonomic processes were operating at this time. This emphasises the need to examine whole populations of fossils both in context, and in relation to each other (cf. Brasier and Antcliffe, 2004). From a broader perspective, it is possible that such processes would also have taken place at other Ediacaran localities around the world, with similar taxonomic consequences.

The introduction of the term 'effaced' preservation will aid in both the description and understanding of the taphonomic processes that operated on the Avalonian seafloor. Effaced preservation emphasises the importance of microbial decay on the Ediacaran seafloor, as microbes were likely the only contemporary organisms capable of breaking down detrital organic matter. Further study of microbial fossils, recently discovered in other late Ediacaran siliciclastic successions (e.g. Steiner and Reitner, 2001; Callow and Brasier, 2009b), should be undertaken to discover more about this important facet of Ediacaran palaeobiology. Indeed microbes, and the products of their degradation of macro-organisms, are likely to be major components of Ediacaran benthic ecosystems (Chapter 7).

Separating taphonomic processes from taxonomy is a crucial first step towards understanding the morphological diversity and disparity present in the late Ediacaran biotic communities. It is also essential in order to draw conclusions about the ecological associations and biological affinities of these organisms, which is a primary goal in understanding the biosphere in the lead up to the Cambrian Explosion.

ACKNOWLEDGEMENTS

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CHAPTER 4

EXPERIMENTAL EVIDENCE IN SUPPORT OF 'EFFACED PRESERVATION'

PREFACE

The Effaced Preservation hypothesis, outlined in Chapter 3, suggests that the irregular ivesheadiomorph fossils preserved on Ediacaran bedding planes in the Avalon region may be products of the microbial decay of macro-organisms on the seafloor. To determine whether microbial decay of organic tissue is a feasible explanation for the formation of ivesheadiomorph impressions, laboratory experiments designed to replicate conditions on the Ediacaran seafloor have been constructed. Visual observation and X-ray computerised tomography (C-T) scanning of these experimental microcosms reveal that the actions of autolysis and microbial decay effectively dampen the surface topography of a dead organism, over timescales of weeks to months. Variation in the temporal extent of microbial activity upon a dead organism, prior to burial, is found to affect sediment properties immediately surrounding the decomposed soft tissues, and may play an influential role in preservation. The preservation potential of these experimentally-produced effaced morphologies is also discussed. It is considered that the effects of microbial activity upon modern macro-organisms and their surrounding sediment are comparable to processes that may have affected the deep seafloor in the late Ediacaran Period.

A detailed discussion of the pot experiments, and extensive images, can be found in Appendix E.

INTRODUCTION

Experimental taphonomy is a proven technique both for tackling problematic fossils (see Briggs, 1995), and for assessing the quality of the fossil record (e.g. Sansom et al., 2010). Previous attempts to experimentally explore the taphonomy of Ediacaran organisms have focused upon the shallow-water assemblages of the Flinders Ranges, Australia (Norris, 1989; Gehling, 1991; McIlroy et al., 2009), and particularly upon cnidarians as possible analogues for 'medusoid' discs (Bruton, 1991). In contrast, the deep-water assemblages of the Avalon region have been largely overlooked; only one study, discussing the methods by which impressions of multifoliate rangeomorphs may be produced, has applied an experimental approach to taphonomic questions regarding this biota (McIlroy et al., 2009).

In Chapter 3, it was suggested that some of the oldest and most enigmatic Ediacaran macro-organisms, the ivesheadiomorphs of the Avalon assemblage, are taphomorphs of other members of the Ediacara biota (Liu et al., 2011). This hypothesis was proposed following the discovery of a spectrum of preservational fidelity on Avalonian bedding planes in Newfoundland and Leicestershire (Chapter 3). The co-occurrence of effaced forms (with exaggerated and irregular first-order morphology) alongside well-preserved forms (exhibiting fine internal details), on individual bedding planes, indicates that post-burial taphonomic processes are unlikely to be responsible for the observed morphological differences. The unusual morphologies of ivesheadiomorphs are instead deemed to result from the slow decomposition of macro-organisms on the seafloor prior to burial by event beds (Liu et al., 2011). The late Ediacaran Period, at the time the Avalonian strata were deposited, is considered to be ecologically non-uniformitarian, in that there is currently no evidence for the pervasive bioturbation, macro-predation, or scavenging processes that rapidly break-down and remove organic material in Phanerozoic ecosystems (e.g. McIlroy and Logan, 1999; Bottjer, 2002; Jensen et al., 2006; Liu et al., 2010; Brasier et al., 2011). It is therefore argued that, apart from autolysis, the only biological processes available in the Ediacaran Period to remove naturally deceased organic material would have been forms of microbially-mediated decomposition (Liu et al., 2011). Microbial decay of organic material on the seafloor can therefore be invoked as an explanation for the preservational spectrum seen in Avalonian macrofossils (Chapter 3). Such a suggestion finds support from several previous studies. For example, microfossils from the Doushantuo Formation in China, and taphonomic studies on extant embryos, both reveal preservational spectra that are postulated to be microbially induced (Raff et al., 2008). Gradation in taphonomic fidelity has also been observed in experiments examining the silicification of microbes (Toporski et al., 2002).

Herein are described *in vitro* laboratory experiments designed to investigate whether microbial decay of organic matter, by non-photosynthetic micro-organisms, can efface the morphology of a macro-organism. Attempts are made to determine whether such effacement can produce structures similar in appearance and form to the Ediacaran ivesheadiomorphs described by Liu et al. (2011), and to assess the preservation potential of these experimentally constructed impressions in the rock record.

EXPERIMENTAL METHODS

In formulating this research, efforts have been made to replicate conditions within Avalonian fossiliferous environments wherever possible. Avalonian ivesheadiomorph-bearing successions were deposited in deep-marine (~1 km depth) basin floor and slope environments, near to a volcanic arc (e.g. Wood et al., 2003). The majority of ivesheadiomorphs occur within turbiditic mudstone or siltstone successions, commonly preserved directly beneath either layers of volcanic tuff, or remobilised volcaniclastic sediment (e.g. Narbonne, 2005).

To recreate the mineralogy of the Mistaken Point Formation, unfossiliferous metapelite from the Mistaken Point Formation, collected from the Bonavista Peninsula, Newfoundland, was crushed and ground to mud/fine-silt grade. This grain-size is consistent with that of sediments of the Conception Group, and provides the substrate upon which the decay experiments were conducted. Plastic pots were filled to a depth of 30 mm with this substrate, and allowed to equilibrate with modern seawater in specially prepared tanks (Fig. 4.1; Appendix E). The tanks were covered on all sides by 15 mm-thick foam boards to block out light (Fig. E1.15), and visible macro-organisms were excluded from the system (in order to prevent bioturbation or scavenging). The tanks were kept at a constant temperature of 12˚C, which is higher than is likely to have been found at depth in the Ediacaran oceans, but was dictated by the demands of other tanks connected to the shared recirculation system. Replicating the pressure at depths of ~1 km (~100 atmospheres), or the speculated higher salinities of the Neoproterozoic (e.g. Knauth, 2005), was not attempted here. Since there is, as yet, no way of confirming the taxonomic composition of the Ediacaran sedimentary microbiota, our microbial population was composed of those organisms found to occur in modern seawater collected off the coast of Newfoundland. To mimic the non-sediment-laden marine contourite currents thought to flow along the slope (cf. Wood et al., 2003), and in order to prevent stagnation, the water in the tanks was continuously circulated. To put decay rates in these experimental tanks into context, it is important to note that the water column in the system was oxygenated, and non-sulfidic (refer to Chapter 1 for current views on Ediacaran ocean chemistry). Biological control methods such as antibiotics were not used, since it is known that microbes were present in the Ediacaran oceans (Chapter 7), and the aim was to encourage rather than inhibit microbial growth.

To determine whether the degree of development of the sedimentary microbial community had an effect on decay rates, experiments were carried out in two tanks (Fig. 4.1). Pots in the first tank (Tank 1) were allowed to equilibrate with seawater for almost two months prior to the addition of organic material. During this settling time, the sediment became inoculated with micro-organisms naturally present in the seawater. In contrast, identical pots in Tank 2 were given only a few days to settle, and therefore did not have time to develop stable microbial sedimentary communities prior to the insertion of macroscopic organic matter.

Body tissues from several different biological kingdoms and phyla were placed on the simulated Precambrian sediment surface in the marine aquaria. Experiments were run using organic tissues from the jellyfish *Aurelia* (extracellular matrix and epithelial tissues composed mainly of proteins, collagen, mucus and water), *Nereis* polychaete worms (again mainly collagen-based), and seaweed (*Fucus*, comprising various polysaccharides and cellulose; Fig. 4.1). The range of organisms utilised reflects the current uncertainty surrounding both the biological affinities of Ediacaran organisms, and the organic material from which they were constructed. This selection was limited by the natural availability of suitable taxa on the Newfoundland coastline. Two dead jellyfish specimens were cut into several pieces (of 3–4 cm in diameter), in order to provide enough material to meaningfully document temporal variation in burial times. Dead *Nereis* specimens were inserted whole into the pots, but their size was limited by the natural variation found within the local sampled population.

Organic material was left to decay for predetermined lengths of time before being covered by pulverised tuff (Fig. 4.1), collected from the Drook Formation of Pigeon Cove, Newfoundland. Prior to burial, organic matter in the pots was photographed using a digital camera at three to four day intervals, to monitor changes in carcass morphology. In order to ensure that tuff did not settle indiscriminately over all pots in a tank, a large cylindrical tube was used to direct it onto individual pots. The mineralogical constitution and chemical compositions of both the Drook Formation tuff, and the Mistaken Point Formation metapelite, are likely to have changed since initial deposition (relative to modern marine sediments and

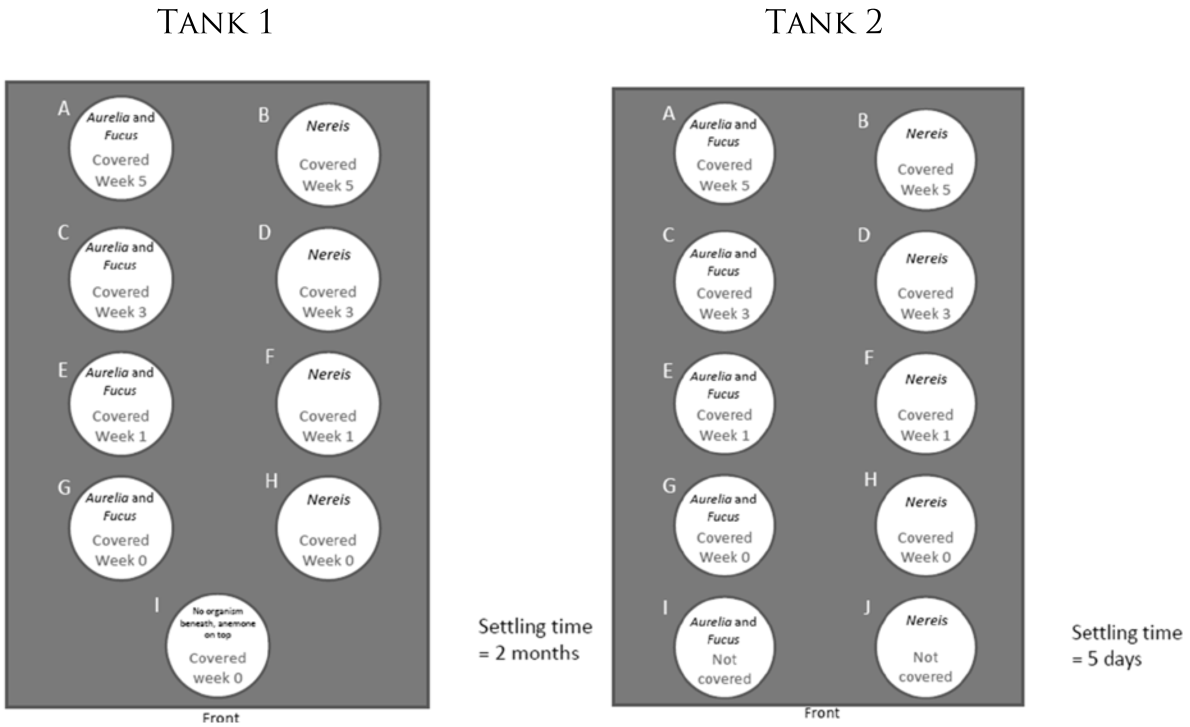

Fig. 4.1. Experimental set-up of the aquaria, detailing the location and contents of the pots, and the length of time over which material in them was allowed to decay prior to burial. Settling time refers to the period over which the sediment in the pots was allowed to equilibrate with the seawater prior to addition of organic material (initiated at Week 0 for all pots). Time covered refers to the point at which tuff was added to the pots, smothering the decaying organic material within. The anemone in Fig. 4.6 was placed on top of the sediment in Pot 1I. The *Arenicola* specimen in Fig. 4.7 was placed on a thin layer of sediment coating the bottom of Tank 1.

tuffs), due to the actions of biological processes, lithification, mineral alteration, low-grade metamorphism, and diagenesis (processes and resultant petrological features outlined in Boggs Jr., 2009). In spite of this, bulk geochemical composition is not thought to be significantly different to that found in Avalonian palaeoenvironments. The effect of microbial activity upon organic matter represents the primary focus of this study.

The experimental vessels remained in the tanks for one year following the introduction of the tuff, allowing the sediment to settle and organic material to decay completely. The pots were then removed and scanned at 1 mm intervals in a Toshiba Xpress/GX medical C-T scanner (operating at 130 kV and 200 mA), based within the Department of Earth Sciences, Memorial University of Newfoundland. The 1 mm spacing between C-T (computerised tomography) slices represents the highest resolution of scanning permitted by the equipment available. Rendering the individual x-ray cross sections to produce 3-D models (using SPIERS software, developed by Mark Sutton and Russell Garwood; see for example Sutton et al., 2001) allowed the interface between the tuff and the mud to be mapped non-destructively, revealing changes to the surface topography created by microbial decay of the organic material.

In addition to the pot experiments described above, the decay of two metazoan specimens in the marine tanks was documented, to observe the processes associated with autolysis and microbially-mediated decay. These specimens, the sea anemone *Urticina eques* (phylum Cnidaria, order Actiniaria), and the annelid worm *Arenicola marina* (Phylum Annelida, Class Polychaeta), were transferred to the experimental tanks immediately following death in other experimental systems (where they were involved in research into locomotion and bioturbation respectively). To put decay rates into context, the sediment onto which these additional organisms were added had been equilibrating in the tanks for just over two months prior to the start of the surficial decomposition experiments (Fig. 4.1). The two sets of observations are delineated as ‘pot’ and ‘surficial’ experiments respectively.

RESULTS

Pot Experiments

Organic material was introduced into the experimental pots as outlined in Figure 4.1. As expected, different organic tissues were found to take variable amounts of time to decay under the influence of marine microbes. Jellyfish (Kingdom Animalia, Phylum Cnidaria, Subphylum Medusozoa) and nereid (Kingdom Animalia, Phylum Annelida, Class Polychaeta) specimens, both built primarily around collagen, were noticeably effaced by microbial activity in as little as one week, and took several weeks to decay completely (Appendix E). Conversely, seaweed (Subkingdom Thallophyta, Class Phaeophyceae) took considerably longer, not being significantly degraded by microbes until at least four weeks into the experiment (Fig. 4.2; see Appendix E for a comprehensive suite of images from the pot experiments). This variation is likely to have resulted from a combination of factors, including the size of the specimens (surface area-to-volume ratios are likely to be integral to this), the type and structure of organic tissue present, and the composition of the microbial community. Due to the extended periods of time necessary for algal organic matter to degrade, it was not possible to obtain data on a complete spectrum of seaweed decay in the allotted time period. Further experimental work over extended periods of time will be necessary to confirm whether algal material can be effaced in a similar way to metazoan tissue. Conversely, the decay of *Nereis* specimens took place too rapidly to document at a three-day imaging resolution. Measurement protocols in future experiments will need to be modified accordingly.

In general, it can be stated that the gross surface topography of organic material was initially enhanced in all specimens, while overall fidelity of anatomical features decreased. Randomly positioned irregular lobes and troughs were created by microbial trapping and binding of sediment on the upper surface of the *Aurelia* specimens (Fig. 4.2; Appendix E). This trapped sediment was derived from the ground-tuffaceous particles added fortnightly to individual pots (Fig. 4.1; pelagic sedimentation rates for the Conception Group are yet to be quantified). Further experimentation will be required, under controlled conditions of gradual sediment accumulation, to determine the degree to which surface morphology can be enhanced in this manner, and the identities of the microbes involved in the baffling of sedimentary grains. The

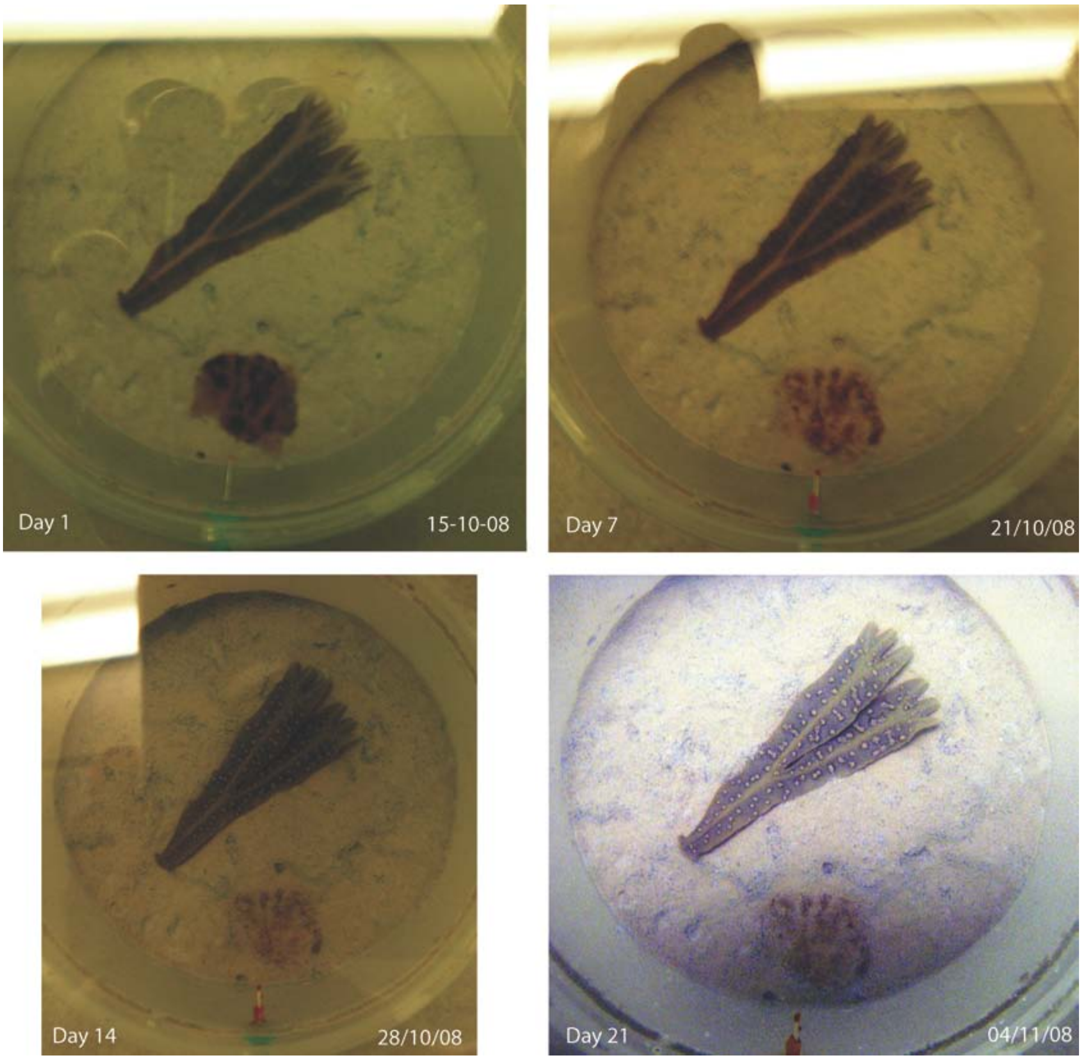

Fig. 4.2. Images of Pot 2C, taken at weekly intervals in the decay process. The pot originally contained a sample of *Fucus* seaweed (top), and a chunk of *Aurelia* jellyfish (bottom). Note the gradual trapping of sediment onto the surface of both the jellyfish and seaweed, and the formation of irregularly positioned lobes upon the decomposing jellyfish even by day 7. Sediment surface in this pot is 100 mm in diameter.

distribution of lobate structures upon specimens appears to be random (Appendix E). These structures are broadly analogous to those seen in ivesheadiomorph fossils from the Avalon terrane. Neither the *Fucus* nor the *Nereis* tissues formed such lobes; worm specimens were all too small for such features to be observed, while the seaweed had not decayed sufficiently over the studied interval to trap detritus on its surface. The different tissue composition and flatter morphology of the algal material may be responsible for its slower and more subtle decay relative to the metazoan remains. It remains to be seen whether algal organic matter can form ivesheadiomorph-like lobate topography during decay.

One of the most striking observations from these experiments was that organic matter decayed at different rates in the two tanks. The only difference between conditions in the tanks was the amount of time that the sediment in the pots had spent equilibrating within the system prior to the introduction of organic material. Pots in Tank 2 had spent just five days in the tank prior to the insertion of organic matter, while those in Tank 1 had resided for two months (Fig. 4.1). Decay rates in Tank 2 were considerably slower, with organic material taking several weeks longer to decay than comparable pots in Tank 1 (see Appendix E for full images and an extended discussion). This difference in rates was noted through observations of digital images, and is a qualitative assessment of the relative degree of effacement individual specimens had undergone in the two tanks (Appendix E). Although it would be useful to quantify exactly when specific morphological features were lost by individual specimens (an approach employed successfully by Sansom et al., 2010), this was not possible here, given the fragmentary nature of the *Aurelia* material, and the limited morphological characteristics of *Fucus*.

It is suggested that this difference in decay rates was caused by the maturity of the microbial community inhabiting the sediment at the start of the experiment. In Tank 1, microbes from the water column are likely to have infiltrated the sediment prior to the introduction of organic material, developing a stable microbial profile. Pots in Tank 1 are therefore hypothesised to have contained better-developed colonies than those in Tank 2, since they had a longer time interval over which to colonise the fresh sediment surfaces. When organic material was added to the pots, it is suggested that the microbial communities in Tank 1 were in a better position to capitalise on this food source (possessing larger populations, greater densities, and more advanced microbial profiles), resulting in faster rates of decomposition.

C-T Data

C-T scanning was employed to visualise the covered sediment-water interfaces in the experimental pots in a non-destructive manner. The C-T scans provided both vertical sections through each pot (e.g. Figs. 4.3–4.4), and 3-D renderings of the total volume of sediment within the pots (e.g. Figs. 4.5, E1.17). It must be remembered that the C-T scanner measured x-ray absorption (essentially density contrasts between different materials), rather than imaging specific objects or materials. In individual C-T slices, black colours therefore represent areas of low density (e.g. air), while white colours denote regions of high density (e.g. solid rock). All C-T images have been calibrated using the SPIERS program to

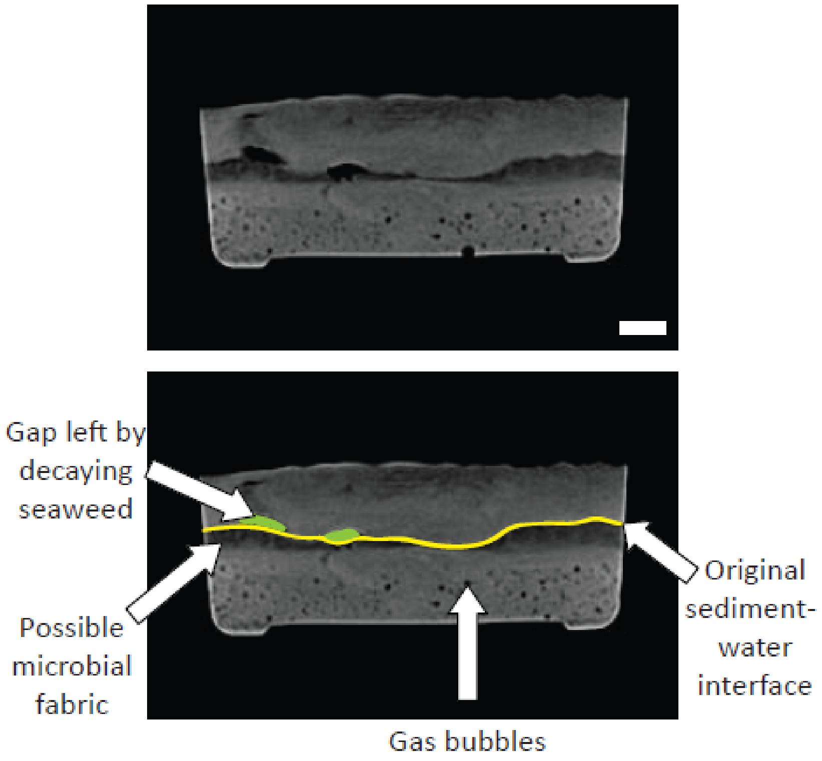

Fig. 4.3. Individual C-T slice through experimental Pot 1G, following burial beneath ‘tuff’, image taken 10 weeks into the experiment. **Top**: Original C-T image. **Bottom**: Annotated image, with the original sediment-water interface and seaweed locations highlighted. White colours represent regions of high density, black represents regions of low density. Gas bubbles can clearly be picked out as black circles (i.e. regions of low x-ray absorbance).

accentuate the differences in density contrast observed within the pots, and to remove mechanical artefacts.

Vertical C-T sections through the pots reveal a number of interesting features. Firstly, the original sediment-water interface (upon which the organic material was deposited) can be identified clearly as a boundary between tuff above, and a darker region of sediment directly beneath (Fig. 4.3). The location of the seaweed specimens was picked out in several pots by regions of low contrast, suggesting that a void now exists in the spot where the seaweed once lay (Fig. 4.3). Unfortunately, there was no evidence for remains or impressions of either *Nereis* or *Aurelia* in the C-T slice imagery.

Rounded circular structures with low densities are gas bubbles (Fig. 4.3), likely to be have formed while filling the pots with sediment prior to emplacement in the tanks. Intriguingly, bubbles are absent in the few millimetres of the sediment immediately below the original sediment-water interface, potentially due to a lower overburden pressure near the surface permitting the bubbles to escape. These same regions also appear darker in C-T images of pots from Tank 1 than the surrounding sediment. The consistent occurrence of a darker region in almost all pots from Tank 1, immediately beneath the sediment-water interface, suggests that this may represent a distinct horizon. Interestingly, this darker region is not present in most pots from Tank 2 (Fig. 4.4); only sediment in Pots 2I and 2J, which were not covered by tuff and whose surfaces therefore remained in contact with the seawater for several months, displayed such a boundary. This could imply that the darker layer is related to the development of a microbial profile/community within the sediment.

Once the C-T slices for individual pots were combined, the resulting models revealed the 3-dimensional location of various interfaces within the pot (e.g. Fig. 4.5). The 3-D models have been ‘smoothed’ in order to remove small anomalous outlier points, and to give each model a

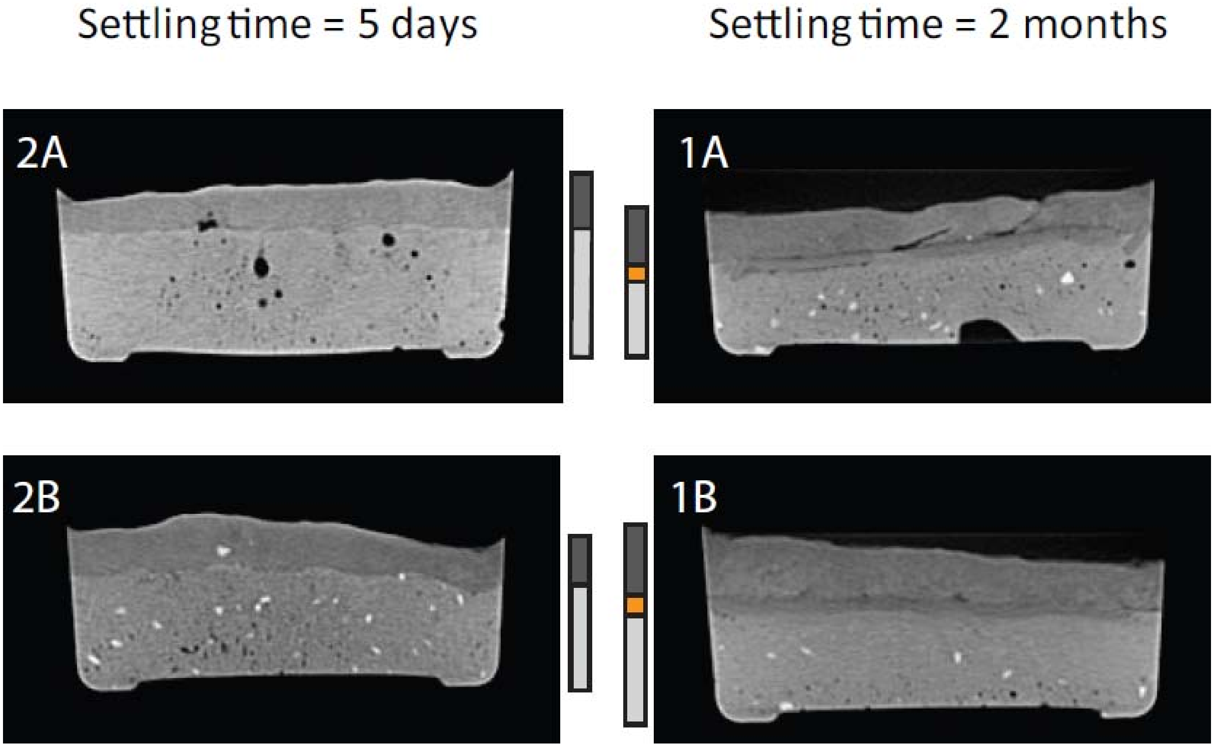

Fig. 4.4. Comparison of C-T sections through four pots, demonstrating the presence of a darker layer of contrast immediately beneath the original sediment-water interface in pots from Tank 1 (absent in Tank 2). The bars in the centre of the image emphasise the location of the layer boundaries in their neighbouring pots, with orange picking out the layer of dark contrast (only present in pots from Tank 1).

more realistic, less angular, appearance. Due to the limited (1 mm) scan resolution available to us, the smoothing process actually enables the modelled surface topography to better resemble the actual sediment profile (though since the process is automated, smoothing does introduce a degree of error into the dataset). 3-D renderings support the suggestion that gas bubbles are largely confined to regions of the sediment below ~1 cm beneath the sediment-water interface (Fig. 4.5E), but the resolution of the scanner was not sufficient to identify anything more than basic outlines of the morphology of the organic material (e.g. the seaweed specimens; Fig. 4.5). Due to their small size relative to the horizontal resolution of the

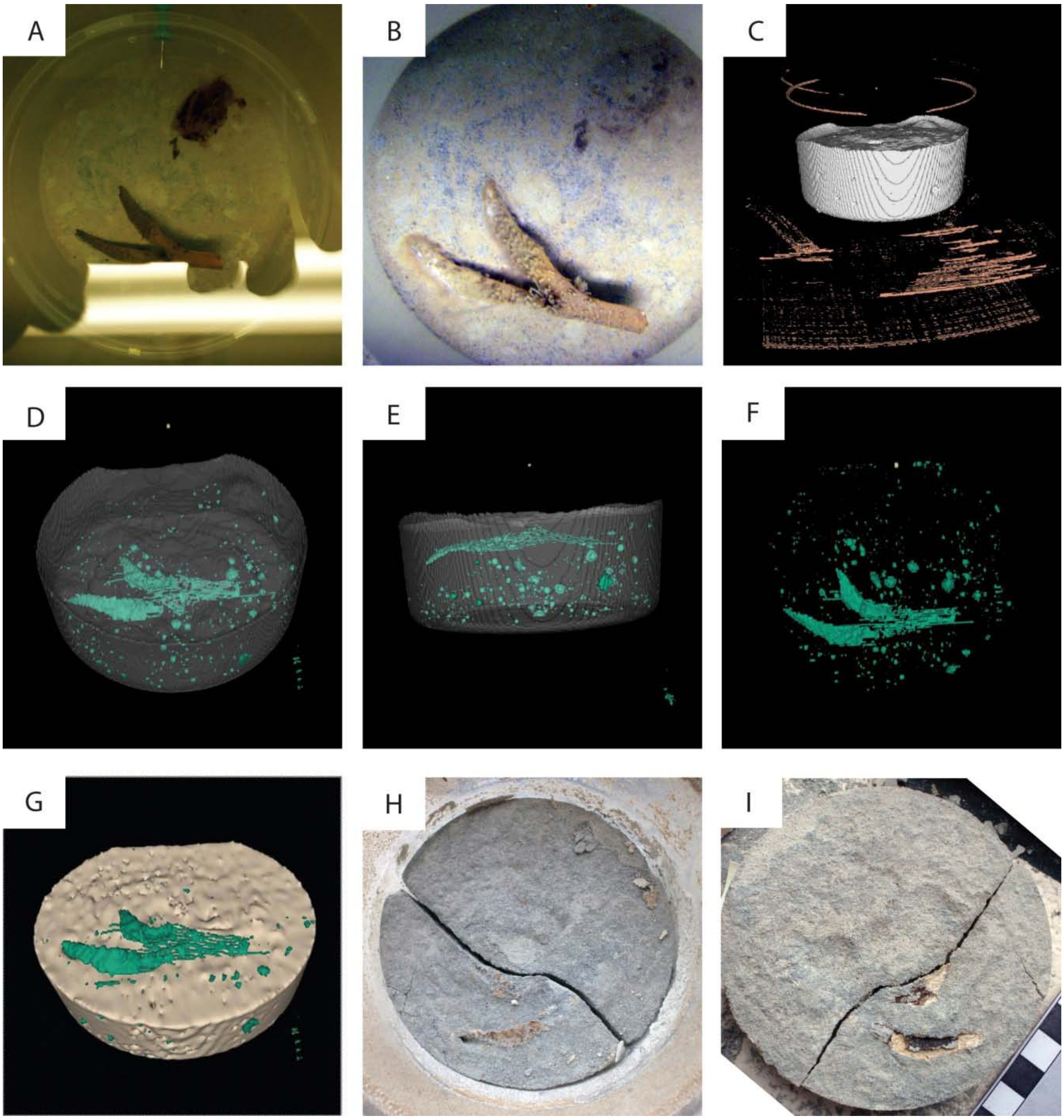

Fig. 4.5. A variety of images from Pot 2A. **A**: The pot immediately following insertion of organic material. **B**: The pot after two weeks of decay. **C**: C-T rendering of the whole pot. **D**: C-T images of the pot with ‘gaps’ (regions of low x-ray absorption) highlighted in green. The outline of the *Fucus* specimen is clearly visible, even after one year. **E**: Lateral view of the pot C-T image, showing that bubbles mostly occur well-below the sediment-water interface. **F**: C-T model as in D, but with sediment ‘removed’. **G**: 3-D C-T model of the original sediment water interface with tuff ‘removed’. Void left by the seaweed appears green. **H**: Sediment-water interface after two years, pot sediment has been dried out and split open. **I**: Counterpart of H, displaying the remnants of seaweed organic material (now a flaky black film). Scale increments in the lower right-hand corner of image I are 10 mm. For further C-T rendering images, see Fig. E1.17, Appendix E.

scanner, impressions of the jellyfish and *Nereis* could not be confidently identified from the C-T-derived models.

After the pots had been removed from the tanks and dried out, observation of the edges of the compacted sediment revealed the expression of the interfaces seen in the C-T scans. Interestingly, the ‘dark layer’ seen in C-T cross sections (Fig. 4.3) is not visible in the dried-out sediments. Unexpectedly, it was found that many of the dried sediment blocks could be split along interfaces observed in the C-T data. In cases where an interface coincided with the original sediment-water interface (Tank 2), it was possible to observe the topography of the surface and its artificial ‘fossil’ impressions directly (see Fig. 4.5H–I). Remnants of seaweed material still remained as dehydrated carbonaceous films even after a year beneath the tuff. Where all organic material had decayed away, surfaces were noted to be topographically uneven, though it was difficult to differentiate between topography created by the presence of a decaying organism, the original topography in the sediment, and variations caused by settling, compaction, and (following drying out of the pots) desiccation.

Summary of pot decomposition studies

C-T scanning of experimental taphonomic microcosms clearly has potential for use in taphonomic research, and can reveal the interfaces between different levels within sediments in a non-destructive manner. However, both much higher scanning resolutions, and larger samples of organic material, are required to definitively identify decay features or subtle morphological characteristics in fossil impressions using this technique. The maturity of the incumbent microbial community within a sedimentary profile is found to be an important factor in controlling rates of decay of organic matter. This has implications for Avalonian deep-marine environments, which would have been frequently inundated with sediment from event beds, regularly providing a fresh substrate for colonisation by both micro- and macro-organisms. The pot experiments suggest that lobate topography can form on the top surfaces of some organic materials during microbial decay and autolysis (the *Aurelia*; Fig. 4.2), but it was not possible to determine whether those lobate surfaces were preserved by the casting sediment. Impressions of the algal material were retained at the sediment-water interface, suggesting that the absence of ‘preserved’ metazoan impressions in these experiments may be governed by specimen size rather than taphonomic constraints.

Surficial experiments: Aphotic decomposition of the anemone Urticina eques

A dead anemone was inserted into the tank with its tentacles in contact with the sediment. Observations of the decaying *Urticina* revealed that its surface rapidly became covered by a microbial biofilm (Fig. 4.6, compare day 3 and day 8), which included filamentous bacteria and fungal hyphae (Fig. 4.6 day 18, arrowed). This biofilm obscured the fine surface morphology of the verrucae on the body column. The biofilm surface became more pustulose over time, probably due to the trapping of gas bubbles created by decomposition of organic matter beneath its surface (Fig. 4.6, day 11). The pustulose top surface remained until day 22, after which time it became completely smooth (see Fig. 4.6, day 25). Tentacles remained clearly visible as discrete entities until about day 11, and were indistinguishable by day 22 (Fig. 4.6). Larger bulges again developed on the surface of the biofilm from day 29 onwards, as decomposition continued in the anemone interior. The gut was the most decay-resistant part of the organism (Fig. 4.6, day 81, arrowed). The original surface of the anemone remained intact for about 50 days before the polyp collapsed (Fig. 4.6 compare days 31 and 81). After 100 days, the primary body tissues of the anemone had largely decomposed, with only a lumpy, asymmetrical biofilm mantling the sediment surface.

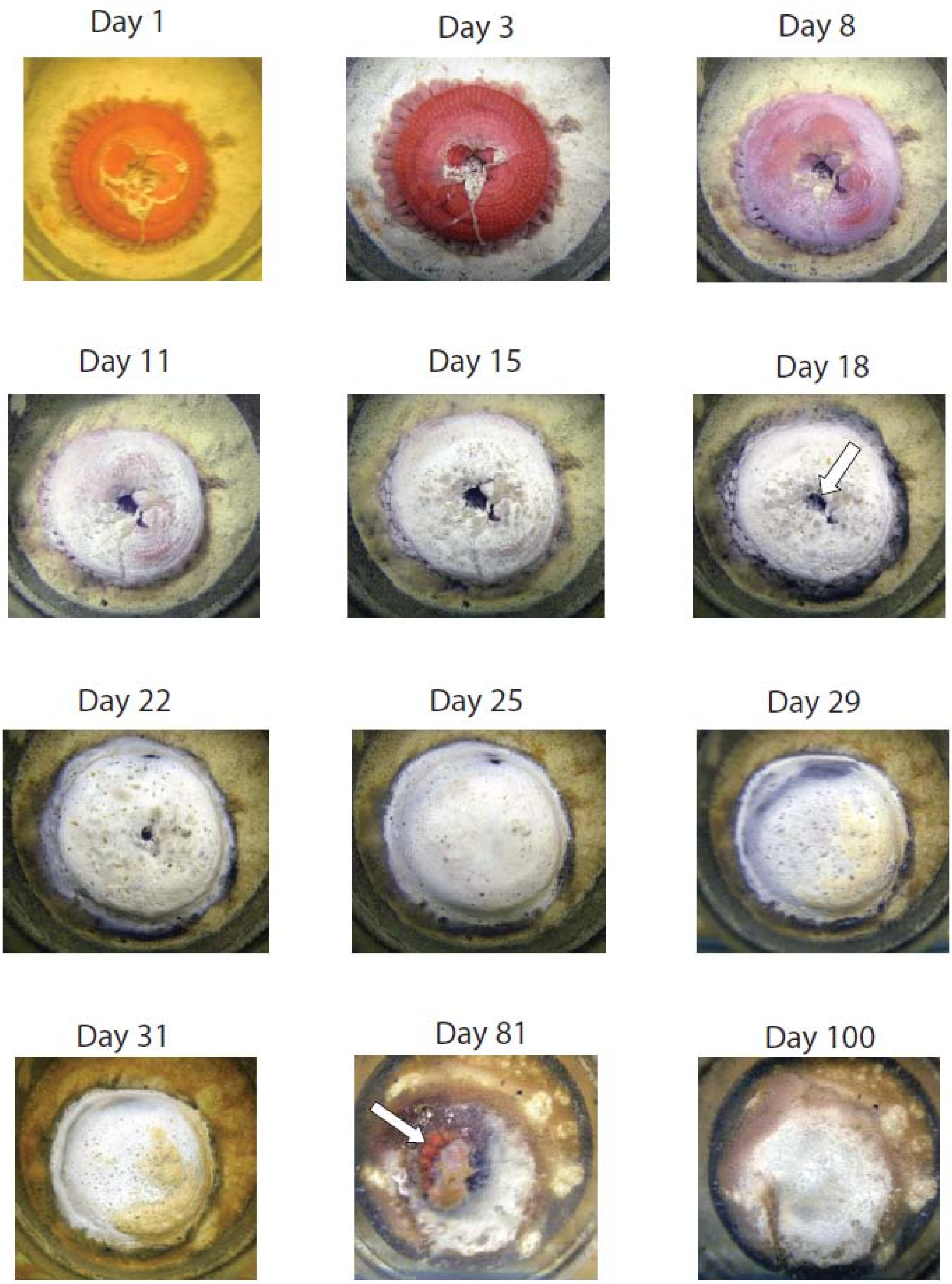
Day 1
Day 3
Day 8
Day 11
Day 15
Day 18
Day 22
Day 25
Day 29
Day 31
Day 81
Day 100

Fig. 4.6. The decay of the sea anemone *Urticina eques* in the experimental tanks, documented over a period of 100 days (15 weeks). Arrows indicate features referred to in the text. Scale bar (day 3) = 10 mm.

Surficial experiments: Aphotic decomposition of the annelid Arenicola marina

Decay of the annelid at the sediment-water interface revealed a similar loss of external morphology to that seen in the anemone *Urticina*, with the carcass gradually enveloped by a microbial biofilm (Fig. 4.7). Initially, growth of a pustulose surface texture, comparable to that noted during decomposition of the anemone (Fig. 4.6), was coupled with loss of fine

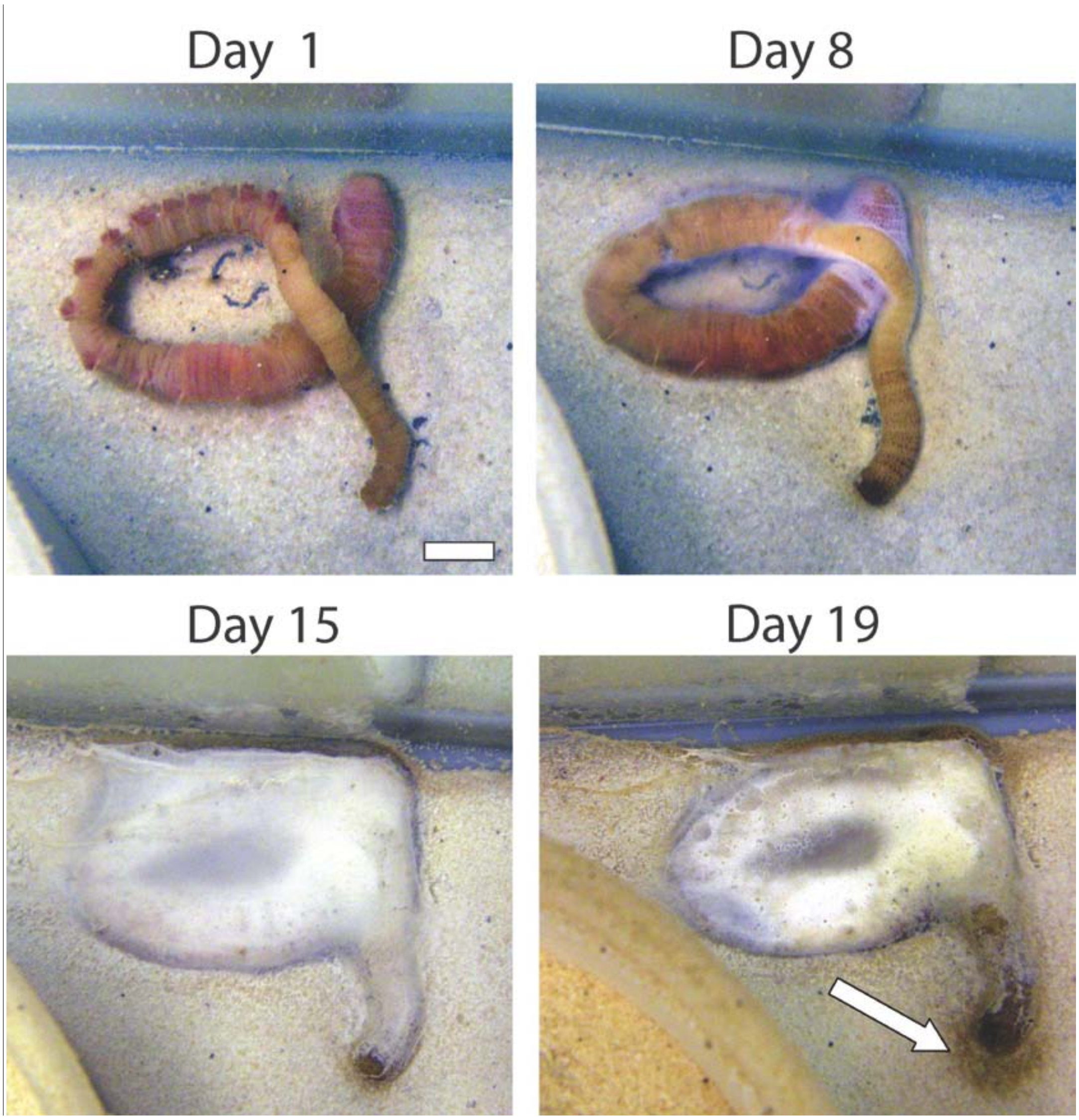

Fig. 4.7. Decay of the annelid worm *Arenicola marina* in our marine tanks. Note the bloating of the specimen (compare day 1 to day 8), the subsequent increase in size, and the fact that the resulting broad morphology of the organism (post biofilm colonisation) is no longer that of a long, thin worm. Arrow at day 19 shows where bodily fluids seeping from the organism have been colonised by microbial growth (black stain on the sediment). Scale bar (day 1) = 10 mm.

morphological features (for example the setae located along the length of the organism; Fig. 4.7, compare day 1 and day 8). An increase in size of the specimen arose due to bloating in the early stages of decay (Fig. 4.7, days 1 to 8), demonstrating one way in which the morphology of an organism can change substantially between death and preservation. Decomposition resulted in the originally coiled worm forming a roughly circular, pustulose microbial mass, similar in shape to the decomposed anemone (Fig. 4.6). The final macroscopic form is not easily identifiable as belonging to an annelid (Fig. 4.7, compare day 1 and day 19).

It was noted that microbial breakdown products and body fluids seeped into the surrounding sediment over the course of the decomposition process (black stain in Fig. 4.6, day 18 onwards; Fig. 4.7, day 19, arrowed), a phenomenon commonly observed in forensic geology, where leachates are often rich in micro-organisms (e.g. Engelbrecht, 1998). These leachates may play a role in early-stage diagenesis and lithification of the sediment. Such fluids seeping from decaying organic matter have previously been observed to harden adjacent substrates (Bruton, 1991), and these decay products represent an interesting avenue for further taphonomic research. Unfortunately, it has not been possible to explore the effects of such fluids upon preservation in these microcosms, since we were inhibited from extracting sediment from beneath the regions infiltrated by the decay products. Doing so would have disrupted the sediment around the organisms, disturbing the overall organic morphology that was the focus of this study. In future studies, such sediment extraction should form a significant target for further exploration.

Summary of surficial decomposition experiments

These observations confirm that, as expected, microbial decay is capable of effacing the remains of metazoan organisms in marine settings under controlled conditions. Growth of microbial communities on the upper surface of a deceased organism is effective at smoothing that surface, and removing evidence of fine original morphological detail. When combined with the actions of autolysis, decomposition by microbial activity can gradually lower the total surface topography of a macroscopic specimen (Fig. 4.6). In our aquaria this process took place over a period of weeks to months, and appeared to be dependent, amongst other variables, upon the size of organism in question. Although there are a myriad of other factors that may influence decay rates, processes, and final decomposed morphologies (see Briggs, 1995, and later discussion in this chapter), decay of these metazoan organisms demonstrates that microbial and autolytic decay are capable of substantially altering the post-mortem morphological characteristics of an organism.

DISCUSSION

The post-mortem microbial effacement of recent marine organic remains, documented herein, is shown to replicate several of the features observed within Ediacaran ivesheadiomorph fossils. Experimental specimens subjected to autolysis and microbial decay can develop irregularly positioned lumps and depressions within the bounds of the overall structure; can suffer gradual loss of fine morphological detail; and can display overall morphologies during the decay process that bear little resemblance to the original organism (Figs. 4.2, 4.6–4.7). This effacement was most noticeable in the cnidarian specimens, since the time intervals at which sediment was added and images obtained were not appropriate for sufficient documentation of *Nereis* or *Fucus* decay. Extension of this study is required to determine whether similar features can be produced by decay of other organic materials. Future work could improve upon this initial study by utilising larger specimens, extending the running time of the experiments, and culturing the microbes partaking in decay in order to determine their precise identities and metabolisms.

The experiments were ambiguous when considering the preservation potential of microbially effaced specimens. Pot experiments suggest that under simulated Ediacaran seafloor conditions, microbially-effaced macro-organisms can produce moulds and casts of their surface impressions (as revealed by seaweed specimens leaving voids, and surface imprints; Fig. 4.5G–I), though their response to deeper burial or compression remains to be investigated. The metazoan tissues (the most effaced examples of the studied organic materials) were not large enough to unambiguously reveal impressions of their remains either in the C-T dataset, or on sedimentary surfaces observed once the pots had been split.

Documentation of two unexpected features to arise from these experiments, the leaching of bodily fluids into the sediment surrounding aerobically decaying organisms, and the preservation of a dark, lower density layer in the C-T imagery in some pots (interpreted to be microbial in origin; Fig. 4.4), demands future investigation. Both decay-derived leachates, and the ‘maturity’ of a microbial population within a substrate, could play significant roles in the preservation of soft-bodied organisms in Ediacaran and younger palaeoenvironments. They may influence not only the rates of decay of organic material, but also the physical properties of the substrate immediately adjacent to the organism. Whether the products of these experimentally-observed processes can be identified in the fossil record is an interesting question. It is known that the early stages of diagenesis can influence fossil preservation within a matter of weeks (Briggs and Kear, 1993, 1994; Briggs, 1995). Therefore, further research into the processes occurring within the first few weeks to months following death could resolve how the final preserved fossil morphology of Ediacaran soft-bodied organisms developed.

The timescale over which decay takes place is strongly dependent on a variety of biological, chemical and physical factors. From a biological perspective, although we consider predation, scavenging, and bioturbation not to have been significant activities in these ecosystems (Chapter 3 and references therein), there are still notable unknowns. While microbial organisms are suggested to be the major agents of biological degradation in the Avalon region, the composition of the microbial communities remains an open question. Although the microbial populations utilised in our experiments were capable of breaking down small samples of organic material on timescales of the order of weeks to months, we cannot conclude with certainty that similar decay in the Ediacaran Period operated on identical timescales. The organic tissue undergoing decay, the structure of the original organism, and its size, are noted herein to have additional significant effects on decay rate (see also Briggs, 1995, 2003).

Modern studies suggest that the enzymatic breakdown of organic material at depth in the oceans is not affected by pressure, but does increase in rate as salinity decreases, and temperature increases (Meyer-Reil and Koster, 1992). These authors also noted that the addition of labile organic matter and nutrients to the sediment-water interface stimulated faster rates of enzymatic breakdown, and that this increased activity occurred not only at the sediment surface, but also at depths of several centimetres within the substrate (Baird et al., 1985; Meyer-Reil and Koster, 1992). Although the postulated decay of organic matter on the Avalonian seafloor could potentially have released abundant labile organic matter at the sediment-water interface (see also Chapter 7), it is considered likely that the depositional environments of the Conception Group and Charnian Supergroup would have witnessed slower rates of microbial decay than those observed in our experiments. This is mainly due to the lower temperatures on the deep-sea floor (modern ocean temperature is roughly 2–4°C at depths of 1 km at latitudes of ~ 50°; Locarnini et al., 2006) inhibiting decay rates relative to those seen in our aquaria (12°C). A longer decay interval would have provided a greater potential for time averaging of different communities, with the result that the duration over which Ediacaran body fossils remained rotting on the seafloor could conceivably have varied from days to years.

The chemistry of the system may also prove to be important in determining Ediacaran decay rates. Experimental decay of embryos has shown that a reducing environment can repress the actions of autolysis (Raff et al., 2008). While the Avalon deep marine environment is considered to have been oxygenated following the Gaskiers glaciation (Canfield et al., 2007), this is not thought to have been the case worldwide (Canfield et al., 2008). There is also evidence to suggest a ferruginous, but non-sulfidic water column in the mid-Ediacaran Period (Canfield et al., 2008). Although the Avalonian depositional environments are not currently thought to have been euxinic, the precise chemistry of these settings is not well documented, and such conditions could have further suppressed decay and autolysis in the Ediacaran.

The interplay between these disparate variables will have governed the precise decay rates of organic matter during the Ediacaran Period. Quantifying these rates represents a significant challenge. However, this research has gone some way to demonstrating the plausibility of the decay mechanisms proposed to have created effaced impressions of macroscopic organisms on the Avalonian seafloor. Although much work can still be done to further refine and test our hypotheses, it is considered likely that the combination of autolysis and microbial decay prior to burial was responsible for the production of ivesheadiomorph fossils during the late Ediacaran Period.

CONCLUSION

The results documented in this chapter demonstrate the value of applying experimental techniques to Ediacaran taphonomic questions. Many avenues of research in this field remain to be explored. It has proven to be relatively easy to replicate conditions on the Ediacaran seafloor, and further studies could potentially do this on a larger scale to investigate numerous taphonomic questions. The interactions of marine currents with microbially-bound sedimentary substrates, the early stage diagenesis and eventual lithification of aqueously deposited volcanic ash, and the physical properties of rangeomorph organic matter are all prospective areas of experimental research. Improvements in our knowledge of all of these topics are required if we are to be confident in our assumptions regarding the palaeoenvironmental and taphonomic processes occurring within Avalonian deep-marine settings. Although ideally some of these experiments would require time-spans of months to years to run to fruition (e.g. in order to grow microbial mats, or allow sediment to undergo diagenetic processes), the considerable promise of this field of research outweighs these temporal obstacles.

The actions of autolysis and microbial decay have been demonstrated to efface both metazoan and algal organic material under controlled conditions. The surface topography of organic matter becomes smoothed, with evidence for high fidelity morphology gradually obscured and removed over intervals of days to months. Combined with trapping and binding of sediment from the water column, microbial activity can significantly alter the surface topography, relief and overall shape of decaying organisms, and can produce irregular lobate morphologies from metazoan remains. The results of such activity are consistent with morphological features seen in the ivesheadiomorphs, a group of proposed taphomorphs from Ediacaran rocks in Newfoundland and the U.K. Replicating these experiments with modern analogous sediments, rather than crushed Precambrian lithologies, has the potential to further advance our understanding of the early stages of preservation and lithification on the Ediacaran seafloor. The possible effect of leachate fluids upon preservation has also never been considered in Ediacaran fossil assemblages. Furthermore, there is currently no evidence for mineralization of soft tissues in the Avalon assemblages (which can take place within hours of death in favourable modern environments; Martill and Harper, 1990), and we must ask why this is the case, considering the bias in late Neoproterozoic environments *toward* exceptional preservation (Brasier et al., 2011).

Microbial decay of deceased individuals on the seafloor prior to burial is rarely seen in later fossil assemblages, potentially due to the introduction of predation, scavenging and pervasive bioturbation by macro-organisms, all of which act to accelerate the breakdown and removal of soft tissues. The taphonomic window in which effaced preservation as described herein can take place is seemingly restricted to the late Ediacaran Period, representing a ‘taphonomic megabias’ (Briggs, 1995). Although microbes were likely to have been fundamental contributors to the decay and breakdown of organic matter, they were also, and remain, critical to the preservation of soft tissues (e.g. Allison, 1986; Gehling, 1999; Raff et al., 2008). The importance of understanding decay as a taphonomic process when interpreting the palaeobiology of soft-bodied fossils (e.g. Briggs, 2003) is thus emphasised.

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CHAPTER 5

THE FŒTID GARDEN OF EDIACARA

PREFACE

The ‘effaced preservation’ hypothesis outlined in the previous chapters has several important implications for Avalonian ecosystems. Recognition of the taxa *Ivesheadia*, *Shepshedia*, *Blackbrookia* and *Pseudovendia* as taphomorphs, and their resulting synonymization as tapho-taxa, has previously been addressed (Chapter 3). Of wider interest are the consequences of this hypothesis for Ediacaran palaeoecology.

Previous studies have largely taken the population densities of Ediacaran siliciclastic bedding planes at face value, inferring them to preserve census populations of living organisms at the time of burial. Based on this assumption, several authors have come to interesting palaeoecological conclusions, most notably that the bedding planes preserve assemblages with a similar ecological community structure to modern suspension feeding animals (Clapham et al., 2003). The conclusion proposed in Chapter 3, that Avalonian assemblages do not represent ‘snapshots’ of ecological communities (i.e., living census populations of Ediacaran biota; *sensu* Seilacher, 1992), but instead comprise a time-averaged assemblage of both living and deceased organisms at the time of burial, forces a re-evaluation of previous palaeoecological interpretations.

Re-analysis of the datasets of Clapham et al. (2003) highlights several interesting points. Firstly, ecological parameters of the kind widely used for the study of extant biological communities cannot be applied with a high degree of confidence to fossil populations. It is therefore inadvisable to speculate on the nature of Ediacaran ecology through comparisons between Ediacaran and modern community structural attributes. Furthermore, a considerable proportion of perceived biomass in these palaeocommunities was actually necromass, the mass of dead organic matter in an ecosystem. The suggestion that abundant decaying carcasses were preserved on the Ediacaran seafloor sees the idyllic scene of a lush ‘Garden of Ediacara’, populated by healthy communities of waving Ediacaran fronds, taking on an altogether more fœtid appearance. Most importantly, similarities with modern animal populations are shown to be undermined by this revised analysis.

This palaeoecological work is currently being written up for submission to the journal *Paleobiology,* under the title ‘*The Fœtid Garden of Ediacara’*, in collaboration with Duncan McIlroy and Martin Brasier. The idea to revise previous palaeoecological studies in light of the effaced preservation hypothesis presented in Chapter 3 was formulated by Duncan McIlroy. All of the planning, data collection, analysis and writing has been undertaken by the author.

AVALONIAN PALAEOECOLOGY

Few workers have previously attempted to study palaeoecology in the Proterozoic. In part, this is because discerning the biological affinities of Proterozoic fossils, let alone their behavioural and ecological roles and capabilities, is often difficult. Proterozoic trophic structure is also likely to have differed substantially from that of the Phanerozoic, due to the absence of many of the major components of modern ecosystems (e.g. metazoans; McIlroy and Logan, 1999).

In successions of Ediacaran age from the Avalon region, two prior studies are notable. Clapham et al. (2002) analysed the size distribution of rangeomorphs from the Conception Group, and demonstrated that rangeomorph communities exhibit a tiered community structure. The same working group then compared community ecological parameters obtained from Mistaken Point fossil assemblages with those of modern epibenthic faunal communities (Clapham et al., 2003), concluding that the community structures of the two groups were similar. These palaeoecological studies are important, since subsequent interpretations of the Ediacara biota as metazoan animals or organisms of animal-grade can commonly be traced back to the palaeoecological studies of Clapham et al. 2003 (e.g. Narbonne, 2005; Bamforth et al., 2008). Whilst the original studies were both bold and innovative, and represent a shift in the way in which Ediacaran research was conducted, it may be argued that they were attempted slightly prematurely.

The Ediacaran fossil assemblages of the Avalon region have previously been regarded as snapshots of benthic communities at the moment they were engulfed by volcanic tuffs and volcaniclastic event beds (Seilacher, 1992; Clapham et al., 2003), in the manner of an ‘Ediacaran Pompeii’ (Narbonne, 2005). Such a scenario envisages all of the preserved organisms to have been alive on the seafloor at the time of burial, with minimal time-averaging of communities on individual bedding planes (Fig. 5.1A; Clapham et al., 2003, p. 530). This interpretation has been used to justify reconstructions of Avalonian palaeoecology in which individual bedding plane fossil assemblages are regarded as true census populations (Clapham et al., 2003). From such studies, it has been suggested (in conjunction with the tiering-model of Clapham and Narbonne, 2002) that the palaeoecology of the Avalonian Ediacara biota is similar to that of modern marine filter-feeding communities (Clapham et al., 2003). This in turn has been used to infer that filter-feeding was a mode of feeding utilised by rangeomorphs, and that the vast majority of Ediacaran organisms in these ecosystems, including rangeomorphs, may therefore have been crown- or stem-group animals (Clapham et al., 2003; Narbonne, 2005, 2010). Although a metazoan interpretation is just one hypothesis among many for the biological affinities of Ediacaran organisms, and other authors have since proposed alternative methods of feeding (e.g. Laflamme et al., 2009), the view that many Ediacaran Avalonian organisms are of animal-grade remains widely accepted by multiple researchers (e.g. Fedonkin et al., 2007a; see also Chapter 1).

The ecological studies cited above are built around assumptions regarding Ediacaran fossil assemblages that are open to question in light of current research. Clapham et al. (2003) suggest that the lack of evidence for either post-mortem transport or infauna in the Avalon successions implies that post-mortem mixing of multiple generations of populations did not occur. From this, they conclude that a combination of both living and recently deceased organisms was not a feature of the preserved Mistaken Point fossil assemblages (Clapham et al., 2003), allowing modern ecological parameters to be applied with confidence. It is, however, entirely reasonable to infer that Ediacaran organisms did not die solely in conjunction with event beds; many would have perished on the seafloor before obrution. Since several Ediacaran forms (the majority of which were sessile) are thought to have been tethered to the seafloor (e.g. Narbonne and Gehling, 2003), many Ediacaran macro-organisms may have remained where they fell upon death. Therefore, post-mortem transport may only have taken place under the influence of extremely strong bottom currents. Such currents are not invoked for the typical Mistaken Point inter-turbidite beds (Wood et al., 2003).

It thus seems logical to predict that dead and decaying organisms would have been buried *in situ* beneath event beds on Ediacaran bedding planes, alongside live individuals, and that their remains may account for a considerable proportion of the preserved 'biomass' in the fossilized assemblages (cf. Chapter 3). The lack of bioturbation in these Avalonian successions (e.g., Sepkoski, 1979; McIlroy and Logan, 1999; Seilacher, 1999; Bottjer et al., 2000; Droser et al., 2002; Jensen et al., 2005; Callow and Brasier, 2009a; though see Liu et al., 2010a; Chapter 6), combined with an absence of evidence for macroscopic scavenging, detritivory, or predatory life forms (Sokolov, 1976; Glaessner, 1984; Seilacher, 1999; Bottjer et al., 2000; though see Fedonkin, 2003) has important implications. It means that autolysis and microbial degradation would arguably have been the main biological processes available to complete the breakdown of organic tissue (Chapter 3; Liu et al., 2011). Fungi and heterotrophic bacteria (utilising osmotrophic and saprophytic methods of feeding) were likely to have been present at the Precambrian sediment-water interface to undertake this process (Brasier et al., 2010). Such breakdown of organic matter is expected to have been considerably slower than rates of decomposition observed in modern marine environments, where scavengers and bioturbating macro-organisms accelerate the process (Chapter 4). It is therefore suggested that prior to the Cambrian, periods of weeks to years may have elapsed before the remains of deceased macro-organisms were completely removed, allowing necromass (the mass of dead organic matter, e.g. Chapman and Gray, 1986) to build up on the seafloor (Chapter 4). This theoretical possibility has support from the suggestion that some fossils in the Avalon fossil assemblages represent the remains of organisms that had already

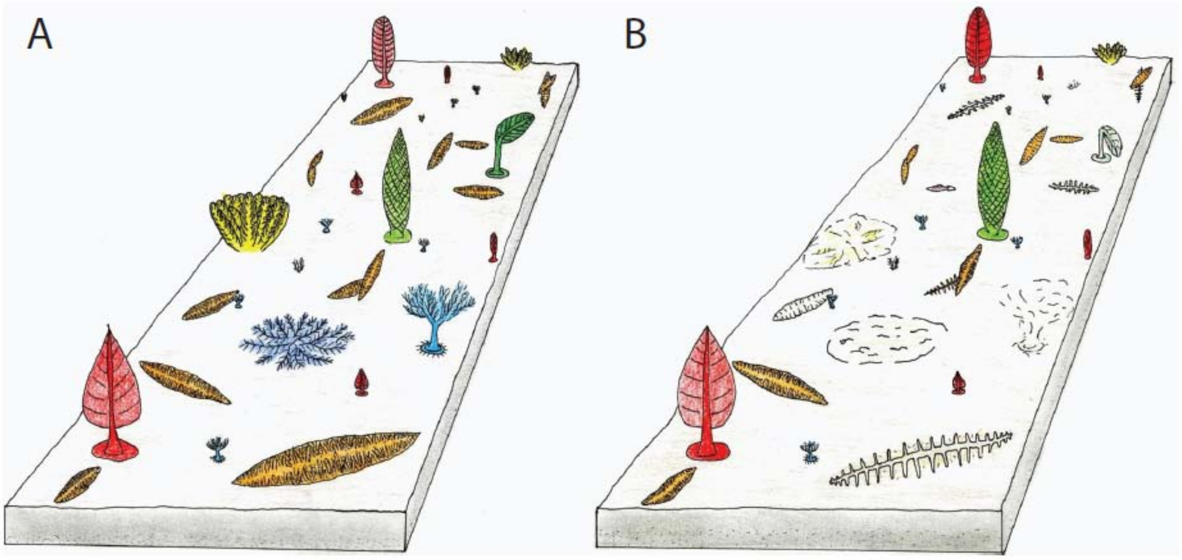

Fig. 5.1. Conceptual diagram showing two alternative possibilities for the original appearance of fossilised Mistaken Point ecosystems. **A**: The established view of all organisms on the surfaces being alive at the time of burial. **B**: The case hypothesised by the effaced preservation hypothesis, whereby many organisms were dead and decaying on the seafloor at the time of burial, resulting in a lower apparent standing population density.

died on the seafloor (Chapter 3), and from experimental work exploring the effects of microbial decay in simulated Ediacaran depositional environments (Chapter 4).

When considered in conjunction with the effaced preservation hypothesis (Chapter 3), it can be argued that Avalonian fossil assemblages preserve ecosystems in which both living (well preserved) and deceased (effaced) soft-bodied organisms can be found preserved together on the seafloor (Fig. 5.1B). That being so, any studies considering these assemblages to represent solely living organisms, and any conclusions drawn from them, are open to question.

METHODOLOGY AND PREDICTIONS

Herein, previous conclusions derived from palaeoecological studies will be reanalysed, considering the Mistaken Point fossil assemblages to represent time-averaged communities (as in Fig. 5.1B), rather than ‘snapshots’ of living communities (e.g. Fig. 5.1A; Clapham et al., 2003). By removing taxa regarded to have been dead at the time of burial from the original Clapham et al. (2003) dataset, it is envisaged that we will be left with a more realistic estimate of the living ‘census’ population. In this way, we hope to determine whether consideration of effaced preservation affects prior interpretations of the ecological structure of these palaeoecosystems. Although it is recognised that a spectrum of preservation of effaced forms exists on Avalonian bedding planes (Chapter 3; Appendix B), in this particular study only the end-members of effacement, the ivesheadiomorphs, will be removed from the previous analyses. This approach has been taken to minimise the degree of subjectivity associated with distinguishing between the various types of effacement in partially degraded specimens. As a result, many specimens of recognisable taxa that can be seen to be poorly preserved and significantly effaced (e.g. Fig. 5.2B) remain in the revised dataset. Subsequently, the revised analyses presented herein will, if anything, underestimate the contribution of taphomorphs to these ecosystems.

Fortunately, the majority of the palaeoecological data obtained by the previous study was published within the original manuscript (Clapham et al., 2003). It has therefore been possible to re-assess many of the structural attributes of the Mistaken Point communities described in Clapham et al. (2003) through re-analysis of their primary data. This re-assessment allows removal of data relating to typical ivesheadiomorphs (termed either *Ivesia* or lobate discs in Clapham et al., 2003). Most importantly, it enables re-calculation of parameters such as species richness, population density, and areal coverage, for all seven beds documented in that study; Bristy (locally referred to as Bristol) Cove, Pigeon Cove (not the same surface as that referred to as Pigeon Cove in Chapter 2), Mistaken Point D, E and G surfaces, Shingle Head, and Lower Mistaken Point. Direct comparisons can therefore be made between results arising from previous studies, and those based upon current assumptions about the taphonomic processes at work on the Mistaken Point bedding planes. Furthermore, the Mistaken Point dataset has recently been re-published (Clapham, 2011, table 1.1), but the newly presented values for total number of fossils on each surface are noted to differ from those in Clapham et al., 2003. Since no explanation is provided for this discrepancy, although the 2011 dataset provides more detailed tallies of individual taxa, the original dataset is utilised herein for consistency.

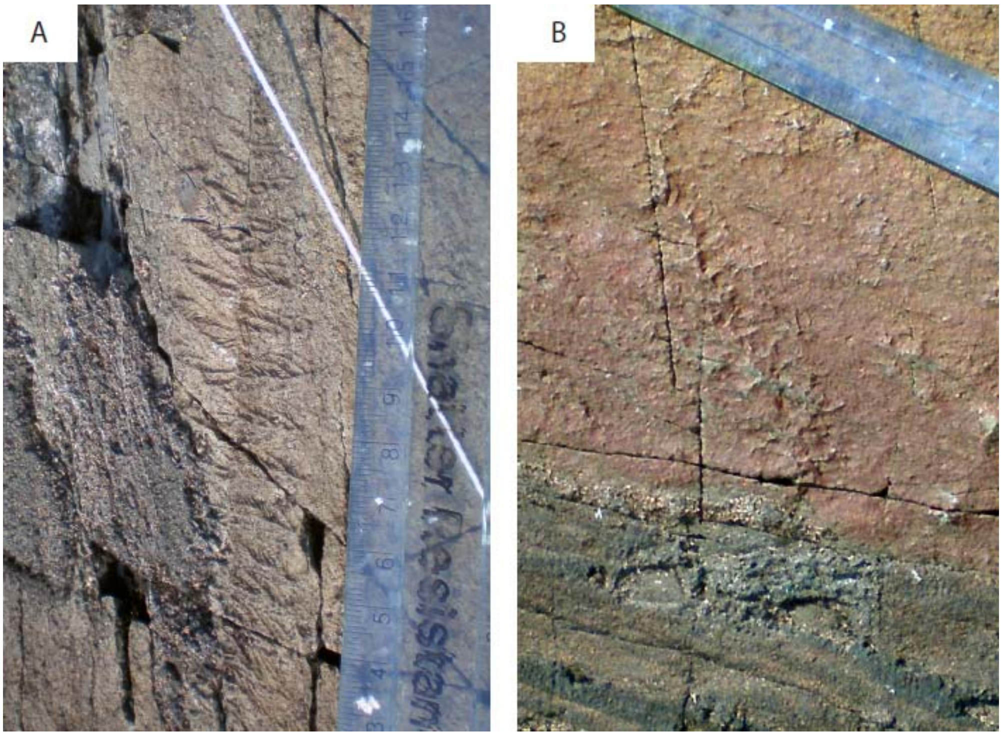

Fig. 5.2. Two contrasting *Fractofusus misrai* specimens from the E Surface of Mistaken Point. **A**: *Fractofusus misrai*, here inferred to have been alive at the time of burial, owing to high fidelity preservation of its rangeomorph branching along the whole length of the organism. **B**: *Fractofusus misrai* specimen considered to have been dead at the time of burial, owing to its incoherent topography and lack of regular internal structure.

It is not expected that the removal of ivesheadiomorph specimens from the dataset will greatly impact the numerical population of the Conception Group assemblages, since ivesheadiomorphs represent a relatively small proportion of the observed specimens (the two ivesheadiomorph taxa together comprise 363 of 7075 individual specimens studied from the bedding plane, just 5%; Clapham et al., 2003; Clapham, 2011). Ivesheadiomorphs do, however, comprise a significant proportion of the areal coverage of the bedding planes (Fig. 5.3), and therefore consideration of effaced preservation is likely to have a significant impact upon estimates of biomass on the seafloor.

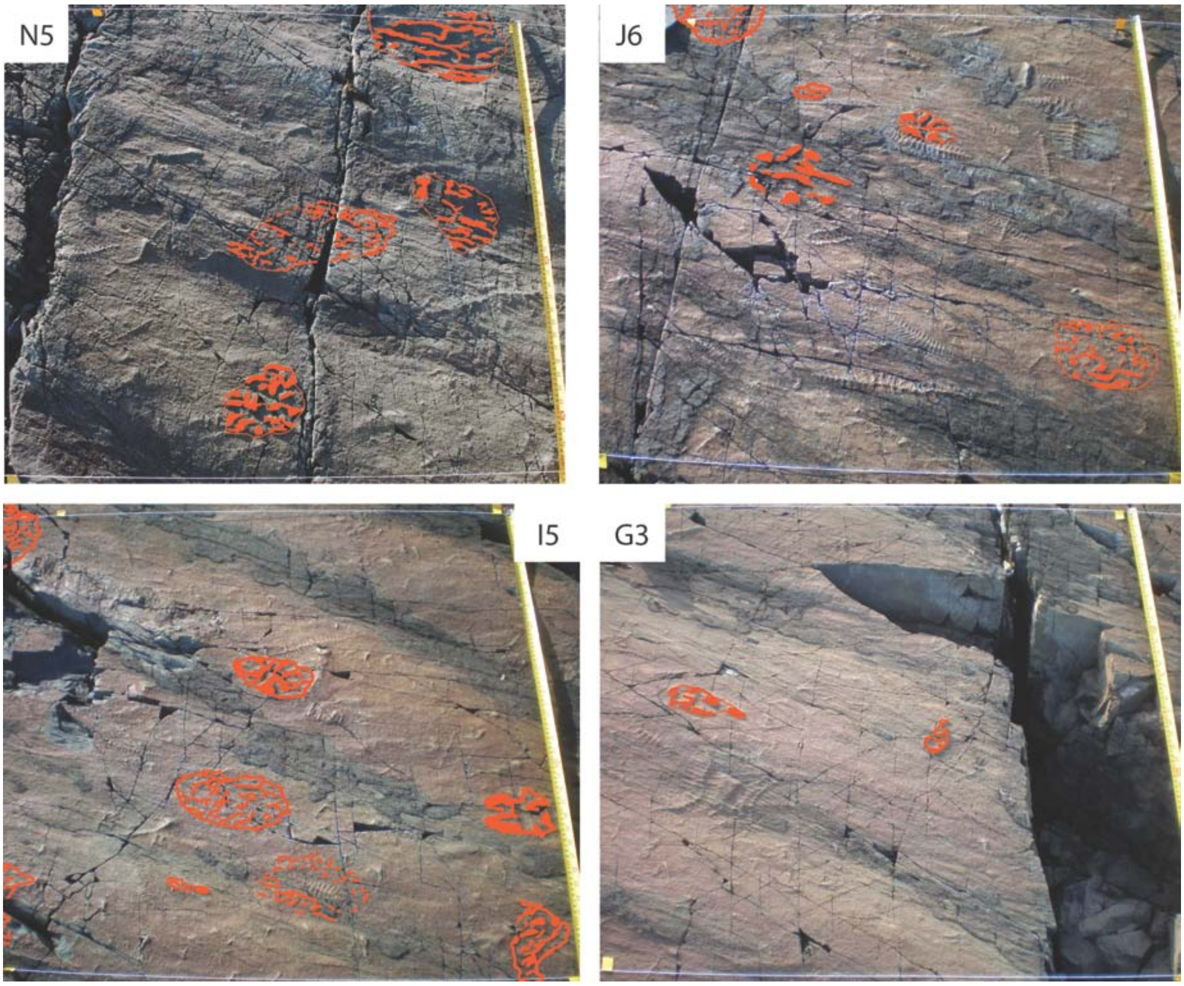

Fig. 5.3. Distributions of ivesheadiomorph structures on the E Surface at Mistaken Point. These images represent a random sample of four 1 x 1 m grid squares from the E Surface, with ivesheadiomorph fossils highlighted in orange. Such specimens are considered to have experienced substantial microbial decay on the seafloor prior to burial, and have therefore been removed from the revised palaeoecological study. The labels N5, J6, I5 and G3 refer to the grid squares in my field-notebook plan of the bedding plane. Note that whilst ivesheadiomorphs do not make up a large proportion of the numerical bedding plane population, they can cover a substantial amount of the area, and therefore indirectly indicate a large volume of necromass on the seafloor.

Ideally, palaeoecological studies of Ediacaran fossil assemblages should focus only on bedding planes exhibiting exceptional quality of preservation (to minimise taphonomic bias); use parameters that are meaningful at the sample sizes available; accurately quantify the basic taxonomic attributes of the assemblages prior to proceeding; and make comparisons with more than one biological group. It is suggested herein that the previous studies of Clapham et al. (2003) may not wholly fulfil these criteria.

VARIABLES AND ASSUMPTIONS

Clapham et al. (2003) measured ecological parameters such as species richness, density, areal coverage, Shannon diversity indices, and single-species spatial patterning for each fossil assemblage. A number of physical and theoretical factors could influence our interpretation of the palaeoecology of the Mistaken Point fossil assemblages. In terms of physical data collection, the quality of preservation is influenced by the amount of ash cover that remains on the bedding planes, as well as by the actions of modern abrasion and weathering. This is particularly evident when comparing bedding surfaces from different stratigraphic levels (Clapham et al., 2003). Within-bed variation is also present, much of which can be attributed to the localised effects of weathering, and even human erosion on some surfaces. This has a significant effect upon the number of small specimens observed, and consequently on perceived population densities, since small delicate forms tend to be preferentially removed by modern erosion (Clapham et al., 2003). The difficulty of accurately identifying small specimens (Chapter 2) is also relevant here, as it arguably impacts upon measured spatial distribution parameters (which are based on nearest neighbour techniques). Other ecosystem parameters, such as species richness and areal coverage, were considered by Clapham et al. (2003) to be relatively robust on the fossil surfaces. That assumption can be challenged, however, if it can be shown that population densities are markedly altered in light of the new effaced preservation taphonomic model (Chapter 3).

Explicit assumptions made by previous studies include: 1) the preservation of census populations; 2) that all preserved organisms are epibenthonic; and 3) there is an absence of post-mortem transportation of fossils or infauna, which would cause mixing of coeval communities (Clapham et al., 2003, p. 530). It is, however, generally accepted that multiple communities can typically be preserved together in most fossil assemblages (e.g. McIlroy, 2004; Tomašových & Kidwell, 2010; McIlroy & Garton, 2010), while time-averaging is suggested to occur in the Ediacara biota through the prolonged presence of necromass on the seafloor (preserved as ivesheadiomorphs; Liu et al., 2011).

The ecosystem structural parameters previously applied to the Mistaken Point fossil assemblages also require that the ‘census’ population is accurate, recording a complete taxonomic inventory for the assemblage. Such taxonomic agreement has not been obtained even now, but in 2003 there was considerable uncertainty surrounding the taxonomy of the Avalonian Ediacara biota. Many specimens in the original study were assigned informal names, possessing no official diagnoses, to resolve the problem of identification (e.g. “duster” or “ostrich feather”; Clapham et al., 2003). While this represented a sensible way to address this problem at the time, numerous new taxa have since been described from the region (e.g. Laflamme et al., 2004; Gehling and Narbonne, 2007; Hofmann et al., 2008; Flude and Narbonne, 2008; Bamforth and Narbonne, 2009; Brasier and Antcliffe, 2009), some of which do not directly correlate with the scheme used to delineate specimens in 2003 (e.g. the “spindle” group in Clapham et al. (2003) incorporates specimens of both *Fractofusus andersoni* and *Fractofusus misrai* Gehling and Narbonne 2007). Furthermore, it is extremely rare for fossil assemblages to preserve 100% of the organisms present within them (e.g. Conway Morris, 1985). Combined with our currently incomplete understanding of general rangeomorph biology, these points all hinder attempts to objectively address the taxonomic diversity of Ediacaran fossil ecosystems, with the result that measurement of proxies such as species richness, ecosystem diversity, and species spatial patterning in Ediacaran assemblages arguably becomes rather inexact.

Finally, the discussion of the Mistaken Point assemblages as benthic "*megafauna*" (e.g. Clapham et al., 2003, p. 540) makes the implicit and non-objective assumption that Mistaken Point organisms comprised a fauna, and therefore constitute animals. While a metazoan biological affinity provides a valid null hypothesis with which to compare the Mistaken Point assemblages, it is not the only possible option. The assertion that the Mistaken Point assemblages contain communities of animals (Clapham et al. 2003) seems to stem from the suggestion that Ediacaran communities possessed a vertically stratified community structure (termed 'tiering'), comparable to that exhibited by more recent animal populations (Clapham and Narbonne, 2002, p. 630). The interpretation of the tiered structure of Ediacaran ecosystems as a characteristic feature of animal-grade organisms has been questioned elsewhere (Sperling et al., 2007), those authors noting that tiering is an ecological response to nutrient collection utilised by heterotrophs, and is not unique to metazoan ecosystems. The Ediacaran literature clearly demonstrates a lack of acceptance for the animal affinities of the Ediacara biota of Avalonia (e.g. Seilacher 1992; Peterson et al. 2003; Grazhdankin & Gerdes 2007; Antcliffe and Brasier 2008; see Chapter 1), and even if metazoans were present in these ecosystems, there exists the distinct possibility that they coexisted with non-metazoan macro-organisms. Alternatively, if the vendobiont hypothesis of Seilacher (1992) is correct, we do not know the 'normal' ranges of ecosystem parameters for vendobiont communities, or their extent of overlap with known animal communities. As such, it is premature to uncritically assume that a fossil assemblage belongs uniquely specific to one biological group, and the approach of comparing palaeoecological parameters from fossil assemblages only with those of animal communities (cf. Clapham et al., 2003), is therefore considered to be of restricted value.

These points demonstrate the limitations of the approach used by Clapham et al. (2003) to investigate Ediacaran palaeoecology. Nevertheless, since several subsequent studies have taken these prior results at face value, it is worth scrutinising the exact parameters utilised in the earlier study to determine their reliability and utility in palaeoecological analysis of Avalonian successions. Such work demonstrates that the applicability of some of the original parameters to Conception Group fossil assemblages (Clapham et al., 2003) can be called into question.

RESULTS

Prior studies maintain that Mistaken Point palaeocommunities exhibit species richness and diversity values that are typical of modern epibenthic communities, and variation in single-species spatial patterning similar to that seen in modern animal communities (Clapham et al., 2003). Those authors argue that Mistaken Point community structure is therefore similar to that of modern slope communities (Clapham et al., 2003). Fresh evaluation of Avalonian taphonomic models allows us to question these assumptions about ecosystem structure, by examining the effects that temporal mixing could have had upon the interpretation of the data.

Species Richness

Species richness is a measure of the number of distinct taxonomic species within a community. While this is relatively easy to calculate in extant ecosystems, application of this parameter to fossil assemblages is affected by several biases, as previously discussed (p.152), and therefore should be interpreted with caution.

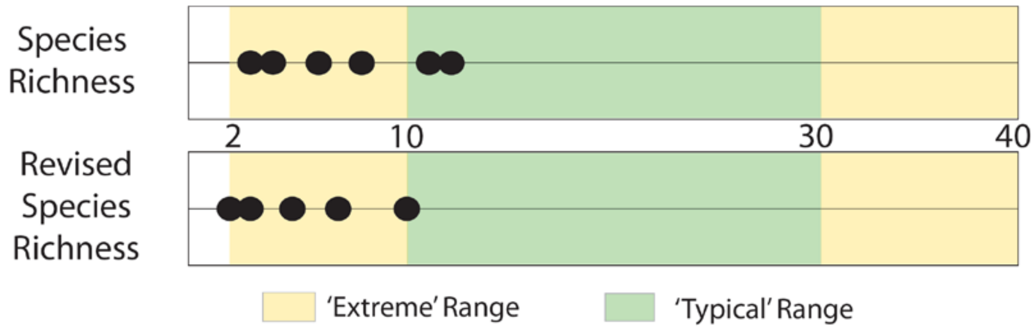

Fig. 5.4. Species richness data for Mistaken Point Ediacaran fossil assemblages, modified from the data of Clapham et al., 2003. **Top**: Data from Clapham et al. (2003, fig. 9). **Bottom**: Species richness values for the communities in which the ivesheadiomorph 'species' have been removed. The green box represents the 'typical' range of values for modern epibenthic marine communities, while the yellow boxes delineate the 'extreme' range. The 'typical' and 'extreme' terminology is not defined in the original study. Furthermore, the bounding values appear to be simply arbitrary, summarising the patterns observed in four studies of extant slope communities cited in Clapham et al., 2003. Note that all revised values fall outside the 'typical' range, *contra* Clapham et al., 2003. Original and revised values for each locality are presented in Appendix F1.

Values for species richness, based on the published data of Clapham et al. (2003), are here recalculated and shown in Figure 5.4 (lower figure). These new results reveal that, for at least six of the seven studied beds, species richness decreases by one or two taxa when ivesheadiomorph fossils (*Ivesia* and lobate discs) are omitted from the original census. Revised species richness values fall to between two and ten species for the seven bedding planes studied at Mistaken Point (Fig. 5.4). Consequently, bedding plane assemblages from the Conception Group no longer fall within the 'typical' range for modern slope species richness (*contra* Clapham et al., 2003), although they all still lie within the 'extreme' range (Fig. 5.4). Removal of the ivesheadiomorph taxa from the census data also decreases the total number of (presumed) living organisms in individual communities by as much as 32.8% (this value is for Pigeon Cove; other beds see falls of up to 7.9%; Appendix F1). However, given the youthful state of Avalonian taxonomy at the time the original study was completed, true diversity is likely to have been greater than has been measured herein.

Population density

Densities of fossils on the bedding surfaces were taken by Clapham et al. (2003) to represent original Ediacaran population densities on the seafloor. Recalculations in light of our taphonomic models (Chapter 3) show that these densities mostly fall by 1–2 individuals per m^2 (ind./m^2), though again the values for Pigeon Cove remain anomalous, with a decrease from 14.3 ind./m^2 to 9.6 ind./m^2 (Fig. 5.5). This sees four Mistaken Point assemblages sit comfortably within the 'typical' modern range of epibenthic communities, and two in the lowermost 'extreme' range (Fig. 5.5). The high outlier value of Bristy Cove (147 ind./m^2) remains (Fig. 5.5). Subsequently, consideration of the most effaced taphomorphs (true ivesheadiomorphs) is not considered to significantly affect Mistaken Point population densities. Of more interest is the fact that primary observations made on the E Surface show that for areas of the surface possessing high quality preservation (e.g. all of the grid squares

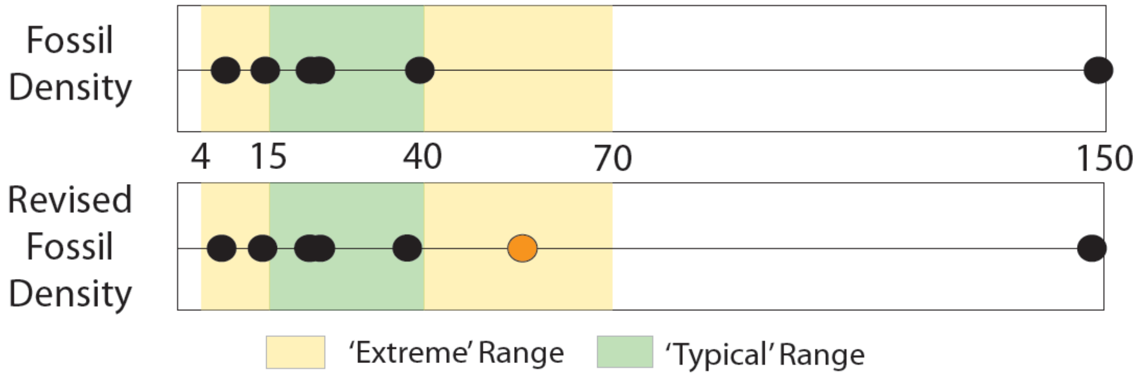

Fig. 5.5. Population density data for Mistaken Point Ediacaran assemblages, modified from Clapham et al., 2003, fig. 9. Values are all individuals/m^2. **Top**: Data from Clapham et al. (2003) study. **Bottom**: Fossil density data revised to incorporate the effaced preservation hypothesis. Note that Bristy Cove is an extreme outlier. Also note that the value for the E surface presented in Clapham et al. (2003) is an average of all the E surface outcrops. The average value for the best preserved section of that surface (E surface East) is presented as an orange point, and is significantly higher than the overall average (and well outside the 'typical range'). See Appendix F1 for data.

figured in Fig. 5.3), population densities of non-ivesheadiomorph organisms are consistently above 45 ind./m^2. This is higher than the E Surface average documented by Clapham et al. (2003; 39.7 ind./m^2), and also lies outside the ‘typical’ range of epibenthic animal communities (Fig. 5.5, orange circle).

Crucially, the two beds showing the highest fossil densities in the Clapham study (beds BC and E; Appendix F1) also exhibit the best resolution of preserved features (≤ 0.5 mm; Clapham et al., 2003). Assuming that the beds showing the best preservation are most likely to accurately reflect the true composition of the communities growing upon them (since they will preserve a greater proportion of the standing community when compared to beds that only preserve large features), this observation of extreme population densities becomes increasingly important to address. Intriguingly, it was noted in the original study that where E surface preservation is best, densities of 50–150 individuals per m^2 are obtained, a range that is significantly higher than is seen in animal communities on modern continental slopes (Clapham et al., 2003, p. 541). This large value is not included in the original density figure (Clapham et al., 2003, fig. 9), with an average value for the whole surface across all its outcrops used instead. The decision not to address these high density values permitted those authors to claim that Mistaken Point fossil densities fall within ranges typical of modern animal communities (Clapham et al., 2003), whereas in reality, the data is not quite so compelling. Population densities well above those seen in modern animal communities argue against a solely animal-based community composition.

Areal coverage and necromass

By calculating the percentage of areal cover (used as a crude proxy for biomass in Clapham et al., 2003) occupied by ivesheadiomorphs on the Mistaken Point bedding planes, and removing this from the ‘biomass’ dataset, the abundance of necromass on the Ediacaran seafloor can be observed. The term necromass is widely used to describe the mass of dead and decaying organic matter in floral ecosystems (e.g. Chapman and Grey, 1986; Palace et al., 2008). It is yet to become commonplace in the marine literature, but does make occasional appearances (e.g. Taylor and Wilson, 2003), particularly in the description of bacterial communities (Parkes et al., 2000).

Areal coverage falls by up to 75% on individual horizons when those fossils considered to have been deceased at the time of burial (the ivesheadiomorphs) are removed. On the E surface, areal coverage almost halves, from 12.4% to 6.6% (Fig. 5.3). Pigeon Cove and Shingle Head also see >60% reductions. Put another way, it can be argued that the areal coverage of dead and decaying tissue (necromass) comprises between 4.7 and 76.4% of the ‘biomass’ preserved in these studied assemblages. The substantial variation in areal coverage between populations is here inferred to result from a combination of the maturity of the ecosystems, environmental conditions, and taphonomic factors. That these figures can be so high suggests that necromass may have been a prominent and important facet of Avalonian ecosystems.

Shannon diversity indices

The Shannon diversity index (Shannon, 1948) measures the diversity and evenness of a population, and 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

Assemblages from four bedding planes were found by Clapham et al. (2003) to fall within the ‘typical’ range of values for modern animal communities (Fig. 5.6). Unfortunately, it is not possible to recalculate Shannon diversity indices for the surfaces studied by those authors, since that would require knowledge of the total number of individuals of every species present on each studied bed. While this information is now available (Clapham, 2011), such an endeavour will not be undertaken, since it can be shown that use of the Shannon diversity index to infer the biological affinity of a fossil community is highly questionable.

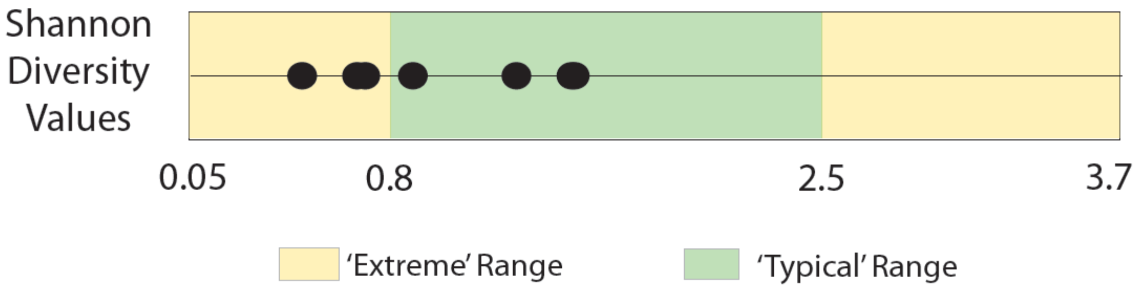

Fig. 5.6. Shannon diversity index values for Mistaken Point Ediacaran communities, figure redrawn from Clapham et al., 2003, fig. 9.

The range of Shannon diversity values stated to characterise modern marine benthic communities (0.05–3.7 = extreme, 0.8–2.5 = typical; Fig. 5.6) encompasses the vast majority of values that one might expect to obtain from any community with a species richness of <30, regardless of the biological affinities of its constituent organisms (Appendix F2). The maximum possible Shannon diversity value in a given community cannot possibly exceed the ‘typical’ range proposed for modern animal ecosystems unless the species richness of the community is ≥13, since the maximum possible Shannon value, H'_{max}, can be shown to equal the natural logarithm of the species richness (i.e. $H'_{max} = \ln S$; Appendix F2). Even then, the population would require maximum evenness. The relevance of this maximum value to communities with low species richness (such as the Mistaken Point localities, which all possess a species richness of <12 in the original study; Fig. 5.4), is therefore severely limited.

The Shannon Index is helpful when making comparisons between known extant biological groups of organisms, but multiple modern groups should be considered when applying it to extinct communities, and the limitations of the methodology should be detailed in full. Shannon index values do not demonstrate that the Mistaken Point assemblages contained animals. They merely show that the fossil assemblages show inherent ecological and/or preservational patchiness.

Spatial distributions

Single-species spatial patterning attempts to elicit any consistent patterns in the distribution of individual taxa on a bedding plane. For the Mistaken Point biota, these patterns have previously been summarised as random patterns being most common (9 occurrences), with aggregated (8; more nearest neighbours than expected) and regular (3; fewer nearest neighbours than expected) patterns less so (Clapham et al., 2003). Only two taxa were found to show consistent patterns across multiple surfaces (Clapham et al., 2003). When the original data (Clapham et al., 2003, table 3) is examined, it becomes apparent that in most cases the quantity of data is insufficient to adequately assess single species spatial patterning. No taxon displays measurable single species patterns from more than three beds. It is therefore debatable as to whether such a small sample size can truly be considered representative of the population, and thus be considered statistically significant (cf. Hammer and Harper, 2006).

In addition, even in the original publication there are conflicting views as to the ways in which the Mistaken Point communities compare with spatial distributions in modern communities. Both random and aggregated/regular single-species spatial patterning can be dominant in modern slope animal communities (Clapham et al., 2003). The same authors then state that Mistaken Point displays "*similar levels of single-species spatial patterning* [to modern marine benthic communities]" (Clapham et al., 2003, p. 541). If modern communities show a range of different patterns, none of which have been proven to be typical of animal-dominated community structure, similar variation in spatial patterning in a fossil ecosystem cannot and should not be taken as indicative of animal ecosystems. Such variation could conceivably be a feature of any biological group or combination of biological groups. Comparison of multiple ecological parameters with data from many extant biological groups is considered necessary before we can use such methods to meaningfully conclude the biological affinities of the Ediacaran, or indeed any, biota.

IMPLICATIONS FOR EDIACARAN PALAEOECOLOGY

It has been posited that similarity between the inferred ecological structure of Conception Group fossil assemblages and modern faunal communities can be used to support a metazoan biological affinity for the Ediacara biota (Clapham et al., 2003). The methods used to assess Mistaken Point palaeoecology in previous studies were, however, governed by prior assumptions about the metazoan affinities of the preserved organisms (as evidenced by comparison of Mistaken Point data only to modern metazoan epibenthic communities; Clapham et al., 2003). This work demonstrates that previously identified similarities between fossil and modern data are either not definitively unique to any one biological group, or no longer hold true once the presence of time-averaging in the fossil assemblages is considered. The use of palaeoecological inferences to support a metazoan interpretation for the Ediacara biota is thus found to be poorly grounded at present.

Reconsideration of the Mistaken Point assemblages in light of new taphonomic understanding (Liu et al., 2011) suggests that they do not fall consistently within the typical range of species richness for extant animal communities (Fig. 5.4), though there are limitations to this parameter in that the original species-richness values may not be representative of true taxonomic diversity on the surfaces. The Shannon diversity index is found to be incapable of determining whether an ecosystem possessed a particular grade of organism (be it animal, plant or other). This is particularly true for assemblages with low taxonomic diversity. Observed spatial distributions of fronds in Conception Group assemblages have not been demonstrated to be indicative of any one specific biological community structure. Furthermore, fossil densities on the best preserved beds are commonly found to have been significantly higher than the densities observed in typical modern epibenthic marine communities (Fig. 5.5). These findings challenge the views of Clapham et al. (2003), who argue that the Mistaken Point communities were animals by virtue of a similar ecological community structure. Conversely, the community structures of Mistaken Point and modern animal assemblages are found to differ substantially in several aspects. As a result, it is considered that future comparison of living and fossil biological communities in this way should 1) consider other modern biological groups as null hypotheses for testing; 2) utilise a complete and taxonomically accurate dataset for the fossil assemblage; and 3) apply only palaeoecological parameters that are suitable for measuring the fossil assemblage under consideration.

Finally, it is shown that up to ~76% of the biomass previously inferred to have been present in the Mistaken Point ecosystems (Clapham et al., 2003) was instead likely to have been necromass. This would imply that ambient conditions on the Avalonian seafloor were considerably more fœtid than previously considered, with a large microbial resource of dead and decaying organic matter present in these deep marine environments.

CONCLUSION

A significant degree of caution should be exercised when applying parameters used to measure community structure in modern ecosystems to fossil assemblages. All taphonomic, ecological and taxonomic biases and variables should be stated, and ideally a judgement on the reliability of both the dataset and the interpretations should be provided. When making comparisons with modern ecosystems, rather than choosing specific comparative groups to test expected conclusions, consideration of multiple different modern groups should be a standard criterion.

It might be possible to obtain greater success by approaching the question of Ediacaran palaeoecology from a community interaction perspective. By determining the ways in which different fossil organisms appear to interact with one another on the bedding planes, both spatially and temporally, information about community structure can be obtained independently of time-averaging biases. Similarly, by studying evidence for behaviour in fossil assemblages, we may be able to extract information about the biological affinities of specific taxa or components within the ecosystem, without the need for multiple assumptions regarding the ecology, taphonomy and taxonomy of Ediacaran depositional environments (as in Chapter 6).

The recognition of ivesheadiomorph fossils as the remains of decaying deceased organisms has a number of implications for the validity of pre-existing palaeoecological and palaeobiological models:

1) Conception Group assemblages do not represent snapshots of exclusively living communities. Instead, they represent time-averaged assemblages, containing the remains of both living and deceased organisms at the time of burial.

2) Amounts of biomass on the Ediacaran seafloor were likely to have been significantly lower than previously suggested.
3) Substantial volumes of necromass (dead and decaying Ediacaran organisms) could have existed, and persisted, on the seafloor in Ediacaran benthic ecosystems.
4) Previous ecological studies, attempted before the incorporation of taphonomic analyses, have given rise to questionable assertions that ecological structure of the communities was similar to that of modern animal communities.

It is herein recommended that the assignment of a metazoan grade of organization for the Mistaken Point Ediacara biota as a whole, based upon perceived similarities between fossil and modern community structural attributes, should be regarded as premature. Our understanding of taphonomic and palaeobiological processes must be sound before such ecological analyses can be meaningfully undertaken.

ACKNOWLEDGEMENTS

Jack Matthews is thanked for assistance in the field, while the Parks and Natural Areas Division, Department of Environment and Conservation, Government of Newfoundland and Labrador provided permits to conduct research within the Mistaken Point Ecological Reserve in the summers of 2008 and 2009. The patience of the interpreters from the Portugal Cove South Visitor Centre while I conducted my research was appreciated.

CHAPTER 6

EVIDENCE FOR METAZOAN LOCOMOTION IN THE EDIACARAN ROCKS OF AVALONIA

PREFACE

Evidence for locomotion has never previously been documented from the Ediacaran Conception Group of the Avalon region. The discovery of trace fossils at Mistaken Point in Newfoundland is therefore of considerable significance in the field of Precambrian palaeontological research. The trace fossils described herein provide indirect evidence for the presence of muscular tissue in at least some of the organisms inhabiting the Avalonian marine basins, implying the existence of metazoans ~20 Myrs prior to the Cambrian Period.

The trace fossil assemblage was discovered whilst surveying the bedding planes of Mistaken Point in the summer of 2008. The find was written up as a short paper with Martin Brasier and Duncan McIlroy, and published in February 2010 in the journal *Geology*, under the title *"First evidence for locomotion in the Ediacara biota from the 565Ma Mistaken Point Formation, Newfoundland"*. A Comment, relating to this study, was submitted by Dr. Greg Retallack of the University of Oregon, who queried both the deep-water environmental setting of the assemblage, and the biogenicity of the traces. We responded with a Reply, restating our opinions that the depositional environment at Mistaken Point was unequivocally deep-marine, and the fossil traces were biogenic. Both Comment and Reply were published online by *Geology* in October 2010.

This chapter brings together our two *Geology* papers, describing the trace fossil assemblage in more depth than was possible in the original publications, and discussing the biological and abiological processes that could explain its formation. Additional unpublished material, documenting further examples of Ediacaran trace fossils in the Avalon successions, is also included. The chapter closes by discussing the importance of this discovery for Ediacaran palaeontology and palaeoecology.

ABSTRACT

Evidence for locomotion in the Precambrian fossil record is scant. Previously, reliable Ediacaran trace fossils have all proved younger than 560 million years in age, and consist of relatively simple horizontal burrows and trails from shallow-water deposits. Herein, an assemblage of macroscopic locomotory traces from deep-water environments at Mistaken Point, dated to ~565Ma, is described. These trails extend the record of horizontal ornamented trace fossils back into the Avalonian biotic assemblage. Evidence for locomotion from younger Avalonian successions in both Newfoundland and the U.K. is also discussed, demonstrating that such behaviour is not as rare as previously considered. This new evidence for macroscopic motile organisms on the seafloor suggests that at least some of the first Ediacaran macro-organisms, whose biological affinities are widely debated, could have possessed muscular tissue and been of metazoan grade.

INTRODUCTION

Traces of animal activity are critical for our understanding of organism-sediment interactions in the geological record (McIlroy and Logan, 1999; McIlroy, 2004). Although it is only in rare circumstances that the trace-making organism can be determined directly, trace fossils remain invaluable as a means of documenting the evolution of behaviour (e.g. Fedonkin, 2003). The trace fossil record is mainly confined to the Phanerozoic Eon, largely because complex organisms capable of actively perturbing sediments are required to create them. Even so, Proterozoic trace fossils do exist. Potential Pre-Ediacaran traces documented in the literature (e.g. Kauffman and Steidtmann, 1981; Seilacher et al., 1998; Bengtson et al., 2007), are not widely considered to be the traces of metazoans. The recent discovery that modern protozoans (gromiid foraminifera) can locomote and create traces (Buchanan and Hedley, 1960; Matz et al., 2008) provides an alternative interpretation for both early Proterozoic impressions, and many purported trace fossils described from the Ediacaran Period itself.

Recent reviews of presumed Ediacaran traces have determined that only a few simple burrow makers were present (Seilacher et al., 2005; Jensen et al., 2006). Ediacaran ichnofossils generally occur in shallow-marine environments (Seilacher et al., 2005; Droser et al., 2006) of ~560 Ma or younger, and are thought to have been produced by early bilaterians (Jensen et al., 2006). The ‘White Sea’ assemblages of Russia and South Australia (~555Ma; Martin et al., 2000) reveal questionable markings related to the body fossils *Yorgia* and *Dickinsonia* (Ivantsov and Malakhovskaya, 2002; Fedonkin, 2003; Gehling et al., 2005; McIlroy et al., 2009; Sperling and Vinther, 2010), along with scratch marks associated with *Kimberella*, interpreted as the possible feeding traces of a mollusc-like organism (Seilacher et al., 2003, 2005). These examples, along with several forms from Siberia (see Fedonkin et al., 2007a and references therein), suggest the presence of a diverse array of animals by ~550 Ma (e.g. Fedonkin et al., 2007b). Hitherto, reliable evidence for trace fossils from the oldest

Ediacaran macrofossil-bearing successions (from Avalonia), some 575–560 Ma, has been lacking (Gehling et al., 2000; Jensen et al., 2006).

The scarcity of trace fossils in the Avalon assemblage has been used to suggest that its organisms were sessile, and incapable of escaping smothering ash falls and turbidity currents (Narbonne, 1998; Peterson et al., 2003), a conclusion that potentially sits at odds with interpretations of Ediacaran organisms as early or stem group metazoans (cf. Narbonne, 2005, 2010). Consequently, this has led to serious consideration of a diverse range of sessile biological organisms as candidates for the Ediacara biota, including algae (Ford, 1958), lichens (Retallack, 1994), fungi (Peterson et al., 2003), sessile metazoans (Clapham et al., 2003), microbial colonies (Grazhdankin and Gerdes, 2007), and entirely extinct phyla (Seilacher, 1992). The discovery of macroscopic traces consistent with locomotion along the sediment-water interface from the Mistaken Point Formation of Newfoundland is therefore of considerable importance, and is described herein. These traces suggest that the Avalonian benthos may have included rare ancestors of early animals at 565 Ma.

THE MISTAKEN POINT TRAIL BED

Whilst undertaking a survey of the fossil-bearing beds of Mistaken Point, an assemblage of surface trace fossils was discovered by the author. The trace-bearing bed (MP4 of Appendix D) is located on the southern side of Mistaken Point, within the uppermost Mistaken Point Formation, on the Avalon Peninsula of Newfoundland (Fig. 6.1). Mistaken Point was first brought to the attention of palaeontologists in the 1960s (Anderson and Misra, 1968; Misra, 1969). The site is famous for its spectacular preservation of rangeomorphs, yielding up to 30 distinct Ediacaran body fossil taxa on hundreds of bedding planes (Narbonne et al., 2007).

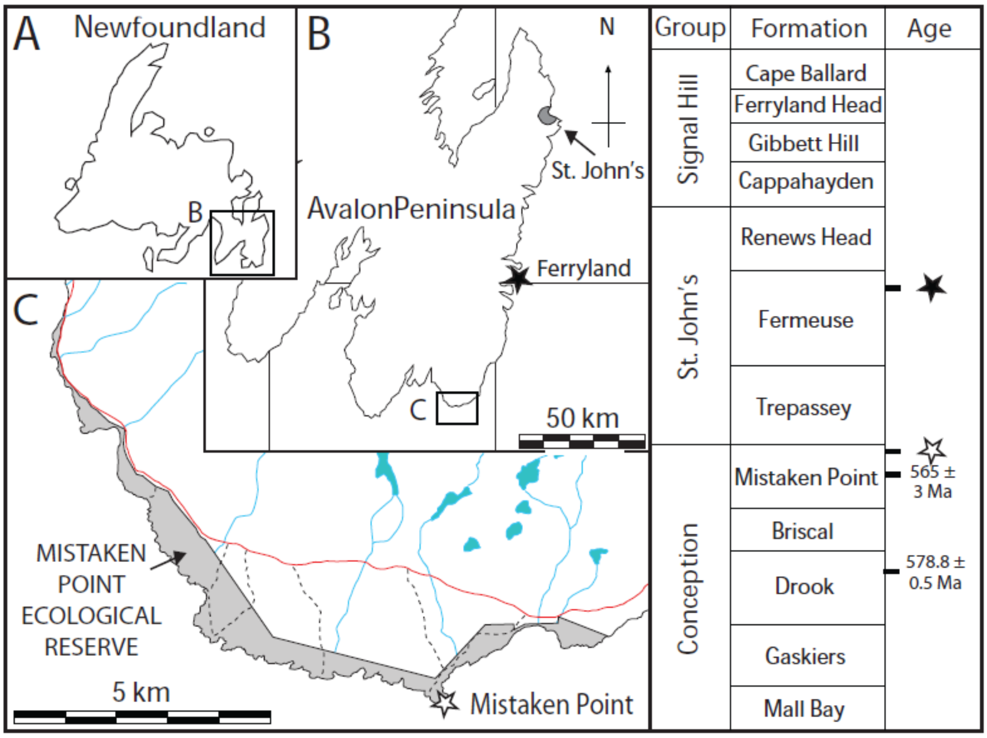

Fig. 6.1. A map and stratigraphic column indicating the location of the trace-bearing bed (MP4; following Liu et al., 2010a, fig. 1). Stratigraphic column not to scale. **A**: Newfoundland, eastern Canada. **B**: The Avalon Peninsula of south-eastern Newfoundland. **C**: The Mistaken Point Ecological Reserve (MPER). The Mistaken Point trail bed is represented by the white star on the southern side of Mistaken Point itself, and is located at N: 46° 37’ 33.1”, W: 053° 09’ 45.3” (bed MP4 in Appendix D). The black star represents the location and stratigraphic position of the possible traces from the Fermeuse Formation of Ferryland (see Fig. 6.10). Dates are taken from Benus (1988), and Van Kranendonk et al. (2008).

The traces are found on a narrow ledge some 53 m stratigraphically above the famous ‘E’ surface (itself dated at 565 ± 3 Ma; Benus, 1988; Fig. 3.1), within massive turbidites close to the base of the overlying Trepassey Formation. The trace-bearing bed sits above an 18 cm-thick, fining-upwards, siltstone to mudstone turbidite bed, which clearly exhibits the T_a, T_c, T_d and T_e components of the turbidite facies model (Bouma, 1962; Fig. 6.2). Cross-bedding within the T_c component indicates a southerly flow direction, broadly consistent with the south-easterly turbidity-current directions obtained from other Mistaken Point Formation beds within the MPER (Narbonne et al., 2005). Unit T_e of the fossil-bearing bed (here consisting of turbiditic muds), displays at its top a 3 mm-thick greenish mudstone, interpreted to be a

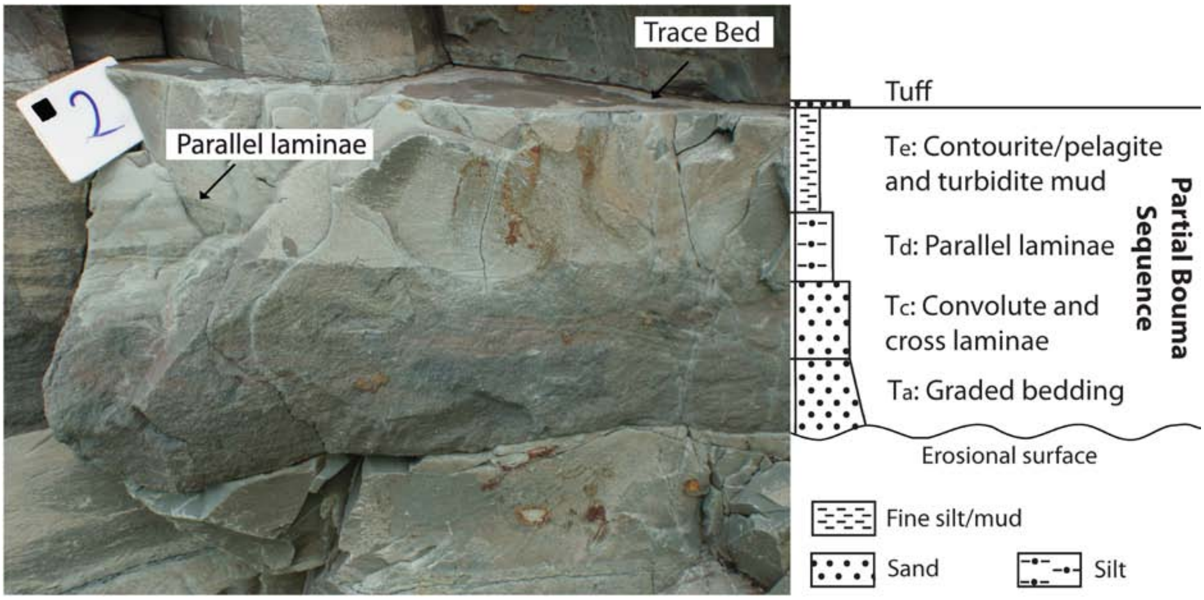

Fig. 6.2. Sedimentology of the trace bearing bed, looking NNE. The traces lie directly above what is interpreted to be a turbidite, here labelled according to the terminology of Bouma (1962), and below a coarse grained pyritic tuff (visible as a thin brown layer covering the bedding surface). Black square on the plastic card is 10 x 10 mm.

contourite deposit (cf. Stow and Piper, 1984), with the traces lying on its upper surface (Fig. 6.2). The bed is capped by 1 mm of coarse-grained brown tuff. This is thought to be either a primary or a reworked water-lain tuff, and is itself overlain by a 12 cm-thick turbidite. The tuff contains numerous oxidised secondary anhedral pyrite crystals, up to 2 mm in diameter (Fig. 6.3B, arrowed). Modern weathering of the relatively soft tuff has revealed the fossiliferous bedding plane. The total exposed area of the trace-fossil bearing surface is roughly two square metres, significantly smaller than that of the extensive fossiliferous bedding planes surrounding it (e.g. the E Surface mentioned in previous chapters, which has an area of ~131 m^2).

Although early publications favoured a shallow marine interpretation for the environment of deposition (Misra, 1971), all subsequent sedimentologically-focused studies of the Mistaken

Point Formation have inferred deep-water turbidite or contourite depositional mechanisms (e.g. Narbonne et al., 2001; Wood et al., 2003; Ichaso et al., 2007). The depositional environment is interpreted to have been a deep-marine (>1 km depth) slope, within a fore-arc basin, adjacent to volcanically active centres (Wood et al., 2003; Ichaso et al., 2007). The preservation of partial Bouma sequences alone is not evidence of deep marine palaeoenvironments; turbidite-like waning flows are well known in prodelta, shoreface, and lacustrine successions (e.g. Dyni and Hawkins, 1981; Nelson, 1982; Pattison, 2005). However, the presence of a >2000 m thick succession of turbiditic strata (Narbonne et al., 2005), without evidence for intercalations of demonstrably shallow-marine textures or sedimentary structures (e.g. wave ripples, dessication cracks), or current re-working, argues against a shallow marine turbidite interpretation. The prevalence of palaeocurrents showing co-axial palaeoflow directions parallel to the inferred basin margin (Wood et al., 2003) also supports this assertion. Therefore, although the precise depth of deposition remains a matter of debate, and these traces themselves have even been used to argue a very shallow depositional environment (Retallack, 2010), we are confident that the deep water interpretation of the Mistaken Point Formation is secure (Liu et al., 2010b).

Impressions on the bedding plane are preserved as positive or negative epirelief casts and moulds, smothered beneath water-lain volcanic ashfalls. Rapid lithification of the overlying ash is thought to be responsible for the preservation of the fossils beneath (see Liu et al., 2011, and references therein). This is consistent with the Conception-type preservation of body fossils seen in adjacent beds (Narbonne, 2005; Chapter 3), implying that the general taphonomic conditions acting upon this bed were similar to those seen throughout the Mistaken Point Formation.

DESCRIPTION OF THE TRACES

The trace-bearing horizon has been mapped in order to document all potential biological impressions (Appendix C). Casts of the most interesting sections are housed in the Oxford University Museum of Natural History under accession numbers OUM ÁT.418/p to OUM ÁT.423/p. Eighty four potential traces were recorded, ranging from 15–172 mm in length, and 1–13 mm in width. Almost all traces consist of a negative epirelief groove running along the surface of the sediment, bounded by positive epirelief marginal ridges (Figs. 6.3, 6.4C–E).

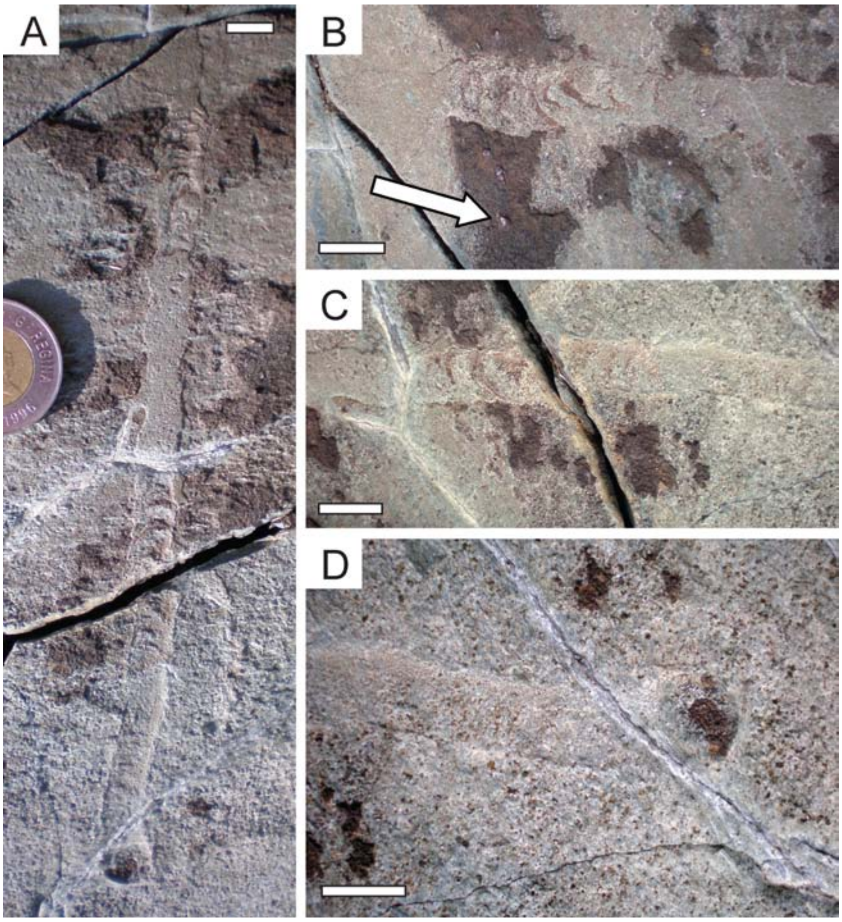

Fig. 6.3. Locomotion trace from Mistaken Point Formation, Newfoundland. Image shows top surface of the bedding plane. **A**: Largest observed trail in the assemblage. **B–D**: Close-up images of positive epirelief crescentic internal divisions in the specimen figured in part A. **B**: Distal end of trail. Note pyrite crystals embedded in ash surrounding the trail (arrowed). **C**: Central section of trail. **D**: Proximal section of trail with terminal circular impression. A cast of this specimen is housed in Oxford University Museum of Natural History (OUM ÁT.418/p). The original specimen remains *in situ* at the site. Scale bars = 10 mm.

Such ridges provide key evidence for movement of an object along the surface of the sediment (Jensen et al., 2005, 2006), and can be used to distinguish trace fossils from abiogenic structures such as synaeresis and desiccation cracks, which lack such features (Parizot et al., 2005). The traces show neither branching nor any systematic increase in width (the width of the largest example varies along its length from 9 to 13 mm; Fig. 6.3A).

Fig. 6.4. Locomotion traces and circular pits on the upper surface of the bedding plane, Mistaken Point Formation, Newfoundland. **A–B**: Isolated circular pits, unrelated to traces. **C**: A trace (arrowed), gently curving but with clear marginal ridges. Traces can curve by as much as 60°–70°. **D**: Two traces (arrowed), one (left) strongly curving, the other ends in a disc (top right). Cast OUM ÁT 423/p. **E**: Three individual traces, exhibiting positive marginal ridges and transverse crescentic internal structure. Specimens in B and E can be found on cast OUM ÁT.419/p. The original specimens remain *in situ* at the site. Scale bars = 10 mm.

Twenty nine of the traces show evidence of internal structure in the form of raised transverse ridges of siltstone (e.g. Fig. 6.5B, D). These transverse internal ridges are most commonly crescentic in shape, extending along the length of the impression at intervals of ~1 mm. At the distal end of several specimens, a negative circular impression (of a diameter equal to the width of the corresponding trace) can also be seen (Figs. 6.3D, 6.4D, 6.5B, D–E). Where these traces also have crescentic internal structure, the concave edge consistently faces the terminal disc. This implies that the disc represents the terminal impression of the trace maker, with the crescents being the impressions left by the posterior edge of the object as it moved over the sediment (with anterior impressions being removed by each subsequent movement). There is no evidence to suggest any preferred orientation of the trails, which can be either straight or gently curved (Figs. 6.4C–D, 6.5, 6.6). When only those traces with internal structures are considered, the axial orientations of the trails on the surface are distributed in all directions (Fig. 6.6A–B), and not seemingly associated with the orientation of tectonic compression (as evidenced by the discs shown in Fig. 6.6C). It does, however, seem that several non-ornamented traces are aligned with the direction of tectonic strain (Fig. 6.6B–C), and could therefore be abiogenic. Some specimens have portions with smooth, positive-relief regions. In the largest specimen, the circular impression and the proximal half of the trace are preserved in negative relief, while the ridges of the crescentic features within the trace are preserved in positive relief. More distally, however, the trace becomes smoother (with no ridges or troughs) with positive epirelief preservation (Fig. 6.3).

Impressions possessing neither internal ornament nor terminal discs (e.g. Fig. 6.5A, C) are also present on the surface. Such impressions commonly consist of individual negative-relief troughs running along the bedding plane, up to 100 mm in length and 14 mm in width (though mostly ≤ 4 mm wide). Marginal positive epirelief ridges of sediment are present in about 50% of such specimens, but there is no evidence for ridges of sediment within the groove of the impression. A handful of impressions are preserved entirely in positive epirelief, but their relationship to the more complex trails is currently unclear. The trails are distributed along

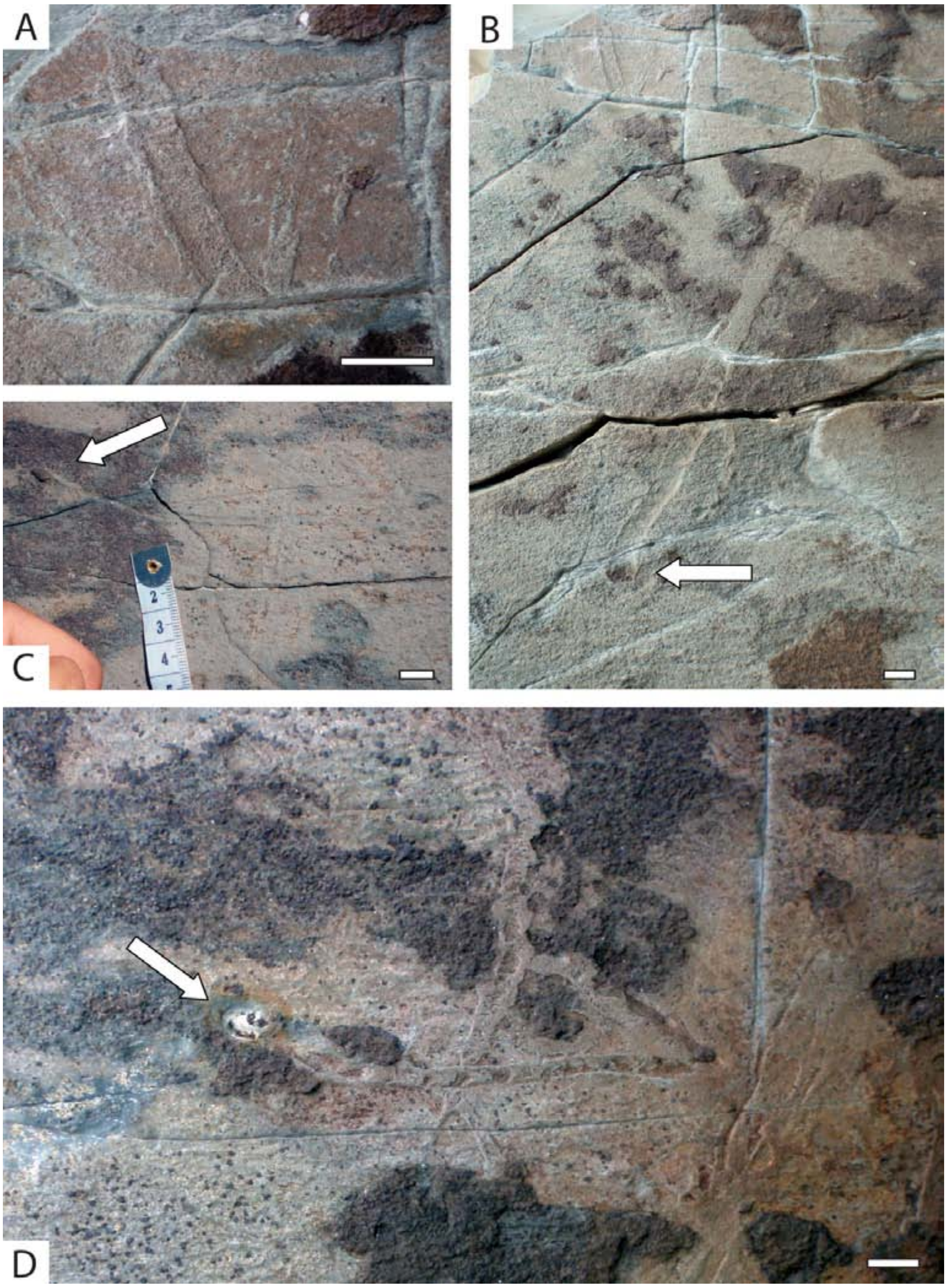

Fig. 6.5. A selection of trace fossils from the upper Mistaken Point Formation, Mistaken Point, Newfoundland. **A**: Two traces lacking internal structure. **B**: The longest trace on the bedding plane, showing transverse hemispheric ridges running down its length, and ending in a terminal negative-relief disc (arrowed). Specimens in A and B can be found on cast OUM ÁT 418/p. **C**: Two simple traces exhibiting cross-cutting relationships, the horizontal one ending in a terminal disc (arrowed). Cast OUM ÁT 421/p. **D**: A series of at least four traces, clearly showing several directions of movement, and cross-cutting relationships. Cast OUM ÁT 421/p. One shows a prominent pit at its end (arrowed). All scale bars = 10 mm.

the entire length of the exposed ledge, and in places they occasionally cluster. Where they interact, it is clear that the traces cut across one another (Fig. 6.5C–D), and neither branch nor bifurcate.

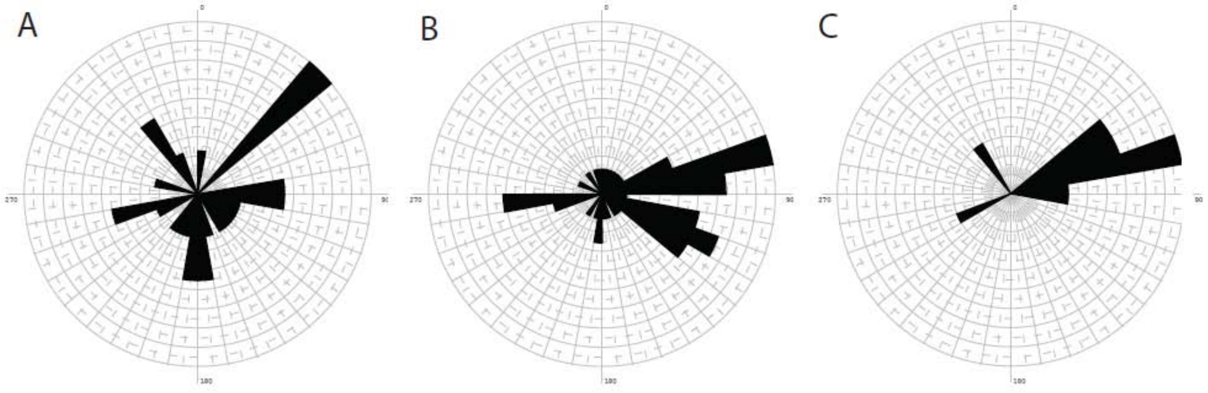

Fig. 6.6. Orientation data for the impressions preserved on the Mistaken Point bed MP4. **A**: Orientations of traces showing internal crescentic ornament, plotted as proceeding in the perceived direction of motion (towards concave face of the transverse internal crescents). n = 29, maximum bin value = 4. **B**: Orientations of all non-ornamented traces. Note that for these traces, direction of motion cannot be determined, therefore they may run at 180° to the documented orientation. n = 53, maximum bin value = 7. **C**: Orientations of the long axes of the negative relief ‘pits’ found on the bedding plane (indicating the primary axis of tectonic strain), n = 11, maximum bin value = 3.

Alongside the linear traces, there are additional impressions preserved on the bed. These include several oval to circular pits, up to 12 mm in diameter, similar to the discoidal impressions found at the end of the trails but not associated with them (Fig. 6.4A–B). Almost all oval pits are elongated in broadly the same direction (ENE–WSW), suggesting that elongation is tectonic in origin (elongation = 1.61 ± 0.21, 1σ; Fig. 6.6C). These pits may be ‘resting’ impressions of the organisms that created the traces. Although they lack the radial or concentric markings diagnostic of *Aspidella* (Gehling et al., 2000; Fig. 6.4A–B), these pits could potentially be an end-member of its morphological spectrum.

One interesting feature is a collection of seemingly associated, non-ornamented trails that are concentrated around a central depression (Fig. 6.7A). At least nine individual linear features emanate from a single point, although on closer inspection, this point is made up of at least four small depressions rather than one large pit. Some of these linear features (at left in Fig. 6.7A) curve significantly back towards the central region, potentially looping, and it is clear that the orientations of each component feature do not correlate with those of fractures or veins running along the surface. There is, however, little in the way of obvious structure or pattern to these impressions, and their origin and affinity remains uncertain. The association could represent 1) locomotion from a central point, as seen in many modern gastropod, echinoderm and annelid taxa on hardground surfaces (e.g. nereid polychaetes in Herringshaw et al., 2010); 2) an association of several trace makers around a central point, possibly a foodstuff; or 3) coincidental occurrence of multiple linear traces or similar impressions. This association is the densest accumulation of trace-like structures on the limited bedding surface.

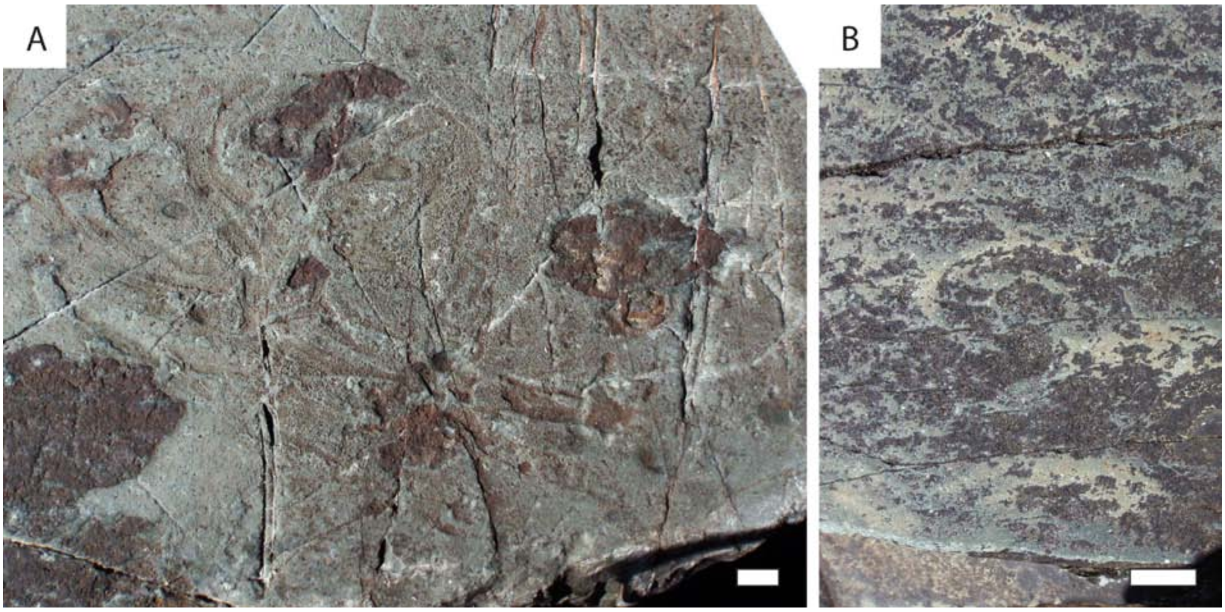

Fig. 6.7. A: A collection of potential traces found at the eastern end of the outcrop, seemingly emanating from a central point. A cast of this specimen is housed at the Oxford University Museum of Natural History, OUM ÁT.420/p. **B**: *Aspidella* specimen (likely to be a rangeomorph holdfast) from the trace bed, the only observed body fossil found on that bed. Scale bar length = 10 mm. Both images show the top surface of the bedding plane.

Although surrounding bedding planes with identical lithologies and similar taphonomic histories can preserve abundant Ediacaran body fossils, the traces and small pits are the only impressions to be found on this particular bed. A detailed search of the surface for body fossils uncovered only one poorly preserved discoidal impression, which is loosely interpreted as *Aspidella* sp. (*sensu* Gehling et al., 2000; Fig. 6.7B). This simple discoidal taxon is currently considered to be the holdfast of a frondose Ediacaran organism (Gehling et al., 2000). The *Aspidella* specimen from the trace-fossil bearing horizon is not directly associated with any of the traces, and is 2–3 times larger than the width of the largest observed trail. Its interpretation is further complicated by additional modern weathering and abrasion resulting from close proximity to the cliff edge. Specimens of *Aspidella*, *Hiemalora* and *Charniodiscus* occur on bedding planes 1–2 m stratigraphically above and below the trace bed, all of which confirm an Ediacaran age for the traces. Unfortunately this bed has not been seen to outcrop elsewhere within the MPER, and it remains the only level within the Mistaken Point Formation in Newfoundland known to exhibit such traces.

DISCUSSION

When documenting evidence for ancient life, it is important to falsify any possible abiogenic mechanisms for producing the features described. Glacially-induced striae, and tectonically-induced bedding cleavage lineations, are common in this region, but cannot explain the formation of the features documented herein; the candidate traces show no consistent orientations, and also exhibit substantial directional changes (Fig. 6.4C–D). Mineral veins of quartz cut vertically through the bed in places, but although they do show a variety of surface expressions even where the vein itself is not visible, they are not capable of showing the characteristic traits of the candidate traces (Appendix C1, Fig. C2.1). While abiogenic conchoidal and “feather” fractures occur on many neighbouring bedding surfaces, such features tend to be irregular, asymmetrical, and are observed to cross-cut sedimentary laminae. In contrast, the candidate traces have both positive and negative expressions with a well-defined, regular internal structure, and do not continue through sedimentary laminae. Importantly, they can also display a circular impression at one end. Although crescentic features can be formed by a circular object being passively dragged along a sediment-water interface, the variety of orientations in the Mistaken Point material cannot easily be explained as tool or scratch marks formed in unidirectional contourite currents (the assumed background hydrodynamic regime; Wood et al., 2003).

The claim by Retallack that the assemblage might represent tool marks known only from shallow water (e.g. Wetzel, 1999; Retallack, 2010) is redundant, because the depositional environment was unequivocally deep marine. The depth of deposition for the Mistaken Point Formation has been questioned on the grounds of an absence of pyrite, the presence of carbonate concretions, supposed oscillation ripples of shallow-water sedimentary origin, and various geochemical proxies (see Retallack 2010 for summary). However, all of these observations can be disputed. The ‘carbonate concretions’ (reported by Benus, 1988) are ferroan concretions consistent with deep water methanogenesis (e.g. Curtis et al., 1986), while earlier accounts of 'oscillation ripples' (Williams and King, 1979) are compressional features of tectonic origin (Benus, 1988; Wood et al., 2003). Higher in the stratigraphy – within the Signal Hill Group – the Ferryland Head Formation displays abundant wave-generated structures, wave-sorted sands, red beds with mudcracks, and rain-pits. These beds are markedly devoid of Ediacaran macrobiota. The presence (not absence) of pyrite in association with Ediacaran macro-fossils, for example with *Fractofusus* at Bristy Cove, is supported by many field observations. The microbial formation of pyrite by sulfate-reducing bacteria requires not only a source of sulfur (commonly seawater sulfate), but also an abundance of organic matter and iron as pre-requisites for growth. Red staining of many Ediacaran beds in the area is likely due to the secondary oxidation of pyrite (Gehling and Narbonne, 2007). That said, even a paucity of pyrite does not unequivocally imply a freshwater environment at the time of deposition.

Interestingly, the only previous study to have inferred a supratidal origin for the Mistaken Point biota is that of Retallack (1994). The 4000+ m Conception Group succession in southeast Newfoundland is mudstone-rich, but devoid of fluvial channel facies. A fully marine interpretation of the succession is also supported geochemically by Canfield et al. (2007), who clearly explain the non-uniformitarian nature of iron cycling in the Proterozoic.

Therefore, comparisons made by Retallack (2010) between our material and tilting marks (created by objects ploughing through modern beach sands; Wetzel, 1999) can be refuted. Firstly, the deep-water post-turbidite/contourite currents were likely to have been too weak to be capable of transporting large clasts, even buoyant ones, along the seafloor. Silts and clays are the only sedimentary particles that appear to have been deposited during ‘quiet’ periods of sedimentation, throughout the entire Conception Group. Skip marks, which can be common in Ediacaran shallow water sediments, are notably absent. If the traces were created passively by saltating hard objects, of organic or inorganic origin, these objects would be expected to remain at the termination of the impression. In contrast, it is observed that where the trails end in circular impressions (Figs. 6.3A, 6.5D), no such objects are found. Most notably, evidence for sediment displacement at the sides of the traces in the form of marginal ridges, a variety of orientations on a deep-water bedding plane, and rounded rather than angular trail extremities, all support a biological interpretation over abiogenic alternatives (cf. Jensen et al., 2005).

Several biogenic features bear some resemblance to our material. The Ediacaran fossil *Palaeopascichnus* was originally described as a trace fossil (Palij et al., 1983), but has since been reinterpreted as a protistan body fossil (Seilacher et al., 2003). *Palaeopascichnus* comprises a number of lunate chambers that, in branching specimens, are clearly not concave but convex in the direction of growth (Jensen et al., 2006). *Palaeopascichnus* also lack discs at their ends, and examples from Newfoundland have more regular spacing of internal ridges than is observed in the candidate traces (Gehling et al., 2000; Figs. 1.3F, A5.1B).

The possibility that these impressions might be body fossils must also be considered. As previously mentioned, the individual circular pits found on the Mistaken Point bedding plane are not readily referable to *Aspidella* (as defined by Gehling et al., 2000), though they are likely to preserve the basal morphology of the object responsible for creating the traces. Tubular body fossils, mostly known from younger Ediacaran assemblages, have often been mistaken for trace fossils (see Jensen et al., 2006). Such body fossils can possess features such as a basal circular disc, transverse segmentation, and dimensions similar to those seen here (e.g. *Funisia*; Droser and Gehling, 2008). *Corumbella werneri*, a tubular body fossil described from Brazil, displays similar overall maximum dimensions to the Mistaken Point traces, but has numerous internal bars, spaced 0.5 mm apart (Babcock et al., 2005). *Corumbella* also possesses an external central groove running along the length of the tube (Babcock et al., 2005), a feature not observed in any of our material. External tube ornamentation and regularly-spaced straight internal ridges are also features of *Calyptrina striata* (Sokolov, 1967); a tubular form of similar dimensions preserved as a carbonaceous impression in the upper Doushantuo Formation of China (Xiao et al., 2002, figs. 2.3–2.6); and also tubular fossils from the western United States (Hagadorn and Waggoner, 2000). Other tubular body fossils such as *Gaojiashania* s.s. from China are demonstrably seen to be composed of a series of articulated discs, which can become disarticulated following death of the organism (Cai et al., 2010). There is no evidence of such disarticulated segments of body fossils in the Mistaken Point material. There are, most importantly, several clear differences between the Mistaken Point material and these previously described Ediacaran tubular body fossils. The presence of marginal sedimentary ‘levees’, combined with clear truncations at cross-over points (Fig. 6.5C–D) rather than superimpositions, strongly suggest a trace fossil rather than tubular body fossil origin for the Mistaken Point material (cf. Jensen et al., 2005). Evidence for arcuate rather than straight transverse markings, widening diameters at points of curvature, and a lack of branching, are all further observations that are inconsistent with preservation of a tubular body fossil (cf. Droser et al., 2005; Jensen et al., 2005, 2006; Liu et al., 2010a; Tacker et al., 2010).

Two trace fossils reported from the latest Ediacaran, *Archaeonassa* and *Bilinichnus* (Jensen et al., 2006), compare with this material in being horizontal and exhibiting raised marginal ridges, but neither displays the prominent crescentic features of the Mistaken Point specimens. Proposed circular trace fossils with limited lateral movement, evidenced by the presence of lunate structures, have been recorded from the late Ediacaran as *Beltanelliformis brunsae* in the Wernecke Mountains of Canada, and *Bergaueria sucta* of the Ukraine (Fedonkin, 1981; Narbonne and Hofmann, 1987). *Bergaueria sucta* has been suggested to represent lateral movement similar to that of modern actinians (Seilacher, 1990), but unlike in the Mistaken Point trails, evidence for lateral movement in *Bergaueria* is limited to a few closely-spaced arcs adjacent to the circular pit (Fedonkin, 1981), which have been considered as structural rather than ichnological impressions by some workers (Jensen et al., 2006).

The Mistaken Point traces bear a passing resemblance to the ‘lower surface expression’ of the ichnotaxa *Plagiogmus* and *Psammichnites*, but both possess a significant vertical component, plus internal ridges that are either straight or convex-forward (McIlroy and Heys, 1997). A lack of meandering rules out *Cochlichnus* and *Torrowangea* (the latter also requires regular constrictions), while *Helminthoidichnites*, although common in the latest Ediacaran, is narrow, sinuous, and shows none of the internal structure present in the ornamented specimens (though it could favourably be compared to the non-ornamented variants from Mistaken Point).

Phanerozoic fossils with meniscate backfill bear some resemblance to the present material. Cross sections of actively backfilled cylindrical burrows such as *Taenidium* (*sensu* Keighley and Pickerill, 1994) can be superficially similar. There is, however, no evidence that the material under consideration represents a cross section of a tubular feature, or extends into the sediment; the impressions appear to be entirely surficial traces. Meanwhile, meniscate backfill is diagnostically a Phanerozoic trait (Brasier et al., 1994). Similarities are also clear between the non-ornamented traces from Mistaken Point (e.g. Fig. 6.5A), and the bilobate trace fossils figured from the late Ediacaran of the Great Basin in the United States (Hagadorn and Waggoner, 2000, figs 5.11–5.12), which are compared in that publication to *Scolicia*. In contrast, our material does not show the parallel basal grooves, ornamented walls, or meniscate backfill seen in *Scolicia* s.s. (Smith and Crimes, 1983). It is therefore considered that the traces from Mistaken Point are ichnological in origin, but cannot be readily assigned to an existing ichnotaxon.

SUGGESTED TRACE MAKERS

In the absence of any strong abiogenic explanations or Ediacaran ichnological affinities for the Mistaken Point impressions, comparison with younger Phanerozoic interface traces is necessary. Modern pennatulacean cnidarians are known to move across the seafloor, and their resting traces can be similar to some of the circular impressions at the ends of our trails (Miller III, 1999). It therefore could be argued that frondose organisms, morphologically similar to *Charniodiscus*, were responsible for forming these traces. The relationship of rangeomorph fronds to pennatulaceans is, however, disputed (see Antcliffe and Brasier, 2007). Furthermore, none of the many thousands of frondose specimens preserved in any Ediacaran biotic assemblage across the globe has ever been found on the same bedding plane as a trace fossil similar to those described here. As such, it is considered highly unlikely that a member of the frondose Ediacara biota was responsible for the formation of these impressions.

Modern organisms with a basal circular morphology, such as echinoids and sea anemones, commonly produce somewhat comparable interface trails, especially in cohesive or mucus-bound sediment (Fig. 6.8). Our observations of a metazoan that moves across the sediment surface by means of ‘shuffling’ (the sand dollar echinoderm, order *Clypeasteroida*, moving on its tube feet), indicate that such a style of locomotion produces a track that is laterally bounded by ridges of displaced sediment, whereas the interior of the track-way remains completely smooth. Similarly, studies of organisms that move by mucociliary creeping (e.g. ceriantharian anemones and platyhelminths; Collins et al., 2000), show that such organisms do not and indeed cannot produce the internal transverse ridges seen in the Mistaken Point trails. Such modes of locomotion are therefore not thought to be responsible for the Mistaken Point impressions.

Actinian cnidarians (sea anemones) may provide a possible biomechanical analogue for these trails (cf. Seilacher et al., 2003), and for discoidal Ediacaran impressions in general (Gehling, 1988; Grazhdankin, 2000). Anemones are capable of crawling across sediment, and can exhibit swimming and burrowing behaviour (e.g., McClendon, 1905; Parker, 1916). Laboratory studies within the Department of Earth Sciences, Memorial University of Newfoundland, using the modern sea anemone *Urticina*, indicate that anemones can produce surface trails with comparable positive marginal ridges to those seen at Mistaken Point, and crescentic internal ridges with concave edges facing the direction of locomotion (Fig. 6.8).

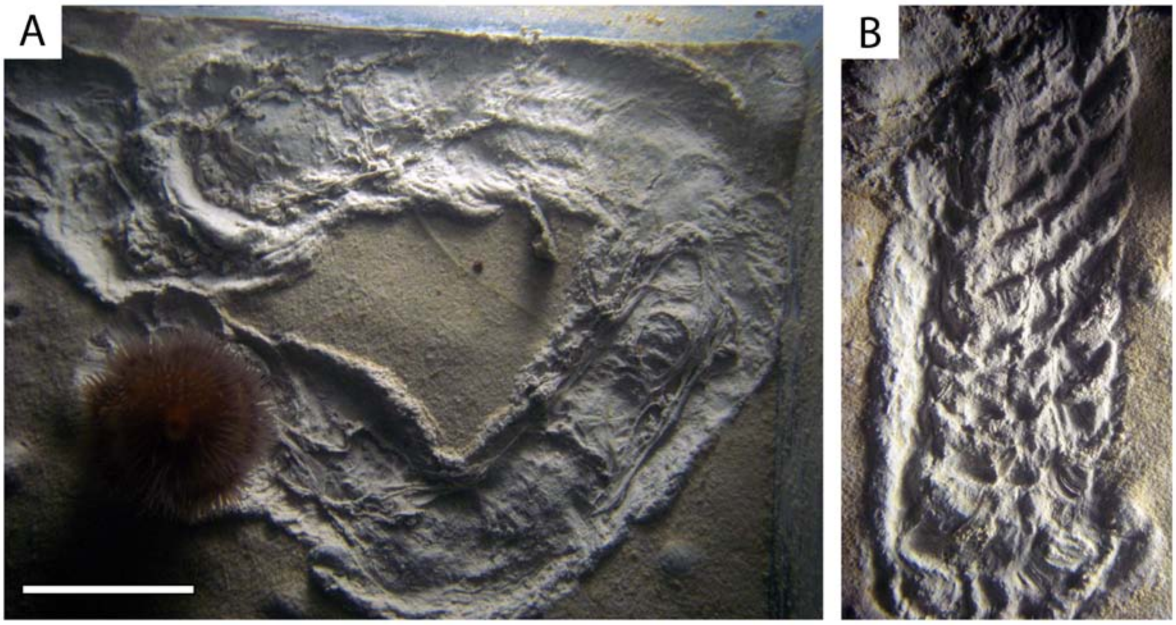

Fig. 6.8. Modern actinian (*Urticina*) trails in mud, produced in our marine aquaria. **A**: Meandering trail, clearly showing concave-forward hemispherical structures (at top) and positive marginal ridges. Mucus trails are present throughout the impression. **B**: Straight anemone locomotion trace, showing assymetrical hemispherical ridges, spaced at regular intervals. Scale bar (applying to both images) = 30 mm.

The anterior impressions made by the anemones are usually obliterated during subsequent movement, except where the trail ends as a circular disc. The traces vary slightly in width along their length because the organisms move by a muscular, non-uniform inflation of their base (Fig. 6.9). Actinian trails also contain regions where ridges are absent and the sediment is smooth, potentially explained by locomotion across a more consolidated substrate, or by deposition of mucus (Figs. 6.8–6.9). While capable of crawling, most modern actinians preferentially reside on hard substrates, explaining the paucity of such traces in ancient sediments. In this way, many features of the Newfoundland traces may be best explained by an actinian-like mode of locomotion.

Against this possibility might be raised the suggestion of a mollusc-like trace maker. For example, recent work has demonstrated that modern gastropods are capable of forming surface locomotory traces that include crescentic meniscae (Getty and Hagadorn, 2009).

Those workers make reference to the Phanerozoic trace *Climactichnites* as a potential molluscan ichnofossil (Getty and Hagadorn, 2009). It has been noted that gastropodan surface trails in modern intertidal environments are seldom preserved, owing to the destructive actions of erosion and bioturbation (e.g. Getty and Hagadorn, 2009). This would not have greatly affected Mistaken Point, however, since neither the destructive action of wave and tidal currents, nor pervasive bioturbation, are considered to have significantly influenced the deep-marine seafloor. The resting body trace of the *Climactichnites* trace-maker is both

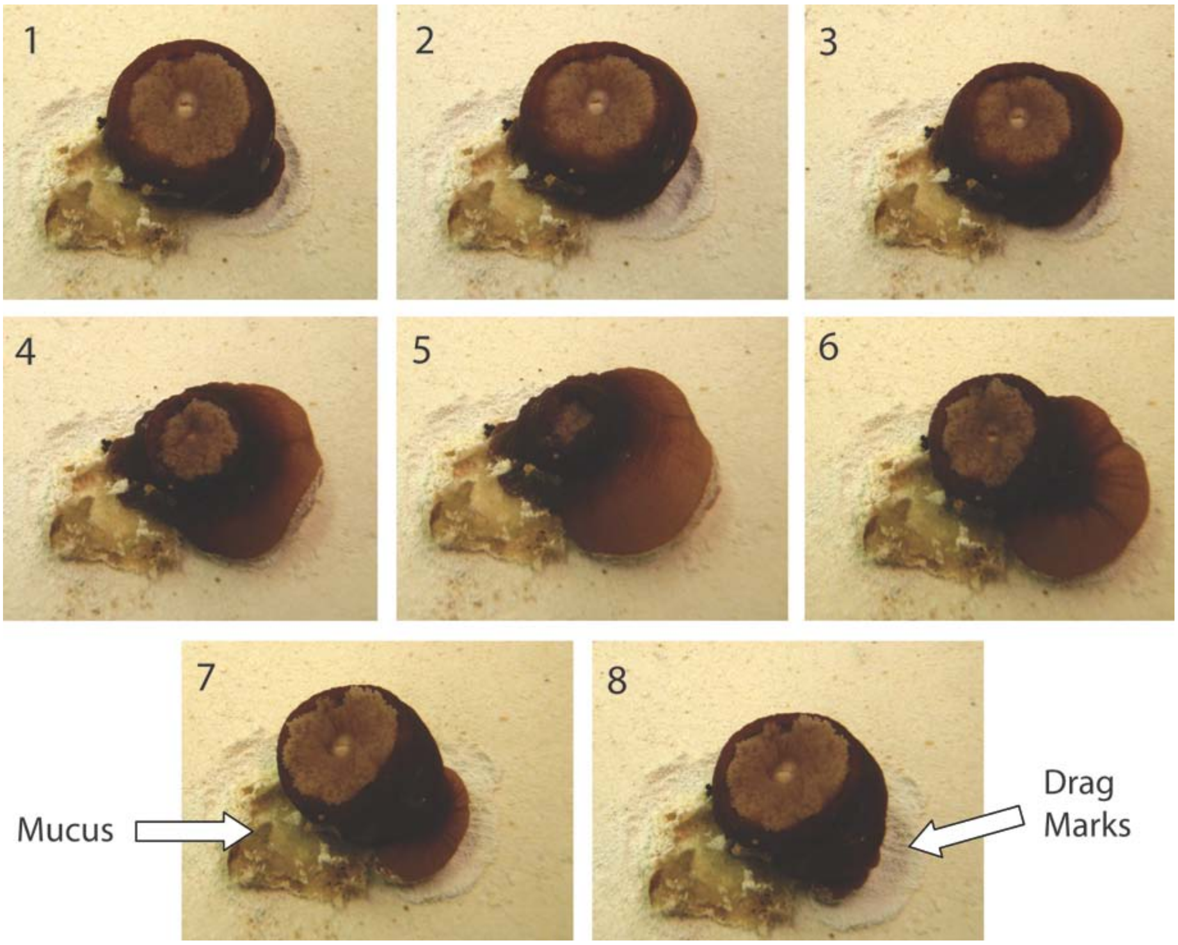

Fig. 6.9. Time-lapse photography of an anemone moving across a soft substrate in laboratory conditions. Movement progresses from left to right. The creature slowly inflates its pedal disc (3,4) until it is fully inflated (5), at which point it attempts to pull itself towards the inflated region as it deflates (6,7), returning eventually to its original shape having moved 1–2 mm. Images were taken between 30 and 75 seconds apart. The drag marks (arrowed) are produced while deflation takes place, and are obliterated as the organism moves over them, with only the impression of the posterior edge of the organism being preserved.

bilaterally symmetrical, and generally elongate (Getty and Hagadorn, 2009; though see Yochelson and Fedonkin, 1993). This contrasts with the broadly circular impressions seen at the termination of the Mistaken Point traces (after accounting for probable tectonic elongation; Fig. 6.6C). Like anemones, gastropods also possess a muscular foot, which would have been the point of contact with the sediment. The waves of muscular contraction utilised by many gastropods during locomotion were once considered to be unlikely to produce ridges perpendicular to the direction of motion in subsequent traces (Yochelson and Fedonkin, 1993). Those workers argued that there is no vertical component of movement involved in that locomotion process to explain movement of sediment to the back of the organism (Yochelson and Fedonkin, 1993). Conversely, Getty and Hagadorn (2009) have described direct observations of the modern gastropod *Viviparus* forming such transverse ridges during locomotion under subaerial conditions. It is also noted that modern gastropods utilise a variety of physical methods to move, including a range of 'stepping' motions (Lissmann, 1945a), not just peristaltic muscle contractions. Molluscs therefore cannot be ruled out as potential creators of the traces. Annelids have also been noted to exhibit the retrograde monoaxial muscular contraction used by molluscs (Lissmann, 1945b; McIlroy and Heys, 1997), but the circular shape of the terminal disc impression seen in the Mistaken Point specimens suggests that, unless the circular discs represent burrow openings, annelids are not responsible for these structures. Locomotion of extant protists (Matz et al., 2008), while capable of forming traces with lateral levees, has not yet been demonstrated to form the internal morphological traits seen in the trails from Mistaken Point.

In summary, experimental and ichnological comparisons indicate that many of the Mistaken Point trace fossils were likely produced by an organism with a muscular basal disc or foot. This organ was capable of exerting a force upon the surrounding sediment in a controlled and rhythmic manner, specifically in a direction opposite to that of forward motion, as evidenced by the crescentic transverse ridges of sediment marking the posterior impression of the organism. As metazoans are the only extant creatures known to possess organs or tissues with these abilities, the creators of these trails can be argued to be of metazoan grade.

Although these traces are preserved beneath tuffs, as with body fossils from the same Formation (Conception-style preservation of Narbonne, 2005), only one such trace-bearing bed has been found to date. The scarcity of these impressions may be a function of water depth, with the trace-makers transported down-slope by currents from shallower depths, or they may have simply been a rare component of the ecosystems. Alternately, special conditions may have been required for their preservation. Jensen et al. (2005) have suggested a low preservation potential for mucus-bound sedimentary traces (such as our laboratory anemone trails), and this has been demonstrated experimentally in shallow settings (Getty and Hagadorn, 2009). Unusually calm conditions at the sediment-water interface may therefore have been necessary to preserve the traces. In our experimental tanks, such conditions permitted trails and mucus streamers to remain on the sediment surface indefinitely. Intriguingly, a number of trace-like impressions and fossils have been observed from the Ediacaran of China and Russia, though they have not generally been described as ichnofossils. Neither '*Gaojiashania*' specimens from the Yudoma River of Siberia (Zhuravlev et al., 2009) nor '*Palaeopascichnus*' from North China (Shen et al., 2007), both of which are composed of serially arranged crescentic segments, are particularly representative of their respective taxa. They do, however, compare well with Siberian material that is likely to be ichnological, dated at around 560–555 Ma, and comparable to *Nenoxites curvus* Fedonkin (Seilacher et al., 2005, fig. 2; Grazhdankin pers. comm. 2011). This important material potentially demonstrates that traces similar to those from Mistaken Point occurred abundantly in the lead up to the Cambrian Period.

ADDITIONAL AVALONIAN TRACES

If the trails described from Mistaken Point are to be accepted as evidence for locomotion by Ediacaran organisms in the Avalon successions ~565 Ma, it would be expected that younger rocks from the Avalon terrane should also preserve evidence for such movement. A detailed search for further examples in the deep-water successions of Newfoundland has so far proved fruitless, although several macroscopic body fossil genera from the assemblages have previously been considered as ichnofossils. The suggestion that the Avalonian taxa *Hadrynichorde catalinensis* Hofmann et al. 2008 and *Parviscopa bonavistensis* Hofmann et al. 2008 are possible trace fossils (Hofmann et al., 2008) is here considered unlikely. The long, thin *Hadrynichorde* is most likely to be a filamentous string similar to many others observed on bedding planes throughout the Avalon region (see Chapter 2). Although *Parviscopa* bears some resemblance to the rasping trace *Radulichnus* (thought to be the feeding trace of *Kimberella* in the White Sea region; Seilacher et al., 2003, 2005; Fedonkin et al., 2007b), the positive epirelief nature of the impressions, and the lack of an associated trace-maker, rule out acceptance of this grazing interpretation. I consider it more likely that *Parviscopa* is closely affiliated with *Primocandelabrum*, a contemporary organism that differs from *Parviscopa* in possessing a basal attachment disc (Hofmann et al., 2008). Shared biostratigraphic ranges of these taxa in Newfoundland support the possibility that *Parviscopa* is simply a juvenile *Primocandelabrum* that lacks a preserved disc (Fig. 2.17).

The Fermeuse Formation of the St. John’s Group, ~555 Ma, Newfoundland is best known for its preservation of discoidal body fossils in thinly inter-bedded mudstones and siltstones (e.g. *Aspidella terranovica*, *Triforillonia costellae*; Gehling et al., 2000). These impressions can reach up to 110 mm in diameter. Although trace fossils have previously been described as being preserved by Fermeuse-style preservation (Narbonne, 2005; Laflamme et al., 2011; both referring to fossils from the Mackenzie Mountains, Northwest Canada; Narbonne and

Aitken, 1990), bioturbation has never been formally described from the Fermeuse Formation itself (Gehling et al., 2000). Contrary to the opinions of some authors, who consider the Fermeuse Formation to be a deep-water slope deposit (e.g. Gehling et al., 2000; Laflamme et al., 2011), the depositional environment of the upper Fermeuse Formation in Ferryland is likely to have been above storm wave base. Evidence for this assertion includes tempestite deposits, and numerous rippled surfaces whose ripple indices are consistent with formation by waves (personal observation; J. Matthews unpublished Masters thesis, University of Oxford). Such sedimentary features indicate a significantly shallower depositional environment than that inferred for the underlying Mistaken Point and Trepassey Formations.

Negative epirelief grooves, up to 2 mm in width, cut across the surfaces of the finer-grained units in the Fermeuse Formation (Fig. 6.10 A–E). These impressions occur on bedding planes alongside *Aspidella terranovica* and *Palaeopascichnus delicatus*, which are preserved in the typical Fermeuse-style negative epirelief preservation of Narbonne (2005). Many impressions are simple, unornamented, curvilinear troughs on the upper surfaces of bedding planes (Fig. 6.10 C), though some do seem to have evidence for internal structure (Fig. 6.10 B, D–E). The transverse ornament within some impressions is not dissimilar to the arcuate internal ridges of the Mistaken Point specimens (Fig. 6.6), although here it occurs on a smaller scale. Other impressions follow looping trajectories broadly similar to those seen in the Phanerozoic ichnogenus *Gordia* (Fig. 6.10 D). All of the figured specimens occur on the same bed (Fig. 6.10 A), with potential traces in surrounding beds being rare. As at Mistaken Point, this dearth of examples requires an explanation, with taphonomic, environmental and coincidental factors all possible contributors. Marginal ridges indicative of sediment displacement are absent, and some specimens (Fig. 6.10 B–C) vary in width along the length of the impression. However, the variety of observed orientations, along with suggestions of cross-cutting where impressions overlap, suggest that a trace fossil interpretation cannot be dismissed lightly.

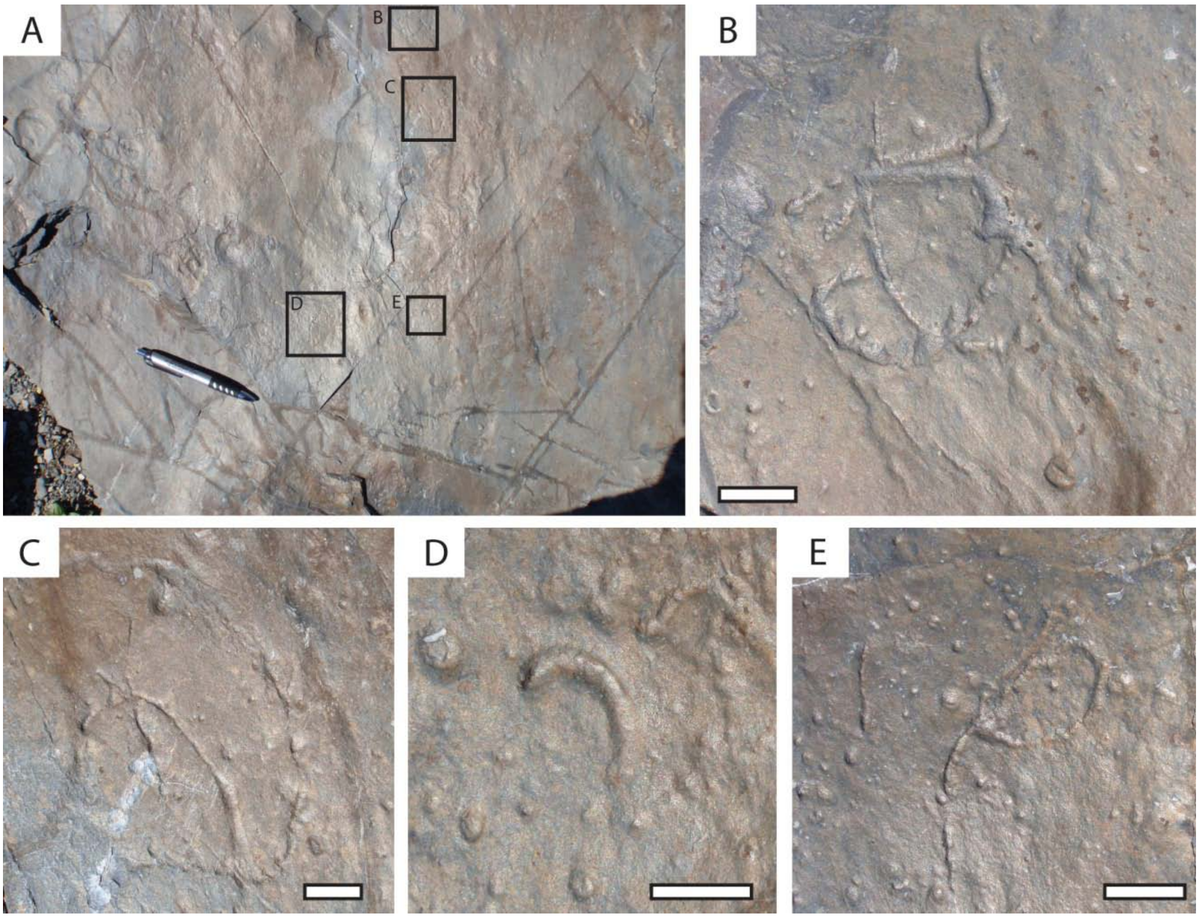

Fig. 6.10. Possible trace fossils preserved in negative epirelief from the Fermeuse Formation, Ferryland, Newfoundland. The locality is situated in a road-cut section on the west side of Route 10, near the church, in Ferryland. **A**: Overview of the block containing the specimens documented in B–E. **B**: A group of narrow troughs showing a variety of directional changes and orientations on the bedding plane. **C**: Further examples of grooves running across the surface, exhibiting cross-cutting relationships. **D**: Simple curved trace displaying fine internal transverse ridges. **E**: A specimen that appears to coil back on itself to form a loop. All images include broadly circular negative epirelief impressions of *Aspidella terranovica*, preserved at a variety of scales. All scale bars = 10 mm.

The absence of a terminal discoidal impression in the Fermeuse specimens, and the small number of examples, leaves the identities of the trace makers in doubt. The Fermeuse Formation impressions display several similarities with proposed trace fossils from the latest Ediacaran of North Carolina (Tacker et al., 2010, fig. 8a), but no possible trace makers are proposed for those impressions. Similarities with simple burrows from younger Ediacaran assemblages could imply small bilaterian trace-makers in this instance, but further work is required to fully document this assemblage.

The Ediacaran successions from Llangynog, in Carmarthenshire, Wales, contain proposed simple branching burrows and meandering feeding traces (Fig. 6.11; Cope, 1977; Carney et al., 2000). Some workers consider these to be fragmentary tubular body fossils rather than traces (Gehling et al., 2000), but this suggestion can be dismissed using the arguments previously outlined in the discussion of the Mistaken Point impressions (pp. 182–183). The Carmarthenshire traces occur in association with a discoidal assemblage of body fossils, in the shallow marine Coed Cochion Member of the Coomb Volcanic Formation (Cope and Bevins, 1993). The trace fossil assemblage from Llangynog records only horizontal movement by small organisms with a width of <1 mm, either on the sediment surface (Cope and Bevins, 1993), or perhaps beneath a microbial mat. Although the lithology (finely laminated volcaniclastic siltstones) and taphonomy compares more closely with the Longmyndian, the predominantly large discoidal body fossil assemblage from Llangynog (Cope, 1977) is more

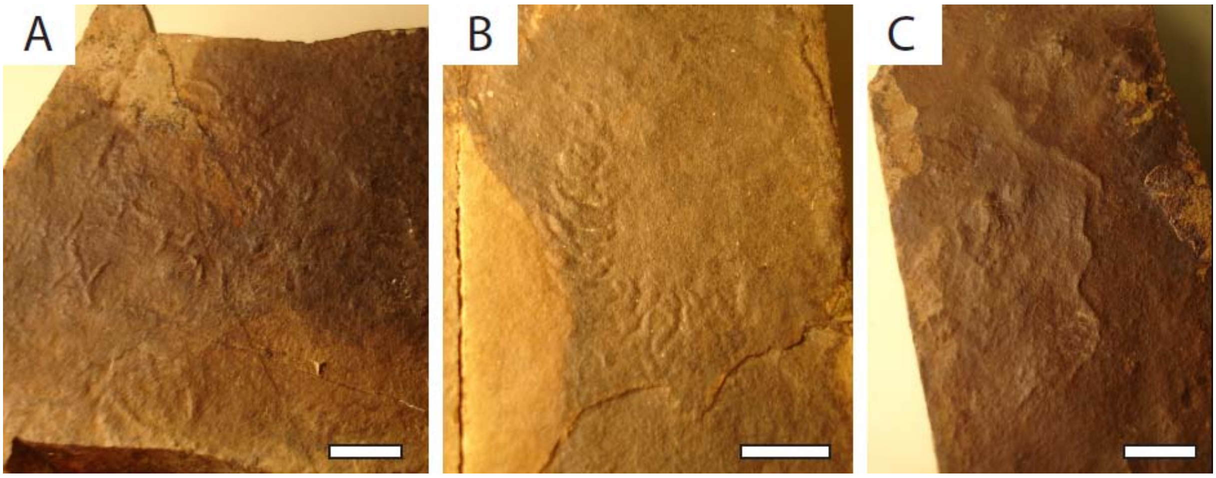

Fig. 6.11. Features interpreted as trace fossils from Llangynog, Carmarthenshire, Wales. Specimens all held at the National Museum of Wales, and figured in Carney et al., 2000. **A**: Simple branching trace, NMW 79.16G.8. **B**: Meandering feeding trace, NMW 79.16G.6. Labelled as *Palaeopascichnus* in fig. 4e, Cope and Bevins, 1993. **C**: Horizontal meandering burrow, NMW 79.16G.7. Scale bars = 10 mm.

akin to that of the late Avalonian Fermeuse Formation of Newfoundland (cf. Gehling et al., 2000). The exact age and stratigraphic position of this inlier remain to be determined, and direct comparisons between the ichnofossil assemblage of Carmarthenshire and those of other Avalonian sites should therefore be treated with caution at present.

The shallow-marine-to-fluvial settings of the Longmyndian Supergroup of Shropshire (Pauley, 1991), and the deep-water Charnian Supergroup of Leicestershire, U.K. (Carney, 2000), show little evidence for convincing trace fossils. *Medusinites* aff. *asteroides* occurs in the fine siltstones of the Burway Formation, a shallowing-upwards marine unit within the Longmyndian Supergroup. It is a circular impression 1–3 mm in diameter, preserved in positive hyporelief, with a small pimple in the centre (McIlroy et al., 2005). *Medusinites* specimens have been described as ichnofossils on the basis of cross-sections, which show thin tubes of fine sand cutting up through finer grained sedimentary laminae, seemingly connecting individual specimens at different sedimentary levels (McIlroy et al., 2005). These tubes are interpreted to show vertical movement of the organism in response to localised sedimentation (McIlroy et al., 2005), quite different behaviour to that required to produce the horizontal Mistaken Point, Fermeuse and Carmarthen traces. The identity of the organism thought to have created the *Medusinites* impressions remains uncertain. From field observation of the surface impressions of *Medusinites*, the writer has yet to be convinced of their diagnosis as trace fossils. The ‘worm burrows’ of the Longmynd, *Arenicolites didymus* (Salter 1856; 1857) have been reviewed elsewhere, (McIlroy et al., 2005), and their status as u-shaped worm tubes remains doubtful (Callow et al., Submitted). Meanwhile, the Old John and North Quarry localities of Charnwood Forest contain features described as ‘worm’ trails (Boynton and Ford, 1995, figs. 18–19), but these are contentious and require further study. Finally, an assemblage of trace fossils reported from the North Carolina slate belt (potentially part of the Avalon Terrane), which includes not only horizontal forms such as *Gordia*, *Planolites* and *Helminthopsis*, and potential vertical burrowers (Gibson, 1989), is likely to be either youngest Ediacaran in age (Weaver et al., 2006), or even Cambrian.

From this discussion, it is evident that locomotion, although relatively simple and predominantly restricted to horizontal surface movements, was present in several later Ediacaran, shallow-water Avalonian assemblages. The comparative scarcity of such impressions in earlier and deep-water settings still requires explanation. Such impressions are not evident in most Avalonian fossil assemblages, despite similar preservational and environmental conditions to those at Mistaken Point being widespread. One explanation for this is that these trace-makers were washed in from shallower depths by storms or density currents. Such a phenomenon is well known from younger fossil localities (e.g. the Burgess Shale of Canada; Conway Morris, 1979). Less plausibly, unusual or as yet unrecognised conditions were required for their preservation, or they could simply have been a rare biological component of all ecosystems at this time. The microbial mats commonly observed throughout late Ediacaran siliciclastic successions (e.g. Brasier et al., 2010) may have hindered the preservation of surficial trace fossils (Jensen, *pers. comm.* 2011). While these finds provide a search image for potential traces in Ediacaran rocks from Avalonia, caution must always be exercised when interpreting potential ichnofossils from Precambrian rocks. Nevertheless, it can be argued that Avalonian ecosystems younger than 565 Ma included organisms that were not entirely non-motile.

IMPLICATIONS FOR PALAEOBIOLOGY

The large, distinctive Mistaken Point interface traces demonstrate the existence of deep-water, putatively metazoan, locomotion by ~565 Ma. Small horizontal surface trails, and burrows within microbial mats, are documented in the slope and shallow-marine environments of the

Fermeuse Formation in Newfoundland, as well as in the Llangynog inlier of Wales. These fossils, from more proximal environments, are likely to be broadly contemporaneous with the grazing traces, simple surface traces, and under-mat miners of the Flinders Ranges, White Sea and Namibian assemblages seen just prior to the Cambrian boundary.

The possible presence of motile metazoans in the Avalon biota has significant implications for the palaeoecology of the oldest Ediacaran ecosystems, which were previously thought to consist entirely of non-motile suspension feeders or osmotrophs (Clapham et al., 2003; Narbonne, 2005; Laflamme et al., 2009). Locomotion requires additional levels of energy and metabolism, suggesting that the ecology of the Avalonian seafloor was perhaps quite complex in places, approaching that of later marine ecosystems. Motile organisms would have been capable of escaping areas of environmental stress. They would have had the capacity to search for nutrients, and they could potentially have freed themselves from the (often surprisingly thin) ash layers that regularly smothered their ecosystems. We consider it possible that an organism comparable with an actinian-grade cnidarian was responsible for the Mistaken Point traces. If correct, comparison with actinian locomotion by inflatable pedal disc implies that muscular tissue (necessary to allow control of hydrostatic inflation; Batham and Pantin, 1950), may well have been present in some Ediacaran organisms.

The general scientific consensus of increasing bioturbation across the Ediacaran-Cambrian transition (e.g. Crimes and Droser, 1992; Seilacher and Pflüger, 1994; McIlroy and Logan, 1999; Bottjer et al., 2000; Callow and Brasier, 2009a) sees undermat miners and grazers of the Ediacara and Nama successions joined by vertical burrows at the base of the Cambrian (e.g. Crimes, 1992; Droser and Bottjer, 1993; Droser et al., 2002). The first appearance of *Treptichnus pedum* at that boundary indicates the emergence of complex vertical bioturbation (Narbonne et al., 1987; Landing, 1994; though see Jensen et al., 2000). The finds from

Avalonia described herein are consistent with this view, and help to clarify our understanding of the transition from the non-motile Precambrian to a Cambrian world full of movement.

Finally, the trace makers may have been some of the first macroscopic ecosystem engineers – organisms capable of changing the geochemical and physical properties of their environments through their behaviour (Herringshaw et al., 2010). The emergence of vertical burrowing in the Cambrian arguably changed the chemistry of the sediment-water interface upon which these organisms lived (Brasier et al., 2011). However, workers are yet to investigate the initial impact made by the innovation of horizontal surface locomotion upon the physics and chemistry of the sediment-water interface.

CONCLUSION

The rocks of Mistaken Point in Newfoundland have yielded the earliest potentially metazoan macroscopic surface locomotory trails in the geological record, extending the occurrence of such traces back by around 5 Myrs, to *c*.565 Ma. We consider that these impressions are consistent with locomotion traces produced by an actinian-like organism. The fact that these traces are directly associated with an Ediacara biota lends support to the hypothesis that at least some elements of the Avalon-type biota could have been motile animals. It is likely that the circular impressions at the ends of the trails represent moulds of the lower surface of the trace maker, and it is noted that these moulds superficially resemble characteristics of the Ediacaran forms *Aspidella*, *Hiemalora,* and *Charniodiscus*. When combined with evidence for locomotion from younger and shallower Avalonian deposits, these finds demonstrate that organisms with the ability to move actively were potentially distributed throughout the Avalon region during the late Ediacaran Period.

ACKNOWLEDGEMENTS

Thanks are extended to Parks and Natural Areas Division, Department of Environment and Conservation, Government of Newfoundland and Labrador for granting a permit to conduct research within the Mistaken Point Ecological Reserve in the summer of 2008. I am grateful for the field assistance and advice of Jack Matthews, Richard Callow, Latha Menon and Emma Nicholson in both Newfoundland and the U.K., while Richard Thomas (Mistaken Point Ecological Reserve Manager) furnished additional support. Art King provided helpful discussion on the stratigraphy of the site, while John Cope kindly provided access to specimens from Carmarthenshire housed in the National Museum of Wales. The Oxford University Museum of Natural History housed casts of this material. Constructive reviews from Marc Laflamme and Sören Jensen greatly enhanced the *Geology* manuscript.

CHAPTER 7

REASSESSING OUR KNOWLEDGE OF THE EDIACARA BIOTA

PREFACE

The material presented in this thesis demonstrates how research into Ediacaran taphonomy, palaeontology, ichnology, petrography and ontogeny can provide insights into both the nature of Ediacaran organisms, and the characteristics of Ediacaran ecosystems. The Ediacaran Period is shown to be a time where uniformitarian thinking must be adapted to account for the fundamental differences in biology and ecology between that interval and the subsequent Phanerozoic. It is not that traditional uniformitarian principles do not apply in the Neoproterozoic – they almost certainly do – but the biota, ocean chemistry, climate, and tectonic cycling of this era were sufficiently dissimilar to require careful consideration before traditional biological and physical processes and interactions can be invoked.

This final chapter summarizes the most significant findings of the thesis, and explores their theoretical and philosophical implications for the history of life on Earth. The importance of microbes in Avalonian ecosystems is highlighted, and evidence both for and against the presence of metazoans in the Avalon biotic assemblage is objectively assessed. Finally, further research directions that would form a natural progression to this study are outlined.

THE ENIGMATIC EDIACARAN PERIOD?

The Ediacaran Period is often viewed as a critical and interesting interval in the history of life, which, despite its strange organisms, ultimately holds the answers to the ancestry of the metazoan clade (e.g. Budd, 2008; Edgecombe, 2009). Nevertheless, the array of different phylogenetic models presented for the Ediacara biota has generated a significant amount of confusion (see discussion in Chapter 1). As the Ediacaran Period and its biota are increasingly brought to the attention of the general public (e.g. Attenborough and Kaplan, 2010, and the accompanying television series), we must ensure that it is the wonder of these strange fossils, rather than their weirdness, which is conveyed to the population at large.

The initial appearance of the Ediacara biota

The interpretation of the Avalonian Ediacara biota presented herein differs substantially from that of previous works. Rangeomorphs described from the Drook Formation of Pigeon Cove represent the smallest known rangeomorph specimens, extending the minimum size bounds for which rangeomorphs can be preserved in Avalonian siliciclastic successions, and providing a new search image/strategy for other workers in these areas (Chapter 2). These rangeomorph fossils are interpreted as a population of juveniles. Together with other fossils on the same bedding plane, they document one of the earliest examples of community succession in the geological record of megascopic life. Furthermore, the specimens suggest that rangeomorphs possessing undisplayed branch architecture (Brasier and Antcliffe, 2009) may have been the first to evolve, with displayed branching being a derived feature. A focused study of rangeomorph ontogeny and taphonomy is now required to confirm that this is an evolutionary, and not an ontogenetic, feature (ongoing research at the University of Oxford). Importantly, the Pigeon Cove biota increase the known generic macrofossil diversity at *c*.579 Ma, and hint at either a rapid 'explosion' of morphological diversity immediately following the Gaskiers glacial event (cf. Shen et al., 2008b), or a longer, as yet unknown ancestry stretching back into the early Ediacaran.

Recent discoveries made since the start of this doctoral project support the suggestion that metazoan evolution may have begun prior to the Ediacaran Period, in the Cryogenian. Ancient macrofossils, such as the ~600 Ma potential eukaryotic algae from the Lantian Formation of China (Yuan et al., 2011), and ~750 Ma discoidal fossils of the Kurgan Formation of Kazakhstan (Meert et al., 2011), demonstrate that large organisms existed on Earth prior to the Gaskiers glacial. Observations from several different disciplines suggest that one of the most basal metazoan groups, the Porifera, may have been present from ~700 Ma. Sterane biomarkers from the Huqf Supergroup of Oman suggest the continuous presence of demosponges in pre-Marinoan (>635 Ma) rocks through to the Cambrian (Love et al., 2009), a finding bolstered by recent discoveries of ~635 Ma, three-dimensional, cm-scale structures from Australia, interpreted as possible early sponges (Maloof et al., 2010). Some Early Neoproterozoic acritarchs have also been suggested to be sponges on the basis of distinctive cruciform patterns resembling spicules on their surfaces (Butterfield, 2009b), while possible Late Ediacaran spicule-bearing macrofossils have been described from Russia (*Fedomia mikhaili*; Serezhnikova and Ivantsov, 2007). Combined with molecular clock studies that have hinted at age ranges extending into the Cryogenian for the basal metazoa (Peterson and Butterfield, 2005; Sperling et al., 2007, 2010), the case for the presence of stem group sponges prior to the Ediacaran is looking increasingly strong.

Such findings demonstrate that there is still much to learn about the early evolution of macroscopic forms. The presence of potential poriferan or other metazoan body fossils in the Avalon biota remains to be proven (see also Sperling et al., 2011; Chapter 1). Although metazoans may have resided in Avalonian ecosystems, their relationship with the Ediacara biota and the exact triggers for their evolution present significant future research directions. Further finds such as those at Pigeon Cove will hopefully lead us to solutions to these questions.

Understanding problematic morphologies

Although many Ediacaran taxa have so far defied classification, owing to their unusual architectures, symmetries and structures, one Avalonian group has been more enigmatic than most. The ivesheadiomorphs have proven difficult to classify due to their lack of consistent internal morphology, and their unique high-relief arrangements of lobes and depressions. The interpretation presented herein suggests that ivesheadiomorph taxa represent taphomorphs of rangeomorph and other Ediacaran organisms that had died and decayed on the seafloor prior to burial by event beds (Chapter 3). Field evidence in support of this hypothesis includes; 1) the preservation on individual bedding planes of a spectrum of morphologies, ranging from well-preserved rangeomorph taxa to completely effaced ivesheadiomorphs; 2) a long stratigraphic range for the group (encompassing the entire ranges of all rangeomorph taxa), and; 3) the fact that no two ivesheadiomorphs are ever morphologically identical. Ivesheadiomorph morphology seems to be determined not by a definitive body plan, but by secondary, preservational, factors. Recognition of these fossils as taphomorphs not only identifies the provenance of *Ivesheadia* and similar forms, and the reasons for their unusual appearance, but also uncovers several previously unrecognised processes and interactions occurring at the Avalonian sediment-water interface.

Experimental taphonomy supports the suggestion that ivesheadiomorphs obtained their unusual morphologies as a result of the break-down of organic matter by microbial activity, in the absence of predators, scavengers, and bioturbating organisms (Chapter 4). Experimental techniques also demonstrate that the remains of macro-organisms degraded in this way could feasibly be preserved in the rock record. There remain multiple Ediacaran macrofossils that possess problematic morphologies, both from the Avalon region (e.g. *Thectardis avalonensis*), and other global terranes. Consideration of taphonomic explanations for their overall appearance, alongside more traditional morphometric or biological studies, may enable us to continue decoding Ediacaran fossils successfully in the future.

Avalonian ecosystems

The presence of taphomorphs, which represent organisms that were not alive at the time of burial, also needs to be considered when assessing the palaeoecology of Avalonian ecosystems. Substantially time-averaged communities are preserved on these bedding planes, which do not represent census populations of living organisms. Several prior studies of these ecosystems have therefore overestimated standing diversities of Ediacaran organisms (e.g. Clapham et al., 2003; Shen et al., 2008b), not only by mistakenly considering the ivesheadiomorphs to be palaeobiological taxa, but also by failing to distinguish fossils that represent living organisms from those that were likely to have been deceased (Chapter 5). Quantifying the duration over which fossilized organisms were subjected to effacement prior to burial is, although interesting in principle, likely to prove difficult. Furthermore, estimates of global Ediacaran diversity and disparity that include ivesheadiomorphs as palaeobiological taxa may be expected to have artificially inflated levels of those parameters (e.g. Shen et al., 2008b). Values for these parameters will be much lower once the presence of taphomorphs is fully incorporated into the studies of the Ediacara biota worldwide.

The lack of soft-bodied organisms preserved in a partially decayed state on bedding planes from the later Ediacaran, or indeed the Phanerozoic, points to a shift in taphonomy through the Ediacaran Period. It seems that a brief taphonomic window existed following the initial emergence of macroscopic organisms in deep marine ecosystems, in which decaying matter could be preserved alongside living creatures. The advent of macroscopic agents of degradation and decay (utilising scavenging, predation or pervasive bioturbation) subsequently removed ivesheadiomorphs and similar taphomorphs from the fossil record. Although soft-bodied organisms can be preserved in younger deposits, this generally occurs only under environmental conditions that preclude the activities of decay agents (e.g. the Cambrian Burgess Shale, Butterfield, 1990; or the Ordovician Fezouata Formation, Van Roy et al., 2010). When such conditions are combined with rapid sedimentation or mineral nucleation, the potential for the preservation of ivesheadiomorph-type taphomorphs is removed. Preservation of casts of microbial masses growing upon dead organisms therefore appears to have been an entirely Ediacaran phenomenon. Although such preservation can be explained by uniformitarian processes, the temporal restriction of ivesheadiomorphs to the Ediacaran Period results from the absence of several more characteristically Phanerozoic phenomena, such as bioturbation and scavenging.

The Ediacaran Period is, in the view of this author, losing its reputation as an enigma. As we gradually explain individual aspects of the biota, scientific consensus is beginning to shift towards viewing the Ediacara biota as a set of serious and surmountable puzzles. It is hoped that my own research career will contribute to further opening up Ediacaran palaeontology, both from a scientific and an educational point of view. Attention will now turn to two biological groups at the forefront of current Ediacaran research. Firstly, microbes, which despite being largely under-studied, are likely to have been a significant component of Avalonian ecosystems. The bearing this doctoral research has had upon the possible presence of metazoans, a group that has dominated Ediacaran thinking for decades, will then be discussed.

THE IMPORTANCE OF MICROBES IN AVALONIAN ECOSYSTEMS

The interactions between Ediacaran macro-organisms and microbial communities in the Avalon region have received little attention in the past. Microbial fossils are, however, of fundamental importance in understanding how Proterozoic ecosystems responded to the evolution of macroscopic organisms (cf. Seilacher and Pflüger, 1994; Brasier, 2009). We know that ultimately, macro-organisms colonised the sediment-water interface, pushing microbes into new, previously unexploited niches, and consequently changing the nature of sediment chemistry, marine biology, and fossil preservation (e.g. Brasier et al., 2011). The way in which this transition progressed warrants considerable future study.

Microbes (a term used herein to denote both microscopic prokaryotes and eukaryotes) have a long and established fossil record stretching from the Archaean Eon to the present day (e.g. Knoll, 2003 and references therein). Although debate continues as to the precise first appearance of particular microbial lineages (e.g. Schopf, 1993; Mojzsis et al., 1996; Brasier et al., 2002, 2005; Whitehouse et al., 2009), it is generally accepted that bacteria were present by ~3.5 Ga (Knoll, 2003; Wacey, 2009). Evidence for this, with varying degrees of reliability, comes in the form of fossilised macro-structures (such as stromatolites; Walter et al., 1980; though see Brasier, 2011), biomarkers (Summons et al., 1999), micro-borings produced by endolithic bacteria (Furnes et al., 1994; McLoughlin et al., 2007), microbially induced sedimentary structures (Noffke et al., 2006), and geochemical data (e.g. Ohmoto et al., 1993; Rosing, 1999).

Unlike the earliest Proterozoic fossil occurrences, where evidence for biogenicity cannot simply be taken at face value (e.g. McLoughlin et al., 2008; Wacey, 2010), confidence in the biogenicity of most Ediacaran microfossils is undoubted. Ediacaran microbes likely represented a wide range of prokaryotic metabolic pathways (e.g. osmotrophy, chemoautotrophy, photoautotrophy; Brasier et al., 2010). The Ediacara biota also shared their ecosystems with members of many of the major eukaryotic lineages, including heterotrophs (Porter, 2006), and several multicellular clades of uniseriate, multiseriate and coenocytic filaments (probably photoautotrophic) and complex vesicles (both prokaryotic and eukaryotic; Butterfield, 2009).

The fossil record of Ediacaran micro-organisms has previously been considered to be dominated by two categories of structures – organic walled microfossils (e.g. testate amoebae and acritarchs), which are considered to have inhabited the water column, and macroscopic surface fabrics created by microbial mats or biofilms. Acritarchs are common in many Ediacaran successions (Vidal and Moczydlowska-Vidal, 1997), but not the Avalon terrane. Although acritarchs are considered to have resided in the plankton during life, their limited suite of morphological characteristics makes definitive identification of their affinities difficult; comparisons with protistan cell-coats, reproductive structures, and egg cases have previously been proposed (see discussion in Vidal and Moczydlowska-Vidal, 1997). Some workers even consider them to be animal resting cysts (Cohen et al., 2009a). The Doushantuo Formation of China preserves a diverse assemblage of microfossils, including possible ciliates (Li et al., 2007) and proposed metazoan embryos (Xiao et al., 1998), but this unusual abundance is explained by a positive taphonomic bias towards remarkable phosphatic preservation (Xiao et al., 1998), which is largely atypical of the Avalon biota (Brasier et al., 2011).

Microbialites such as stromatolites and thrombolites were present prior to and during the Ediacaran Period (Shapiro, 2004 and references therein), but are almost completely absent from the relatively high latitude siliciclastic marine settings of the Avalon terrane, largely because syndepositional cementation is not a common feature of siliciclastic depositional environments (Noffke et al., 2002). Instead, the Avalon terrane preserves a suite of surface sedimentary textures that have been classified under a variety of different names. Microbially Induced Sedimentary Structures (MISS; Noffke et al., 2001; Noffke, 2009), potentially including microbial mats, biofilms and wrinkle structures (exhibiting reticulate, elephant skin, and linear fabrics amongst others; Hagadorn and Bottjer, 1997; Gehling, 1999; Porada and Bouougri, 2007), and most recently Textured Organic Surfaces (TOS, defined as a 'subset' of MISS that also considers the preservation of macroscopic organisms as well as the actions of microbes; Gehling and Droser, 2009), have all been described from Ediacaran bedding planes (e.g. Gehling, 1999; Gehling et al., 2005; Callow and Brasier, 2009a; Brasier et al., 2010; Laflamme et al., 2011). These subtly different terms are united in describing sedimentary impressions that record evidence of the presence or activity of microbes. In many Avalonian localities, these surface fabrics are evident as bubble-mat or wrinkle fabrics on the surfaces of the bedding planes (Fig. 7.1).

During the Ediacaran Period, microbial mats were a common component of both the shallow and deep marine seafloor. Their proposed role in the preservation of macrofossils, whereby they catalysed the rapid lithification of sediment in contact with organic matter, has already been discussed (Chapter 3; Gehling, 1999). Chapters 3–5 also demonstrated how breakdown of benthic organic matter sees microbes influencing fossil preservation in Avalonian marine environments. In addition to this, the presence of microbes was also likely to have been fundamentally important to the living components of the Ediacara biota. Microbial mats, bound by EPS membranes, would have potentially helped to tether organisms anchored within the sediment (e.g. *Charniodiscus* sp.) to the seafloor, preventing them from being uprooted by oceanic currents (Laflamme et al., 2011). There is purported evidence from Australian and Russian successions that some Ediacaran macro-organisms residing on the mats actively grazing upon them (e.g. "*Radulichnus*" traces produced by *Kimberella*; Seilacher et al., 2003, 2005), though discussion of absorptive feeding in *Dickinsonia* ('ghost' traces or *Epibaion*, Ivantsov and Malakhovskaya, 2002; Fedonkin, 2003; Ivantsov, 2011) remains controversial (McIlroy et al., 2009; Sperling and Vinther, 2010). In Avalonian strata, the extent of organism-mat interactions is relatively poorly studied. In spite of this, microbial fossils, and evidence for microbial activity, are clearly widespread in Avalonian successions. In shallow water settings, microbes are observed not just as microbial mat fabrics, but also preserved as individual fossilized filaments and spheroids (often in high fidelity; Callow and Brasier, 2009b). Indeed, microbial colonies may have been able to grow to such sizes that they themselves represent components of the Ediacaran macrobiota (Grazhdankin and Gerdes,

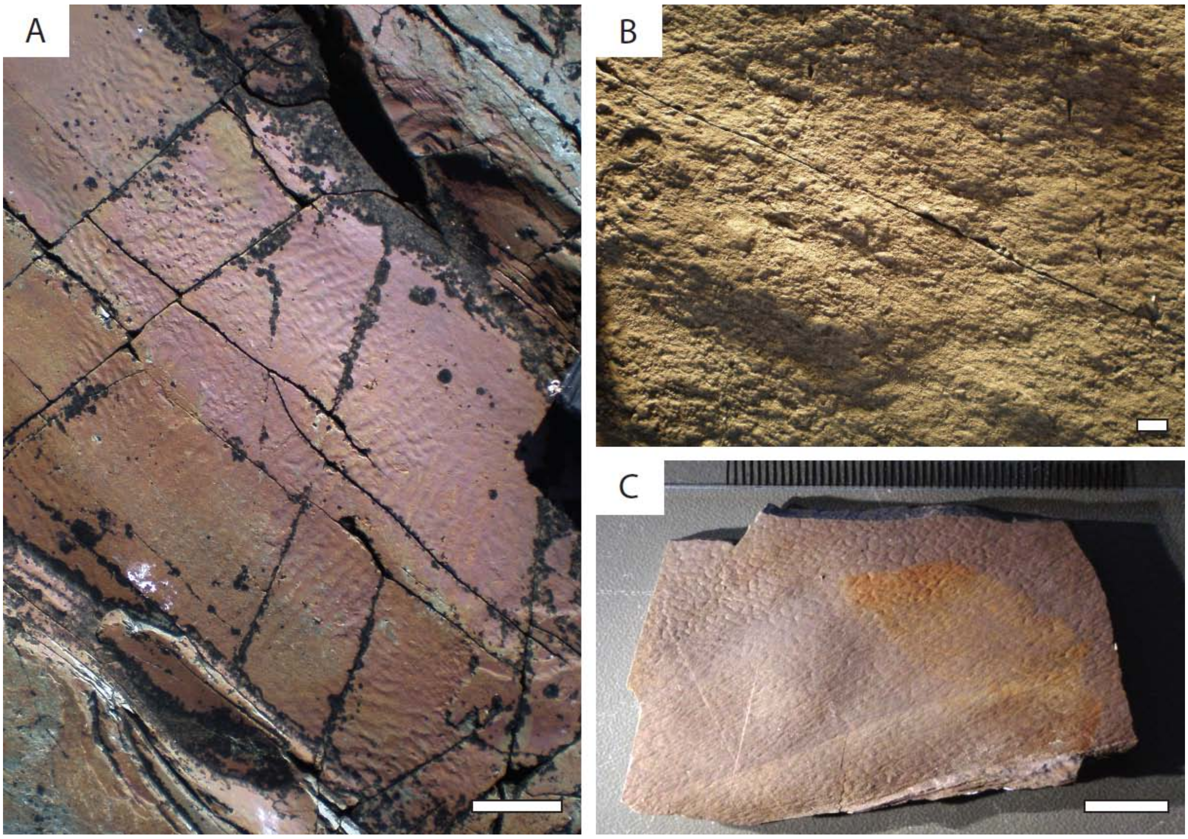

Fig. 7.1. Microbial mat fabrics from the Avalon region. **A**: Microbially-induced wrinkle surface from locality WH6, Mistaken Point Formation, Western Head, Newfoundland. **B**: Bubble-mat fabric from the bedding plane surface at Memorial Crags, Bradgate Formation, Charnwood, U.K. Image taken from cast. **C**: Elephant skin microbial mat from locality BV2, the Synalds Formation, Batch Valley, Longmynd, U.K. Specimen L-BV2-5. Scale bar in A = 50 mm. Scale bars in B–C = 10 mm. The cast photographed in B is the property of the British Geological Survey, and is housed in Keyworth, Nottinghamshire, U.K. Fig. 7.1B reproduced with the permission of the British Geological Survey © NERC. All rights reserved.

2007). Filamentous fossils described from the Conception Group of Newfoundland (Chapter 2) provide further evidence for the preservation potential of microbial organisms from deeper palaeoenvironments, and this often-overlooked but seemingly abundant component of the biota merits further study.

One subject that has not previously been considered is the potential impact of microbes upon nutrient cycling at the sediment-water interface. The decay and breakdown of large carcasses on the seafloor, implied by the effaced preservation hypothesis, could have released a substantial amount of finely disseminated organic matter into the environment immediately adjacent to the sediment-water interface. The degree to which non-photosynthetic biofilms and mats release or trap organic material is of interest here. If dissolved organic carbon was, as has been hypothesised (e.g. Sperling et al., 2011), a major food source for rangeomorph organisms utilising osmotic metabolisms (Laflamme et al., 2009), such microbial decay may have provided a substantial food reservoir, large enough to sustain the often dense assemblages of large macro-organisms. Such a scenario deserves consideration, and could reveal yet another important role for microbes in Ediacaran ecosystems.

THE PRESENCE OF METAZOANS

Determining whether early metazoans were present in Ediacaran successions is one of the primary objectives in Ediacaran palaeontology. The synonymization of the Avalonian genera *Ivesheadia*, *Shepshedia*, *Blackbrookia* and *Pseudovendia* (some of which had previously been interpreted as the remains of animals, e.g. Boynton and Ford, 1995) within the tapho-taxon ivesheadiomorpha, removes several proposed metazoan taxa from the Ediacaran literature (Chapter 3). Furthermore, a palaeoecological line of evidence commonly used to support an animal interpretation for the Ediacara biota (that of Clapham et al., 2003) is negated by demonstration that those palaeoecological studies do not stand up to either critical scrutiny, or consideration of effaced preservation (Chapter 5). It is also proposed that some aspects of the Avalonian biota, including several macroscopic organisms, are likely to be microbial in nature, such as the filamentous fossils found in abundance on exceptionally-preserved bedding planes (Chapter 2). While such findings do not preclude the presence of metazoans in the ecosystems, they demonstrate that if they were present, they likely shared the ecosystem with macroscopic members of other biological Kingdoms and Domains.

Nevertheless, some aspects of the research presented in this thesis are consistent with the presence of metazoans in Avalonian benthic ecosystems. The decay experiments documented in Chapter 4 demonstrate that the microbial decay of metazoan tissue (amongst others) is capable of producing effaced morphological features and impressions similar to those found as ivesheadiomorphs on Avalonian horizons. More importantly, evidence for locomotion in rocks ~565 Ma extends the record of such traces by 5–10 Myrs (Chapter 6). The Mistaken Point locomotion traces, comprising simple horizontal straight-to-curving surface impressions, suggest that some rare components of the Avalon biota possessed muscular tissues (Liu et al., 2010a). Such trace-makers were potentially capable of exerting a force on their surrounding substrate in order to facilitate movement, and thus were likely to have been of metazoan grade. Further examples of locomotion traces from younger Avalonian localities in Newfoundland and the U.K. demonstrate that this was not an isolated phenomenon (Chapter 6). Although we cannot yet assign specific Ediacaran fossils to the metazoa, or determine the phylum to which the original Mistaken Point trace-makers belonged, these trace fossils may constrain the first appearance of muscular tissue to the Avalon biotic assemblage, improving our understanding of metazoan evolution.

In conclusion, it is considered likely that metazoans were present in Avalonian ecosystems in the Ediacaran Period, but body fossils of such forms remain to be identified. Identifying taphomorphs and abiogenic impressions in Ediacaran assemblages, and critically testing those taxa and palaeoecological datasets proposed to demonstrate metazoan traits, is essential if we are to determine the true biological affinities of the Ediacaran macrobiota.

SUMMARY

The findings presented in this thesis paint an interesting picture of Avalonian Ediacaran fossil assemblages, which does not conform to the views of previous workers. Although this work does not directly provide biological affinities for the Ediacara macrobiota, it addresses several of the fundamental issues that have impeded that goal in the past. Insufficient fossilized morphological characteristics, a lack of preserved original organic material, and a wide range of preservational fidelity, require a multidisciplinary approach to assess the true importance of Ediacaran macrofossils in the history of life.

Creating a consistent taxonomy for the Ediacara biota is vital if the patterns observed in those palaeocommunities are to be considered robust. Removing tapho-taxa and constraining the stratigraphic ranges of fossil groups are essential steps towards determining the relationships and ecological patterns within the Ediacara biota. A better appreciation of the morphological variability imparted by taphonomic processes on the Ediacaran macro-organisms, and the processes by which this occurs, can enable us to make better informed interpretations about preserved Ediacaran biogenic structures.

From this work we can conclude seven major points:

1) The initial evolution and radiation of the Ediacara biota requires reassessment, following the discovery of a diverse assemblage of juvenile rangeomorph taxa just three million years after the Gaskiers glacial event.
2) Avalonian bedding plane fossil assemblages represent time-averaged communities of both living and deceased organisms at the time of burial.
3) The effaced fossil morphologies observed on Avalonian bedding planes can be replicated in the laboratory by subjecting extant organic matter to microbial decay and autolytic processes.
4) Microbial activity was likely to have been abundant and diverse on the Avalonian seafloor, with microbes playing an important role in the preservation, degradation, and maybe even nutrition of Ediacaran macro-organisms.
5) Modern palaeoecological methods cannot be reliably applied to fossil assemblages, due to taphonomic biases. Previous studies suggesting the Mistaken Point biota were animals based on the ecological structural attributes of the Mistaken Point assemblages are contested.
6) Animals possessing muscular tissue, and capable of locomotion, were arguably present in Avalonian ecosystems, though they do not appear to have been a dominant component of the deep marine environments.
7) Ediacaran palaeocommunities in the Avalon region were likely to include a diverse range of organisms belonging to several Domains, Kingdoms, and Phyla, in a similar way to the diverse ecosystems of the modern world. The biological affinities of Ediacaran taxa should be evaluated on a case-by-case basis, rather than shoehorning them all into one biological group.

These findings further our knowledge of Ediacaran palaeocommunities, but additional work is required before our level of understanding approaches that of the Phanerozoic biotas. As illustrated herein, important discoveries remain to be made in Ediacaran rocks, both in terms of exceptional finds (including remarkable preservation and new organisms), and original theoretical concepts. Further exploration of well known and new localities, combined with the application of both traditional and innovative analytical techniques, will continue to enhance our understanding of the Ediacara biota and its importance in the history of life.

FUTURE WORK

A key tenet of this thesis has been consolidating our basic understanding of the Ediacaran Period; the taxonomy and taphonomy upon which research into evolutionary processes at this time are based. Although the Ediacara biota may eventually enable us to ascertain when, how and why metazoans evolved, our immediate goals should focus upon strengthening our understanding of the fundamental palaeontology and taphonomy of these assemblages.

Firstly, workers should attempt to constrain the stratigraphic and temporal extent of Ediacaran macrofossils below the level of Pigeon Cove beds, utilising sedimentary successions from Newfoundland and elsewhere. This will allow correct placement of the Ediacara biota within a Proterozoic to Cambrian context. Exploration of Ediacaran strata worldwide, at all levels, by multiple scientists, is necessary both to find more taxa, and to identify redundant taxa for synonymization. A consistent global taxonomy for the Ediacara biota is achievable, and consideration should soon be given to the production of an official treatise on the biota. Such a process is necessary if we are to determine the evolutionary and ontogenetic relationships between taxa. Accurate radiometric dates, from numerous fossil-bearing levels, would greatly assist in correlating fossil assemblages between regions.

If the Conception Group trace fossils (Chapter 6) are accepted as the first evidence for metazoan locomotion, it is necessary to determine the identity of the trace makers, and find further fossilized vestiges of such impressions. The realm of microbial fossils also deserves extensive study, and attempts should be made to identify the specific biological groups to which they belong, be that through morphological analogy or experimental analysis. Microbes are conspicuous and seemingly influential components of Avalonian ecosystems, and they therefore must be considered if we are to fully understand the biology of the Ediacaran macrobiota.

Appreciating the taphonomic processes that have enabled these remarkable organisms to be preserved is vital if we are to make informed and reasoned judgements regarding their morphology, biology, and ecology. Taphonomic processes include not only secondary actions such as post-burial diagenesis, but also the sedimentological, biological, microbial and chemical means by which these remains were preserved. Although considerable advances have been made in the field of Ediacaran taphonomy in recent years, many of them by this working group (e.g. McIlroy and Logan, 1999; Mapstone and McIlroy, 2006; Callow and Brasier, 2009a; McIlroy et al., 2009; Brasier et al., 2011; Liu et al., 2011), important questions remain. Neither ash gently settling through a deep water column, nor volcaniclastic turbidity currents, can satisfactorily explain the preservation of Avalonian rangeomorphs on many surfaces. Similarly, very little is known about the relative roles of ash and microbes in the early lithification of fossil surfaces above and below Ediacaran fossils. Experimental taphonomy, which has proved its utility in this study (Chapter 4), has enormous potential to inform our understanding of these issues. Investigation of the biogeochemistry acting upon the near-fossil pore-water system is one way in which advances in our understanding of this area could be made. Further work to verify the environments of deposition of many of the Avalonian settings would also be beneficial in this regard. For example, the documentation of positive evidence for deep-water depositional environments in the Conception Group would remove a lot of the scepticism currently surrounding the depth of these successions (e.g. Retallack, 2010).

Rigorous and thoughtful scientific endeavour will enable us to further our knowledge of this unique and stimulating period in the history of life on Earth. Once the foundations of Ediacaran palaeontology are sufficiently robust, we can then begin to meaningfully discuss the evolutionary significance of the Ediacara biota, and compare palaeoecology or taxonomic diversity across disparate terranes. It must be remembered that we are still in the early years of intensive Ediacaran research. Countless discoveries await us, which will likely be equally as unexpected and unusual as those that have already been made. Although we are currently achieving significant advances in this field, there remains much to be done before we can truly appreciate the significance and biology of this, most intriguing, time interval.

REFERENCES

Abrajevitch, A. & R. Van der Voo 2010: Incompatible Ediacaran paleomagnetic directions suggest an equatorial geomagnetic dipole hypothesis. *Earth and Planetary Science Letters*, **293,** 164-170.

Allen, P. A. & J. L. Etienne 2008: Sedimentary challenge to Snowball Earth. *Nature Geoscience,* **1,** 817-825.

Allison, P. A. 1986: Soft-bodied animals in the fossil record: The role of decay in fragmentation during transport. *Geology,* **14,** 979-981.

Anderson, M. M. & S. B. Misra 1968: Fossils found in the Pre-Cambrian Conception Group of South-eastern Newfoundland. *Nature*, **220,** 680-681.

Ansted, D. T. 1866: *The physical geography and geology of the county of Leicestershire*. Nichols and Sons, Westminster. 70 pp.

Antcliffe, J. B. & M. D. Brasier 2007a: *Charnia* and sea pens are poles apart. *Journal of the Geological Society, London,* **164,** 49-51.

—— 2007b: Towards a morphospace for the Ediacara biota. *In*: P. Vickers-Rich & P. Komarower (eds): *The Rise and Fall of the Ediacaran Biota*, Geological Society, London, Special Publications, **286,** 377-386, London.

—— 2008: *Charnia* at 50: Developmental models for Ediacaran fronds. *Palaeontology,* **51,** 11-26.

Attenborough, D. & M. Kaplan 2010: *First Life*. Harper Collins, London. 288 pp.

Babcock, L. E., A. M. Grunow, G. R. Sadowski & S. A. Leslie 2005: *Corumbella*, an Ediacaran-grade organism from the Late Neoproterozoic of Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **220,** 7-18.

Bailey, J. V., S. B. Joye, K. M. Kalanetra, B. E. Flood & F. A. Corsetti 2007: Evidence of giant sulphur bacteria in Neoproterozoic phosphorites. *Nature*, **445,** 198-201.

Baird, B. H., D. E. Nivens, J. H. Parker & D. C. White 1985: The biomass, community structure, and spatial distribution of the sedimentary microbiota from a high-energy area of the deep sea. *Deep-sea Research*, **32,** 1089-1099.

Bamforth, E. L. & G. M. Narbonne 2009: New Ediacaran rangeomorphs from Mistaken Point, Newfoundland, Canada. *Journal of Paleontology*, **83,** 897-913.

Bamforth, E. L., G. M. Narbonne & M. M. Anderson 2008: Growth and Ecology of a Multi-branched Ediacaran Rangeomorph from the Mistaken Point Assemblage, Newfoundland. *Journal of Paleontology*, **82,** 763-777.

Batham, E. J. & C. F. A. Pantin 1950: Muscular and hydrostatic action in the sea-anemone *Metridium senile* (L.). *Journal of Experimental Biology*, **27,** 264-289.

Bengtson, S., B. Rasmussen & B. Krapež 2007: The Paleoproterozoic megascopic Stirling biota. *Paleobiology*, **33,** 351-381.

Benus, A. P. 1988: Sedimentological context of a deep-water Ediacaran fauna (Mistaken Point, Avalon Zone, eastern Newfoundland). *In*: E. Landing, G. M. Narbonne & P. M. Myrow (eds): *Trace Fossils, Small Shelly Fossils and the Precambrian-Cambrian Boundary*, Vol. **463,** 8-9, New York State Museum and Geological Survey Bulletin.

Billings, E. 1872: On some fossils from the Primordial rocks of Newfoundland. *Naturaliste Canadien*, **6,** 465-479.

Black, M. 1933: The algal sediments of Andros Islands, Bahamas. *Royal Society of London Philosophical Transactions Series B*, **222,** 165-192.

Bogdanova, S. V., S. A. Pisarevsky & Z. X. Li 2009: Assembly and breakup of Rodinia (some results of IGCP Project 440). *Stratigraphy and Geological Correlation*, **17,** 259-274.

Boggs Jr., S. 2009: *Petrology of sedimentary rocks*. 2nd ed., Cambridge University Press, Cambridge, 600 pp.

Bottjer, D. J. 2002: Enigmatic Ediacara Fossils: Ancestors or Aliens? *In*: D. J. Bottjer, W. Etter, J. W. Hagadorn & C. M. Tang (eds): *Exceptional Fossil Preservation*, 11-33, Columbia University Press, New York. 424 pp.

Bottjer, D. J., J. W. Hagadorn & S. Q. Dornbos 2000: The Cambrian substrate revolution. *GSA Today*, **10,** 1-7.

Bouma, A. H. 1962: *Sedimentology of some Flysch deposits: a graphic approach to facies interpretation*. Elsevier, Amsterdam. 168 pp.

Bowring, S. A., P. M. Myrow, E. Landing & J. Ramenzani 2003: Geochronological constraints on terminal Neoproterozoic events and the rise of metazoans. *Geophysical Research Abstracts*, **5,** Abstract 13219.

Boyle, R. A., T. M. Lenton & H. T. P. Williams 2007: Neoproterozoic 'snowball Earth' glaciations and the evolution of altruism. *Geobiology*, **5,** 337-349.

Boynton, H. E. 1978: Fossils from the Pre-Cambrian of Charnwood Forest, Leicestershire. *Mercian Geologist*, **6,** 291-296.

—— 1999: New fossils in the Precambrian of Charnwood Forest, Leicestershire, England. *Mercian Geologist*, **14,** 197-200.

Boynton, H. E. & T. D. Ford 1979: *Pseudovendia charnwoodensis* - A new Precambrian Arthropod from Charnwood Forest, Leicestershire. *Mercian Geologist*, **7,** 175-177.

—— 1995: Ediacaran fossils from the Precambrian (Charnian Supergroup) of Charnwood Forest, Leicestershire, England. *Mercian Geologist*, **13,** 165-182.

—— 1996: Ediacaran fossils from the Precambrian (Charnian Supergroup) of Charnwood Forest, Leicestershire, England - revision of nomenclature. *Mercian Geologist*, **14,** 3.

Brasier, M. D. 1992: Background to the Cambrian Explosion. *Journal of the Geological Society, London*, **149,** 585-587.

—— 2009: *Darwin's Lost World. The Hidden History of Animal Life.* Oxford University Press, Oxford. 304 pp.

—— 2011: Towards a null hypothesis for stromatolites. *In*: S. D. Golding & M. Glikson (eds): *Earliest life on Earth: Habitats, environments and methods of detection*, 115-125, Springer Science+Business Media B.V., Dordrecht. 316 pp.

Brasier, M. D. & J. B. Antcliffe 2004: Decoding the Ediacaran enigma. *Science*, **305,** 1115-1117.

—— 2008: *Dickinsonia* from Ediacara: A new look at morphology and body construction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **270,** 311-323.

—— 2009: Evolutionary relationships within the Avalonian Ediacara biota: new insights from laser analysis. *Journal of the Geological Society, London*, **166,** 363-384.

Brasier, M. D. & J. F. Lindsay 2001: Did supercontinent amalgamation trigger the Cambrian Explosion? *In*: A. Y. Zhuravlev & R. Riding (eds): *The ecology of the Cambrian radiation. Perspectives in palaeobiology and Earth history*, 69-89, Columbia University Press, New York.

Brasier, M. D., J. Cowie & M. Taylor 1994: Decision on the Precambrian-Cambrian boundary. *Episodes*, **17,** 95-100.

Brasier, M. D., O. R. Green, A. P. Jephcoat, A. K. Kleppe, M. J. Van Kranendonk, J. F. Lindsay, A. Steele & N. V. Grassineau 2002: Questioning the evidence for Earth's oldest fossils. *Nature*, **416,** 76-81.

Brasier, M. D., O. R. Green, J. F. Lindsay, N. McLoughlin, A. Steele & C. Stoakes 2005: Critical testing of Earth's oldest putative fossil assemblage from the ~3.5 Ga Apex chert, Chinaman Creek, Western Australia. *Precambrian Research*, **140,** 55-102.

Brasier, M. D., R. H. T. Callow, L. R. Menon & A. G. Liu 2010: Osmotrophic Biofilms: From Modern to Ancient. *In*: J. Seckbach & A. Oren (eds): *Microbial Mats: Modern and Ancient Microorganisms in Stratified Systems*. Cellular Origin, Life in Extreme Habitats and Astrobiology, Vol. **14,** 131-148, Springer Science+Business Media B.V., Dordrecht. 500 pp.

Brasier, M. D., J. B. Antcliffe & R. H. T. Callow 2011: Evolutionary Trends in Remarkable Fossil Preservation Across the Ediacaran-Cambrian Transition and the Impact of Metazoan Mixing. *In*: P. A. Allison & D. J. Bottjer (eds): *Taphonomy: Process and Bias Through Time*. 2nd edition, Topics in Geobiology, Vol. **32,** 519-567, Springer Science+Business Media B.V. 599 pp.

Briggs, D. E. G. 1995: Experimental taphonomy. *Palaios,* **10,** 539-550.

—— 2003: The role of decay and mineralization in the preservation of soft-bodied fossils. *Annual Reviews in Earth and Planetary Sciences*, **31,** 275-301.

Briggs, D. E. G. & A. J. Kear 1993: Fossilization of Soft Tissue in the Laboratory. *Science*, **259,** 1439-1442.

—— 1994: Decay and Mineralization of Shrimps. *Palaios,* **9,** 431-456.

Bristow, T. F. & M. J. Kennedy 2008: Carbon isotope excursions and the oxidant budget of the Ediacaran atmosphere and ocean. *Geology,* **36,** 863-866.

Bruton, D. L. 1991: Beach and laboratory experiments with the jellyfish *Aurelia* and remarks on some fossil "medusoid" traces. *In*: A. Simonetta & S. Conway Morris (eds): *The Early Evolution of Metazoa and the Significance of Problematic Taxa*, 125-129, Cambridge University Press, Cambridge.

Buchanan, J. B. & R. H. Hedley 1960: A contribution to the biology of *Astrorhiza limicola* (Foraminifera). *Journal of the Marine Biological Association, U.K.,* **39,** 549-560.

Budd, G. E. 2008: The earliest fossil record of the animals and its significance. *Philosophical Transactions of the Royal Society, London, Series B,* **363,** 1425-1434.

Burki, F., K. Shalchian-Tabrizi, M. Minge, A. Skjæveland, S. I. Nikolaev, K. Jakobsen & J. Pawlowski 2007: Phylogenomics reshuffles the Eukaryotic Supergroups. *PLOS one,* **2,** e790.

Butterfield, N. J. 1990: Organic Preservation of Non-Mineralizing Organisms and the Taphonomy of the Burgess Shale. *Paleobiology,* **16,** 272-286.

—— 2005: Probable Proterozoic fungi. *Paleobiology,* **31,** 165-182.

—— 2009a: Oxygen, animals and oceanic ventilation: an alternative view. *Geobiology,* **7,** 1-7.

—— 2009b: Modes of pre-Ediacaran multicellularity. *Precambrian Research*, **173,** 201-211.

—— 2011: Animals and the invention of the Phanerozoic Earth system. *Trends in Ecology and Evolution*, **26,** 81-87.

Cai, Y., H. Hua, S. Xiao, J. D. Schiffbauer & P. Li 2010: Biostratinomy of the late Ediacaran pyritized Gaojiashan lagerstätte from southern Shaanxi, south China: Importance of event deposits. *Palaios*, **25,** 487-506.

Cai, Y., H. Hua, A. Y. Zhuravlev, J. A. Gámez Vintaned & A. Y. Ivantsov 2011: Discussion of 'First finds of problematic Ediacaran fossil *Gaojiashania* in Siberia and its origin'. *Geological Magazine* **148,** 329-333.

Callow, R. H. T. & M. D. Brasier 2009a: Remarkable preservation of microbial mats in Neoproterozoic siliciclastic settings: Implications for Ediacaran taphonomic models. *Earth Science Reviews*, **96,** 207-219.

—— 2009b: A solution to Darwin's dilemma of 1859: Exceptional preservation in Salter's material from the late Ediacaran Longmyndian Supergroup, England. *Journal of the Geological Society, London*, **166,** 1-4.

Callow, R. H. T., D. McIlroy & M. D. Brasier, Submitted: John Salter and the Ediacara Fauna of the Longmyndian Supergroup.

Canfield, D. E., S. W. Poulton & G. M. Narbonne 2007: Late-Neoproterozoic deep-ocean oxygenation and the rise of animal life. *Science*, **315,** 92-95.

Canfield, D. E., S. W. Poulton, A. H. Knoll, G. M. Narbonne, G. Ross, T. Goldberg & H. Strauss 2008: Ferruginous conditions dominated later Neoproterozoic deep-water chemistry. *Science*, **321,** 949-952.

Carney, J. N. 1999: Revisiting the Charnian Supergroup: new advances in understanding old rocks. *Geology Today*, **November-December 1999**, 221-229.

—— 2000: Charnwood Forest. *In*: J. N. Carney, J. M. Horák, T. C. Pharaoh, W. Gibbons, D. Wilson, W. J. Barclay & R. E. Bevins (eds): *Precambrian Rocks of England and Wales*, Geological Conservation Review Series, Vol. **20,** p. 19, Joint Nature Conservation Committee, Peterbrough.

Carney, J. N., J. M. Horák, T. C. Pharaoh, W. Gibbons, D. Wilson, W. J. Barclay & R. E. Bevins 2000: *Precambrian Rocks of England and Wales*. 1st edition, Geological Conservation Review Series, Vol. **20,** Joint Nature Conservation Committee, Peterborough. 252 pp.

Catling, D. C., C. R. Glein, K. J. Zahnle & C. P. McKay 2005: Why O_2 is required by complex life on habitable planets and the concept of planetary "oxygenation time". *Astrobiology*, **5,** 415-438.

Cavalier-Smith, T. 2002: The phagotrophic origin of eukaryotes and phylogenetic classification of Protozoa. *International Journal of Systematic and Evolutionary Microbiology*, **52,** 297-354.

—— 2010: Deep phylogeny, ancestral groups and the four ages of life. *Philosophical Transactions of the Royal Society, London, Series B*, **365,** 111-132.

Chapman, S. J. & T. R. G. Gray 1986: Importance of cryptic growth, yield factors and maintenance energy in models of microbial growth in soil. *Soil Biology and Biochemistry*, **18,** 1-4.

Chumakov, N. M. 2007: Climates and climate zonality of the Vendian: geological evidence. *In*: P. Vickers-Rich & P. Komarower (eds): *The Rise and Fall of the Ediacaran Biota*, Geological Society, London, Special Publications, Vol. **286,** 15-26, London.

—— 2009: The Baykonurian glaciohorizon of the late Vendian. *Stratigraphy and Geological Correlation*, **17,** 373-381.

—— 2010: Precambrian glaciations and associated biospheric events. *Stratigraphy and Geological Correlation*, **18,** 467-479.

Clapham, M. E. 2011: Ordination Methods and the Evaluation of Ediacaran Communities. *In*: M. Laflamme, J. D. Schiffbauer & S. Q. Dornbos (eds): *Quantifying the Evolution of Early Life*. Topics in Geobiology, Vol. **36,** 3-21, Springer Science+Business Media B.V., Dordrecht. 462 pp.

Clapham, M. E. & G. M. Narbonne 2002: Ediacaran epifaunal tiering. *Geology*, **30,** 627-630.

Clapham, M. E., G. M. Narbonne & J. G. Gehling 2003: Paleoecology of the oldest known animal communities: Ediacaran assemblages at Mistaken Point, Newfoundland. *Paleobiology*, **29,** 527-544.

Clapham, M. E., G. M. Narbonne, J. G. Gehling, C. Greentree & M. M. Anderson 2004: *Thectardis avalonensis*: a new Ediacaran fossil from the Mistaken Point biota, Newfoundland. *Journal of Paleontology*, **78,** 1031-1036.

Cloud Jr., P. E. 1968: Atmospheric and Hydrospheric Evolution on the Primitive Earth. *Science*, **160,** 729-736.

Cohen, P. A., A. H. Knoll & R. B. Kodner 2009a: Large spinose microfossils in Ediacaran rocks as resting stages of early animals. *Proceedings of the National Academy of Sciences, USA*, **106,** 6519-6524.

Cohen, P. A., A. Bradley, A. H. Knoll, J. P. Grotzinger, S. Jensen, J. Abelson, K. Hand, G. Love, J. Metz, N. McLoughlin, P. Meister, R. Shepard, M. Tice & J. P. Wilson 2009b: Tubular compression fossils from the Ediacaran Nama Group, Namibia. *Journal of Paleontology*, **83,** 110-122.

Collins, A. G., J. H. Lipps & J. W. Valentine 2000: Modern mucociliary creeping trails and the bodyplans of Neoproterozoic trace-makers. *Paleobiology*, **26,** 47-55.

Compston, W., A. E. Wright & P. Toghill 2002: Dating the Late Precambrian volcanicity of England and Wales. *Journal of the Geological Society, London*, **159,** 323-339.

Condon, D. J., M.-Y. Zhu, S. A. Bowring, W. Wang, A. Yang & Y. Jin 2005: U-Pb Ages from the Neoproterozoic Doushantuo Formation, China. *Science*, **308,** 95-98.

Conway Morris, S. 1979: The Burgess Shale (Middle Cambrian) Fauna. *Annual Review of Ecology and Systematics*, **10,** 327-349.

—— 1985: The Ediacaran biota and early metazoan evolution. *Geological Magazine*, **122,** 77-81.

—— 1993: Ediacaran-like fossils in Cambrian Burgess Shale-type faunas of North America. *Palaeontology*, **36,** 593-635.

Cope, J. C. W. 1977: An Ediacara-type fauna from South Wales. *Nature*, **268,** 624.

Cope, J. C. W. & R. E. Bevins 1993: The stratigraphy and setting of the Precambrian rocks of the Llangynog Inlier, Dyfed, South Wales. *Geological Magazine*, **130,** 101-111.

Costerton, J. W. & P. Stoodley 2003: Microbial biofilms: protective niches in ancient and modern geomicrobiology. *In*: W. E. Krumbein, D. M. Paterson & G. A. Zavarzin (eds): *Fossil and Recent Biofilms*, xv-xxi, Kluwer Academic Press, Dordrecht. 504 pp.

Crimes, T. P. 1992: The record of trace fossils across the Proterozoic-Cambrian boundary. *In*: J. H. Lipps & P. W. Signor (eds): *Origin and early evolution of the Metazoa*, Topics in Geobiology, Vol. **10,** 177-202, Plenum Press, New York.

Crimes, T. P. & M. L. Droser 1992: Trace fossils and bioturbation: the other fossil record. *Annual Review of Ecology and Systematics*, **23,** 339-360.

Curtis, C. D., M. L. Coleman & L. G. Love 1986: Pore water evolution during sediment burial from isotopic and mineral chemistry of calcite, dolomite and siderite concretions. *Geochimica et Cosmochimica Acta*, **50,** 2321-2334.

Dalziel, I. W. D. 1997: Neoproterozoic-Paleozoic geography and tectonics: Review, hypothesis, environmental speculation. *Geological Society of America Bulletin*, **109,** 16-42.

Darwin, C. R. 1859: *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. 1st edition, John Murray, London. 502 pp.

Deflandre, G. 1937: Microfossiles des silex crétacés. Deuxième partie. Flagellés *incertae sedis*. Hystrichosphaerides. Sarcodinés. Organismes divers. *Annales de Paléontologie*, **26,** 51-103.

Dobrzinsky, N. & H. Bahlburg 2007: Sedimentology and environmental significance of the Cryogenian successions of the Yangtze Platform, South China block. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **254,** 100-122.

Droser, M. L. & D. J. Bottjer 1993: Trends and patterns of Phanerozoic ichnofabrics. *Annual Reviews in Earth and Planetary Sciences*, **21,** 205-225.

Droser, M. L. & J. G. Gehling 2008: Synchronous Aggregate Growth in an Abundant New Ediacaran Tubular Organism. *Science*, **319,** 1660-1662.

Droser, M. L., S. R. Jensen & J. G. Gehling 2002: Trace fossils and substrates of the terminal Proterozoic-Cambrian transiton: Implications for the record of early bilaterians and sediment mixing. *Proceedings of the National Academy of Science, U.S.A.*, **99,** 12572-12576.

Droser, M. L., J. G. Gehling & S. Jensen 2005: Ediacaran trace fossils: True and false. *In*: D. E. G. Briggs (ed): *Evolving form and function: Fossils and development*, 125-138, Yale Peabody Museum of National History, New Haven, Connecticut. 288 pp.

Droser, M. L., J. G. Gehling & S. R. Jensen 2006: Assemblage palaeoecology of the Ediacara biota: The unabridged edition? *Palaeogeography, Palaeoclimatology, Palaeoecology*, **232,** 131-147.

Dyni, J. R. & J. E. Hawkins 1981: Lacustrine turbidites in the Green River Formation, northwestern Colorado. *Geology*, **9,** 235-238.

Dzik, J. 2003: Anatomical Information Content in the Ediacaran Fossils and Their Possible Zoological Affinities. *Integrative and Comparative Biology*, **43,** 114-126.

Edgecombe, G. D. 2009: The ever enigmatic Ediacarans. *BioScience*, **59,** 527-528.

Engelbrecht, J. F. P. 1998: Groundwater pollution from cemeteries. *The Water Institute of Southern Africa, Biennial Conference and Exhibition*, **1,** 1-8.

Erwin, D. H. 2008: Wonderful Ediacarans, wonderful cnidarians? *Evolution and Development*, **10,** 263-264.

Etienne, J. L., P. A. Allen, R. Rieu & E. Le Guerroué 2009: Neoproterozoic Glaciated Basins: A Critical Review of the Snowball Earth Hypothesis by Comparison with Phanerozoic Glaciations. *In*: M. J. Hambrey, P. Christoffersoen, N. F. Glasser & B. Hubbard (eds): *Glacial Sedimentary Processes and Products*, Chapter 19, 343-399, Blackwell Publishing Ltd, Oxford. 436 pp.

Fedonkin, M. A. 1981: Belomorskaya Biota Venda. *Trudy Akademii Nauk SSSR*, **342,** 1-100.

—— 2003: The origin of the Metazoa in the light of the Proterozoic fossil record. *Paleontological Research*, **7,** 9-41.

Fedonkin, M. A. & A. Y. Ivantsov 2007: *Ventogyrus*, a possible siphonophore-like trilobozoan coelenterate from the Vendian Sequence (late Neoproterozoic), northern Russia. *In*: P. Vickers-Rich & P. Komarower (eds): *The rise and fall of the Ediacaran biota*, Geological Society, London, Special Publications, Vol. **286,** 187-194, London.

Fedonkin, M. A., J. G. Gehling, K. Grey, G. M. Narbonne & P. Vickers-Rich 2007a: *The Rise of Animals: Evolution and Diversification of the Kingdom Animalia*. 1st edition, John Hopkins University Press, Baltimore. 344 pp.

Fedonkin, M. A., A. Simonetta & A. Y. Ivantsov 2007b: New data on *Kimberella*, the Vendian mollusc-like organism (White Sea region, Russia): palaeoecological and evolutionary implications. *In*: P. Vickers-Rich & P. Komarower (eds): *The rise and fall of the Ediacaran biota*, Geological Society, London, Special Publications, Vol. **286,** 157-179, London.

Fike, D. A., J. P. Grotzinger, L. M. Pratt & R. E. Summons 2006: Oxidation of the Ediacaran Ocean. *Nature*, **444,** 744-747.

Flude, L. I. & G. M. Narbonne 2008: Taphonomy and ontogeny of a multibranched Ediacaran fossil: *Bradgatia* from the Avalon Peninsula of Newfoundland. *Canadian Journal of Earth Sciences*, **45,** 1095-1109.

Ford, T. D. 1958: Precambrian fossils from Charnwood Forest. *Proceedings of the Yorkshire Geological Society*, **31,** 211-217.

—— 1980: The Ediacaran fossils of Charnwood Forest, Leicestershire. *Proceedings of the Geological Association*, **91,** 81-83.

—— 1999: The Precambrian fossils of Charnwood Forest. *Geology Today*, **November-December 1999,** 230-234.

Furnes, H., N. R. Banerjee, K. Muehlenbachs, H. Staudigel & M. de Wit 1994: Early life recorded in Archean pillow lavas. *Science*, **304,** 578-581.

Gardiner, S. & R. N. Hiscott 1988: Deep-water facies and depositional setting of the lower Conception Group (Hadrynian), southern Avalon Peninsula, Newfoundland. *Canadian Journal of Earth Sciences*, **25,** 1579-1594.

Gast, V. & K. Gocke 1988: Vertical distribution of number, biomass and size-class spectrum of bacteria in relation to oxic/anoxic conditions in the Central Baltic Sea. *Marine Ecology Progress Series*, **45,** 179-186.

Gehling, J. G. 1987: Earliest known echinoderm - a new Ediacaran fossil from the Pound Subgroup of South Australia. *Alcheringa*, **11,** 337-345.

—— 1988: A cnidarian of actinian-grade from the Ediacaran Pound Subgroup, South Australia. *Alcheringa*, **12,** 299-314.

—— 1991: The case for Ediacaran fossil roots to the metazoan tree. *Memoir of the Geological Society of India*, **20,** 181-224.

—— 1999: Microbial Mats in Terminal Proterozoic Siliciclastics: Ediacaran Death Masks. *Palaios*, **14,** 40-57.

—— 2007: Fleshing out the Ediacaran period. *In*: P. Vickers-Rich & P. Komarower (eds): *The Rise and Fall of the Ediacaran Biota*, Geological Society, London, Special Publications, Vol. **286,** 425-428, London.

Gehling, J. G. & J. K. Rigby 1996: Long expected sponges from the Neoproterozoic Ediacara fauna of south Australia. *Journal of Paleontology*, **70,** 185-195.

Gehling, J. G. & G. M. Narbonne 2007: Spindle-shaped Ediacara fossils from the Mistaken Point assemblage, Avalon Zone, Newfoundland. *Canadian Journal of Earth Sciences*, **44,** 367-387.

Gehling, J. G. & M. L. Droser 2009: Textured organic surfaces associated with the Ediacara biota in South Australia. *Earth Science Reviews*, **96,** 196-206.

Gehling, J. G., G. M. Narbonne & M. M. Anderson 2000: The first named Ediacaran body fossil, *Aspidella terranovica*. *Palaeontology*, **43,** 427-456.

Gehling, J. G., M. L. Droser, S. R. Jensen & B. N. Runnegar 2005: Ediacaran organisms: relating form and function. *In*: D. E. G. Briggs (ed): *Evolving form and function: fossils and development*, 43-67, Yale University, New Haven, Connecticut. 288 pp.

Germs, G. J. B. 1972: New shelly fossils from Nama Group, South West Africa. *American Journal of Science*, **272,** 752-761.

Getty, P. R. & J. W. Hagadorn 2009: Palaeobiology of the *Climactichnites* tracemaker. *Palaeontology*, **52,** 753-778.

Gibson, G. G. 1989: Trace Fossils from Late Precambrian Carolina Slate Belt, South-Central North Carolina. *Journal of Paleontology*, **63,** 1-10.

Glaessner, M. F. 1958: New fossils from the base of the Cambrian in South Australia. *Transactions of the Royal Society of South Australia,* **81,** 185-188.

—— 1980: *Parvancorina* - an arthropod from the Late Precambrian (Ediacarian) of South Australia. *Ann. Naturhistorisches Museum Wien,* **83,** 83-90.

—— 1984: *The dawn of animal life: A biohistorical study*. Cambridge University Press, Cambridge. 258 pp.

Glaessner, M. F. & M. R. Walter 1975: New Precambrian fossils from the Arumbera Sandstone, Northern Territory, Australia. *Alcheringa*, **1,** 59-69.

Gnilovskaya, M. B. 1983: Vendotaenides. *In:* A. D. Urbanek & A. Y. Rozanov (eds): Upper Precambrian and Cambrian Palaeontology of the East-European Platform, 46-56, Publishing House Wydawnictwa Geologiczne, Warszawa. 158 pp.

Gradstein, F. M., J. G. Ogg & A. G. Smith 2004: *A Geologic Time Scale*. Cambridge University Press, Cambridge. 610 pp.

Grazhdankin, D. 2000: The Ediacaran genus *Inaria*: a taphonomic/morphodynamic analysis. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **216,** 1-34.

—— 2004: Patterns of distribution in the Ediacaran biotas: facies versus biogeography and evolution. *Paleobiology*, **30,** 203-221.

Grazhdankin, D. & A. Seilacher 2002: Underground Vendobionta from Namibia. *Palaeontology*, **45,** 57-78.

Grazhdankin, D. & G. Gerdes 2007: Ediacaran microbial colonies. *Lethaia*, **40,** 201-210.

Grazhdankin, D., U. Balthasar, K. E. Nagovitsin & B. B. Kochnev 2008: Carbonate-hosted Avalon-type fossils in arctic Siberia. *Geology*, **36,** 803-806.

Grey, K. & C. R. Calver 2007: Correlating the Ediacaran of Australia. *In*: P. Vickers-Rich & P. Komarower (eds): *The Rise and Fall of the Ediacaran Biota*, Geological Society, London, Special Publications, Vol. **286,** 115-135, London.

Grotzinger, J. P., S. A. Bowring & B. Z. Saylor 1995: Biostratigraphic and geochronologic constraints on early animal evolution. *Science*, **270,** 598-604.

Grotzinger, J. P., W. A. Watters & A. H. Knoll 2000: Calcified metazoans in thrombolite-stromatolite reefs of the terminal Proterozoic Nama Group, Namibia. *Paleobiology*, **26,** 334-359.

Gürich, G. 1933: Die Kuibis-Fossilien der Nama-Formation von Südwestafrika. *Paläontologische Zeitschrift*, **15,** 137-154.

Hagadorn, J. W. & D. J. Bottjer 1997: Wrinkle structures: Microbially mediated sedimentary structures common in subtidal siliciclastic settings at the Proterozoic-Phanerozoic transition. *Geology*, **25,** 1047-1050.

Hagadorn, J. W. & B. Waggoner 2000: Ediacaran fossils from the southwestern Great Basin, United States. *Journal of Paleontology*, **74,** 349-359.

Hagadorn, J. W., S. Xiao, P. C. J. Donoghue, S. Bengtson, N. J. Gostling, M. Pawlowska, E. C. Raff, R. A. Raff, F. R. Turner, C. Yin, C. Zhou, X. Yuan, M. B. McFeely, M. Stampanoni & K. H. Nealson 2006: Cellular and subcellular structure of Neoproterozoic animal embryos. *Science*, **314,** 291-294.

Halverson, G. P., P. F. Hoffman, D. P. Schrag, A. C. Maloof & A. H. N. Rice 2005: Toward a Neoproterozoic composite carbon-isotope record. *Geological Society of America Bulletin*, **117,** 1181-1207.

Hammer, O. & D. Harper 2006: *Paleontological Data Analysis*. Blackwell Publishing, Oxford. 368 pp.

Herbert, C. L., A. J. Kaufman, S. C. Penniston-Dorland & A. J. Martin 2010: Radiometric and stratigraphic constraints on terminal Ediacaran (post-Gaskiers) glaciation and metazoan evolution. *Precambrian Research*, **182,** 402-412.

Herringshaw, L. G., O. A. Sherwood & D. McIlroy 2010: Ecosystem engineering by bioturbating polychaetes in event bed microcosms. *Palaios*, **25,** 46-58.

Hill, E. & T. G. Bonney 1877: The Precarboniferous rocks of Charnwood Forest.-Part I. *Quarterly Journal of the Geological Society*, **33**, 754-789.

Hoffman, P. F., A. J. Kaufman, G. P. Halverson & D. P. Schrag 1998: A Neoproterozoic Snowball Earth. *Science*, **281,** 1342-1346.

Hofmann, H. J. & E. W. Mountjoy 2010: Ediacaran body and trace fossils in Miette Group (Windermere Supergroup) near Salient Mountain, British Columbia, Canada. *Canadian Journal of Earth Sciences*, **47,** 1305-1325.

Hofmann, H. J., S. J. O'Brien & A. F. King 2008: Ediacaran biota on Bonavista Peninsula, Newfoundland, Canada. *Journal of Paleontology*, **82,** 1-36.

Høgslund, S., N. P. Revsbech, J. G. Kuenen, B. B. Jørgensen, V. A. Gallardo, J. van de Vossenberg, J. L. Nielsen, L. Holmkvist, E. T. Arning & L. P. Nielsen 2009: Physiology and behaviour of marine *Thioploca*. *The International Society for Microbial Ecology Journal*, **3,** 647-657.

Hyde, K. D., E. B. G. Jones, E. Leaño, S. B. Pointing, A. D. Poonyth & L. L. P. Vrijmoed 1998: Role of fungi in marine ecosystems. *Biodiversity and Conservation*, **7,** 1147-1161.

Ichaso, A. A., R. W. Dalrymple & G. M. Narbonne 2007: Paleoenvironmental and basin analysis of the late Neoproterozoic (Ediacaran) upper Conception and St. John's Groups, West Conception Bay, Newfoundland. *Canadian Journal of Earth Sciences*, **44,** 25-41.

Ivantsov, A. Y. 2011: Feeding traces of Proarticulata - the Vendian metazoa. *Paleontological Journal*, **45,** 237-248.

Ivantsov, A. Y. & Y. E. Malakhovskaya 2002: Giant trails of the Vendian animals. *Doklady Akademii Nauk*, **385,** 382-386.

Ivantsov, A. Y., Y. E. Malakhovskaya & E. A. Serezhnikova 2004: Some problematic fossils from the Vendian of the southeastern White Sea region. *Paleontological Journal*, **38,** 1-9.

Jenkins, R. J. F. 1985: The enigmatic Ediacaran (late Precambrian) genus *Rangea* and related forms. *Paleobiology*, **11,** 336-355.

Jensen, S., J. G. Gehling & M. L. Droser 1998: Ediacara-type fossils in Cambrian sediments. *Nature*, **393,** 567-569.

Jensen, S., B. Z. Saylor, J. G. Gehling & G. J. B. Germs 2000: Complex trace fossils from the terminal Proterozoic of Namibia. *Geology*, **28,** 143-146.

Jensen, S., M. L. Droser & J. G. Gehling 2005: Trace fossil preservation and the early evolution of animals. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **220,** 19-29.

Jensen, S. R., M. L. Droser & J. G. Gehling 2006: A Critical Look at the Ediacaran Trace Fossil Record. *In*: S. Xiao & A. J. Kaufman (eds): *Neoproterozoic Geobiology and Paleobiology*. Topics in Geobiology, Vol. **27,** 115-157, Springer, Dordrecht. 300 pp.

Jensen, S., T. Palacios & M. Marti Mus 2007: A brief review of the fossil record of the Ediacaran-Cambrian transition in the area of Montes de Toledo-Guadalupe, Spain. *In*: P. Vickers-Rich & P. Komarower (eds): *The Rise and Fall of the Ediacaran Biota*, Geological Society, London, Special Publications, Vol. **286,** 223-235, London.

Jiang, G., X. Wang, X. Shi, S. Zhang, S. Xiao & J. Dong 2010: Organic carbon isotope constraints on the dissolved organic carbon (DOC) reservoir at the Cryogenian-Ediacaran transition. *Earth and Planetary Science Letters*, **299,** 159-168.

Kasemann, S. A., A. R. Prave, A. E. Fallick, C. J. Hawkesworth & K.-H. Hoffmann 2010: Neoproterozoic ice ages, boron isotopes, and ocean acidification: Implications for a snowball Earth. *Geology*, **38,** 775-778.

Kauffman, E. G. & J. R. Steidtmann 1981: Are these the oldest metazoan trace fossils? *Journal of Paleontology*, **55,** 923-947.

Keighley, D. G. & R. K. Pickerill 1994: The ichnogenus *Beaconites* and its distinction from *Ancorichnus* and *Taenidium*. *Palaeontology*, **37,** 305-337.

Keller, B. M. 1969: The Tommotian stage and the Cambrian Lower Boundary problem. *Akademii Nauk USSR Geologicheskaya Instituta Trudy (Seriya 3)*, **206,** 175-176.

Keller, B. M. & M. A. Fedonkin 1976: New organic fossil finds in the Precambrian Valdai series along the Syuz'ma River. *Izvestiya Akademii Nauk, Seriya Geologicheskaya*, **3,** 38-44.

Kilner, B., C. Mac Niocaill & M. D. Brasier 2005: Low-latitude glaciation in the Neoproterozoic of Oman. *Geology*, **33,** 413-416.

Kirschvink, J. L. 1992: Late Proterozoic low-latitude global glaciation: the Snowball Earth. *In*: J. W. Schopf & C. Klein (eds): *The Proterozoic Biosphere*, 51-52, Cambridge University Press, Cambridge. 1374 pp.

Knauth, L. P. 2005: Temperature and salinity history of the Precambrian ocean: implications for the course of microbial evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **219,** 53-69.

Knoll, A. H. 2003: *Life on a Young Planet: The First Three Billion Years of Evolution on Earth*. Princeton University Press, Princeton, NJ. 304 pp.

Knoll, A. H., M. R. Walter, G. M. Narbonne & N. Christie-Blick 2004: A new Period for the geologic time scale. *Science*, **305,** 621-622.

—— 2006: The Ediacaran Period: a new addition to the geologic time scale. *Lethaia*, **39,** 13-30.

Krumbein, W. E., D. M. Paterson & L. J. Stal 1994: *Biostabilization of Sediments*. Bibliotheks und Informationssystem der Carl von Ossietzky Universitat Oldenburg, (BIS)-Verlag, Oldenburg, 526 pp.

Laflamme, M. & G. M. Narbonne 2008: Ediacaran fronds. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **258,** 162-179.

Laflamme, M., G. M. Narbonne & M. M. Anderson 2004: Morphometric analysis of the Ediacaran frond *Charniodiscus* from the Mistaken Point Formation, Newfoundland. *Journal of Paleontology*, **78,** 827-837.

Laflamme, M., G. M. Narbonne, C. Greentree & M. M. Anderson 2007: Morphology and taphonomy of an Ediacaran frond: *Charnia* from the Avalon Peninsula of Newfoundland. *In*: P. Vickers-Rich & P. Komarower (eds): *The Rise and Fall of the Ediacaran Biota*, Geological Society, London, Special Publications, Vol. **286,** 237-257, London.

Laflamme, M., S. Xiao & M. Kowalewski 2009: Osmotrophy in modular Ediacara organisms. *Proceedings of the National Academy of Sciences, USA*, **106,** 14438-14443.

Laflamme, M., J. D. Schiffbauer, G. M. Narbonne & D. E. G. Briggs 2011: Microbial biofilms and the preservation of the Ediacara biota. *Lethaia*, **44,** 203-213.

Landing, E. 1994: Precambrian-Cambrian boundary global stratotype ratified and a new perspective of Cambrian time. *Geology*, **22,** 179-182.

—— 1996: Avalon: Insular continent by the latest Precambrian. *GSA Special Papers*, **304,** 29-63.

Landing, E., G. M. Narbonne, P. M. Myrow, A. P. Benus & M. M. Anderson 1988: Faunas and depositional environments of the Upper Precambrian through lower Cambrian, southeastern Newfoundland (field trip road log). *In*: E. Landing, G. M. Narbonne & P. M. Myrow (eds): *Trace Fossils, Small Shelly Fossils and the Precambrian-Cambrian Boundary*, **Bulletin 463,** 27-32, New York State Museum and Geological Survey, New York. 81 pp.

Le Guerroue, E. 2010: Duration and synchroneity of the largest negative carbon isotope excursion on Earth: The Shuram/Wonoka anomaly. *Comptes Rendus Geoscience*, **342,** 204-214.

Le Guerroue, E., P. A. Allen & A. Cozzi 2006: Chemostratigraphic and sedimentological framework of the largest negative carbon isotopic excursion in Earth history: The Neoproterozoic Shuram Formation (Nafun Group, Oman). *Precambrian Research*, **146,** 68-92.

Li, C.-W., J.-Y. Chen, J. H. Lipps, F. Gao, H. Chi & H.-J. Wu 2007: Ciliated protozoans from the Precambrian Doushantuo Formation, Wengan, South China. *In*: P. Vickers-Rich & P. Komarower (eds): *The Rise and Fall of the Ediacaran Biota*, Geological Society, London, Special Publications, Vol. **286,** 151-156, London.

Li, Z. X., S. V. Bogdanova, A. S. Collins, A. Davidson, B. De Waele, R. E. Ernst, I. C. W. Fitzsimons, R. A. Fuck, D. P. Gladkochub, J. Jacobs, K. E. Karlstrom, S. Lu, L. M. Natapov, V. Pease, S. A. Pisarevsky, K. Thrane & V. Vernikovsky 2008: Assembly, configuration, and break-up history of Rodinia: A synthesis. *Precambrian Research*, **160,** 179-210.

Lissmann, H. W. 1945a: The mechanism of locomotion in gastropod molluscs. I. Kinematics. *Journal of Experimental Biology*, **21,** 58-69.

—— 1945b: The mechanism of locomotion in gastropod molluscs. II. Kinetics. *Journal of Experimental Biology*, **22,** 37-50.

Liu, A. G., D. McIlroy & M. D. Brasier 2010a: First evidence for locomotion in the Ediacara biota from the 565Ma Mistaken Point Formation, Newfoundland. *Geology*, **38,** 123-126.

—— 2010b: First evidence for locomotion in the Ediacara biota from the 565Ma Mistaken Point Formation, Newfoundland: Reply. *Geology*, **38,** e224.

Liu, A. G., D. McIlroy, J. B. Antcliffe & M. D. Brasier 2011: Effaced preservation in the Ediacaran biota of Avalonia and its implications for the early macrofossil record. *Palaeontology*, **54,** 607-630.

Locarnini, R. A., A. V. Mishonov, J. I. Antonov, T. P. Boyer & H. E. Garcia 2006: *World Ocean Atlas 2005*. Vol. **1**: Temperature. S. Levitus (ed) NOAA Atlas NESDIS 61, U.S. Government Printing Office, Washington, D.C., 182 pp.

Love, G. D., E. Grosjean, C. Stalvies, D. A. Fike, J. P. Grotzinger, A. S. Bradley, A. E. Kelly, M. Bhatia, W. Meredith, C. E. Snape, S. A. Bowring, D. J. Condon & R. E. Summons 2009: Fossil steroids record the appearance of Demospongiae during the Cryogenian period. *Nature*, **457,** 718-721.

MacNaughton, R. B. & R. K. Pickerill 1995: Invertebrate ichnology of the nonmarine Lepreau Formation (Triassic), southern New Brunswick, eastern Canada. *Journal of Paleontology*, **69,** 160-171.

Maithy, P. K. & G. Kumar 2007: Biota in the terminal Proterozoic successions on the Indian subcontinent: a review. *In*: P. Vickers-Rich & P. Komarower (eds): *The Rise and Fall of the Ediacaran Biota*, Geological Society, London, Special Publications, Vol. **286,** 315-330, London.

Maloof, A. C., C. V. Rose, R. Beach, B. M. Samuels, C. C. Calmet, D. H. Erwin, G. R. Poirier, N. Yao & F. J. Simons 2010: Possible animal-body fossils in pre-Marinoan limestones from South Australia. *Nature Geoscience*, **3,** 653-659.

Mapstone, N. B. & D. McIlroy 2006: Ediacaran fossil preservation: Taphonomy and diagenesis of a discoid biota from the Amadeus Basin, central Australia. *Precambrian Research*, **149,** 126-148.

Martill, D. M. & E. Harper 1990: Critical point drying, a technique for palaeontologists. *Palaeontology*, **33,** 423-428.

Martin, M. W., D. V. Grazhdankin, S. A. Bowring, D. A. D. Evans, M. A. Fedonkin & J. L. Kirschvink 2000: Age of Neoproterozoic Bilaterian Body and Trace Fossils, White Sea, Russia: Implications for Metazoan Evolution. *Science*, **288,** 841-845.

Matz, M. V., T. M. Frank, N. J. Marshall, E. A. Widder & S. Johnsen 2008: Giant deep-sea protist produces bilaterian-like traces. *Current Biology*, **18,** 1-6.

McCall, G. J. H. 2006: The Vendian (Ediacaran) in the geological record: Enigmas in geology's prelude to the Cambrian explosion. *Earth Science Reviews*, **77,** 1-229.

McClendon, J. F. 1905: On the locomotion of a sea anemone (*Metridium marginatum*). *Biology Bulletin*, **10,** 66-67.

McIlroy, D. 2004: Some ichnological concepts, methodologies, applications and frontiers. *In*: D. McIlroy (ed): *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*, Geological Society, London, Special Publications, Vol. **228,** 3-27, London.

McIlroy, D. & J. M. Horák 1996: The Neoproterozoic of England and Wales. *In*: P. Brenchley & P. Rawson (eds): *The Geology of England and Wales*, 9-24, Geological Society Publishing House, Bath. 256 pp.

McIlroy, D. & G. R. Heys 1997: Palaeobiological significance of *Plagiogmus arcuatus* from the lower Cambrian of central Australia. *Alcheringa*, **21,** 161-178.

McIlroy, D. & G. A. Logan 1999: The Impact of Bioturbation on Infaunal Ecology and Evolution During the Proterozoic-Cambrian Transition. *Palaios*, **14,** 58-72.

McIlroy, D. & M. Garton 2010: Realistic interpretation of ichnofabrics and palaeoecology of the pipe-rock biotope. *Lethaia*, **43,** 420-426.

McIlroy, D., M. D. Brasier & J. B. Moseley 1998: The Proterozoic-Cambrian transition within the 'Charnian Supergroup' of central England and the antiquity of the Ediacara fauna. *Journal of the Geological Society, London*, **155,** 401-411.

McIlroy, D., O. R. Green & M. D. Brasier 2001: Palaeobiology and evolution of the earliest agglutinated Foraminifera: *Platysolenites, Spirosolenites* and related forms. *Lethaia*, **34,** 13-29.

McIlroy, D., T. P. Crimes & J. C. Pauley 2005: Fossils and matgrounds from the Neoproterozoic Longmyndian Supergroup, Shropshire, U.K. *Geological Magazine*, **142,** 441-455.

McIlroy, D., M. D. Brasier & A. S. Lang 2009: Smothering of microbial mats by macrobiota: implications for the Ediacara biota. *Journal of the Geological Society, London,* **166,** 1117-1121.

McKerrow, W. S., C. R. Scotese & M. D. Brasier 1992: Early Cambrian continental reconstructions. *Journal of the Geological Society, London,* **149,** 599-606.

McLoughlin, N., M. D. Brasier, D. Wacey, O. R. Green & R. S. Perry 2007: On biogenicity criteria for endolithic microborings on early Earth and beyond. *Astrobiology,* **7,** 10-26.

McLoughlin, N., L. A. Wilson & M. D. Brasier 2008: Growth of synthetic stromatolites and wrinkle structures in the absence of microbes – implications for the early fossil record. *Geobiology*, **6,** 95-105.

McMenamin, M. A. S. 1998: *The Garden of Ediacara*. Columbia University Press, New York. 256 pp.

McMenamin, M. A. S. & D. L. S. McMenamin 1990: *The emergence of animals: The Cambrian breakthrough*. Columbia University Press, New York. 217 pp.

Meert, J. G., A. Gibsher, S., N. M. Levashova, W. C. Grice, G. D. Kamenov & A. B. Ryabinin 2011: Glaciation and ~770 Ma Ediacara (?) Fossils from the Lesser Karatau Microcontinent, Kazakhstan. *Gondwana Research,* **19,** 867-880.

Meng, F., P. Ni, J. D. Schiffbauer, X. Yuan, C. Zhou, Y. Wang & M. Xia 2011: Ediacaran seawater temperature: Evidence from inclusions of Sinian halite. *Precambrian Research*, **184,** 63-69.

Meyer-Reil, L.-A. & M. Köster 1992: Microbial life in pelagic sediments: the impact of environmental parameters on enzymatic degradation of organic material. *Marine Ecology Progress Series*, **81,** 65-72.

Miller III, W. 1999: Small Pits Associated with *Renilla* (Cnidaria: Pennatulacea) on a Modern Low-Energy Sandflat, Kiawah Island, South Carolina, U.S.A. *Ichnos*, **6,** 289-292.

Misra, S. B. 1969: Late Precambrian (?) Fossils from Southeastern Newfoundland. *Geological Society of America Bulletin*, **80,** 2133-2140.

—— 1971: Stratigraphy and depositional history of late Precambrian coelenterate-bearing rocks, southeastern Newfoundland. *Geological Society of America Bulletin*, **82,** 979-988.

Mojzsis, S. J., G. Arrhenius, K. D. McKeegan, T. M. Harrison, A. P. Nutman & C. R. L. Friend 1996: Evidence for life on Earth before 3,800 million years ago. *Nature*, **384,** 55-59.

Murchison, R. I. 1845: On the Palaeozoic deposits of Scandinavia and the Baltic Provinces of Russia, and their relations to Azoic or more ancient crystalline rocks; with an account of some great features of dislocation and metamorphism along their northern frontiers. *Quarterly Journal of the Geological Society*, **1,** 467-494.

Narbonne, G. M. 1998: The Ediacara Biota: A terminal Neoproterozoic experiment in the evolution of life. *GSA Today*, **8,** 1-6.

—— 2004: Modular construction in the Ediacaran biota. *Science*, **305,** 1141-1144.

—— 2005: The Ediacara Biota: Neoproterozoic origin of animals and their ecosystems. *Annual Reviews in Earth and Planetary Sciences*, **33,** 421-442.

—— 2007: Canadian Paleontology Conference Field Trip Guide Book, **11,** Geological Association of Canada, Paleontology Division, St John's. 36 pp.

—— 2010: Ocean chemistry and early animals. *Science*, **328,** 53-54.

Narbonne, G. M. & H. J. Hofmann 1987: Ediacaran biota of the Wernecke Mountains, Yukon, Canada. *Palaeontology*, **30,** 647-676.

Narbonne, G. M. & J. D. Aitken 1990: Ediacaran fossils from the Sekwi Brook area, Mackenzie Mountains, Northwestern Canada. *Palaeontology*, **33,** 945-980.

Narbonne, G. M. & J. G. Gehling 2003: Life after snowball: the oldest complex Ediacaran fossils. *Geology*, **31,** 27-30.

Narbonne, G. M., P. M. Myrow, E. Landing & M. M. Anderson 1987: A candidate stratotype for the Precambrian-Cambrian boundary, Fortune Head, Burin Peninsula, southeastern Newfoundland. *Canadian Journal of Earth Sciences*, **24,** 1277-1293.

Narbonne, G. M., R. W. Dalrymple & J. G. Gehling 2001: Neoproterozoic fossils and environments of the Avalon Peninsula, Newfoundland. *Guidebook, Trip B5, Geological Association of Canada/Mineralogical Association of Canada Annual Meeting*, St John's, Newfoundland. 100 pp.

Narbonne, G. M., R. W. Dalrymple, M. Laflamme, J. G. Gehling & W. D. Boyce 2005: Life after Snowball: Mistaken Point Biota and the Cambrian of the Avalon. *North American Paleontological Convention Field Trip Guidebook,* Halifax, Nova Scotia. 95 pp.

Narbonne, G. M., J. G. Gehling & P. Vickers-Rich 2007: The Misty Coasts of Newfoundland. *In*: M. A. Fedonkin, J. G. Gehling, K. Grey, G. M. Narbonne & P. Vickers-Rich (eds): *The Rise of Animals: Evolution and Diversification of the Kingdom Animalia*, 1st edition, 53-68, John Hopkins University Press.

Narbonne, G. M., M. Laflamme, C. Greentree & P. Trusler 2009: Reconstructing a lost world: Ediacaran rangeomorphs from Spaniard's Bay, Newfoundland. *Journal of Paleontology*, **83,** 503-523.

Nelson, C. H. 1982: Modern shallow-water graded sand layers from storm surges, Bering Shelf: A mimic of Bouma sequences and turbidite systems. *Journal of Sedimentary Petrology,* **52,** 537-545.

Noffke, N. 2003: Epibenthic cyanobacterial communities in the context of sedimentary processes in siliciclastic depositional systems (present and past). *In*: W. E. Krumbein, D. M. Paterson & G. A. Zavarzin (eds): *Fossil and Recent Biofilms*, 265-280, Kluwer Academic Press, Dordrecht.

—— 2009: The criteria for the biogenicity of microbially induced sedimentary structures (MISS) in Archean and younger, sandy deposits. *Earth Science Reviews,* **96,** 173-180.

Noffke, N., G. Gerdes, T. Klenke & W. E. Krumbein 2001: Microbially induced sedimentary structures - a new category within the classification of primary sedimentary structures. *Journal of Sedimentary Research,* **71,** 649-656.

Noffke, N., A. H. Knoll & J. P. Grotzinger 2002: Sedimentary controls on the formation and preservation of microbial mats in siliciclastic deposits: a case study from the Upper Neoproterozoic Nama Group, Namibia. *Palaios*, **17,** 533-544.

Noffke, N., K. A. Eriksson, R. M. Hazen & E. L. Simpson 2006: A new window into Early Archean life: Microbial mats in Earth's oldest siliciclastic tidal deposits (3.2 Ga Moodies Group, South Africa). *Geology*, **34,** 253-256.

Normore, L. S. 2010: Geology of the Bonavista map area (NTS 2C/11), Newfoundland. *Current Research, Newfoundland Department of Mines and Energy Geological Survey*, **10-1,** 281-301.

Norris, R. D. 1989: Cnidarian taphonomy and affinities of the Ediacara biota. *Lethaia*, **22,** 381-393.

O'Brien, S. J. & A. F. King 2005: Late Neoproterozoic (Ediacaran) stratigraphy of the Avalon zone sedimentary rocks, Bonavista Peninsula, Newfoundland. *Current Research, Newfoundland and Labrador Department of Natural Resources Geological Survey,* **05-1,** 101-113.

—— 2006: Lithostratigraphic and biostratigraphic studies on the eastern Bonavista Peninsula: an update. *Current Research, Newfoundland and Labrador Department of Natural Resources Geological Survey*, **06-1,** 257-263.

Ohmoto, H., T. Kakegawa & D. R. Lowe 1993: 3.4-Billion-year-old biogenic pyrites from Barberton, South Africa: sulfur isotope evidence. *Science*, **262,** 555-557.

Palace, M., M. Keller & H. Silva 2008: Necromass Production: Studies in undisturbed and logged Amazon forests. *Ecological Applications*, **18,** 873-884.

Palij, V. M., E. Posti & M. A. Fedonkin 1983: Soft-bodied metazoa and animal trace fossils in the Vendian and Early Cambrian. *In*: A. D. Urbanek & A. Y. Rozanov (eds): *Upper Precambrian and Cambrian palaeontology of the East European Platform*, 56-93, Wydawnictwa Geologiczne Publishing House, Warszawa.

Parizot, M., P. G. Eriksson, T. Aifa, S. Sarkar, S. Banerjee, O. Catuneanu, W. Altermann, A. J. Bumby, E. M. Bordy, J. L. van Rooy & A. J. Boshoff 2005: Suspected microbial mat-related crack-like sedimentary structures in the Palaeoproterozoic Magaliesberg Formation sandstones, South Africa. *Precambrian Research*, **138,** 274-296.

Parker, G. H. 1916: Locomotion of sea-anemones. *Proceedings of the National Academy of Science, U.S.A.*, **2,** 449-450.

Parkes, R. J., B. A. Cragg & P. Wellsbury 2000: Recent studies on bacterial populations and processes in subseafloor sediments: A review. *Hydrogeology Journal*, **8,** 11-28.

Pattison, S. A. J. 2005: Storm-influenced prodelta turbidite complex in the lower Kenilworth Member at Hatch Mesa, Book Cliffs, Utah, U.S.A.: Implications for shallow marine facies models. *Journal of Sedimentary Research*, **75,** 420-439.

Pauley, J. C. 1991: A revision of the stratigraphy of the Longmyndian Supergroup, Welsh Borderland, and of its relationship to the Uriconian volcanic complex. *Geological Journal*, **26,** 167-183.

Peat, C. 1984: Precambrian microfossils from the Longmyndian of Shropshire. *Proceedings of the Geologist's Association*, **5,** 17-22.

Peterson, K. J. & N. J. Butterfield 2005: Origin of the Eumetazoa: Testing ecological predictions of molecular clocks against the Proterozoic fossil record. *Proceedings of the National Academy of Science, U.S.A.*, **102,** 9547-9552.

Peterson, K. J., B. Waggoner & J. W. Hagadorn 2003: A fungal analog for Newfoundland Ediacaran fossils? *Integrative and Comparative Biology*, **43,** 127-136.

Pflug, H. D. 1966: Neue Fossilreste aus den Nama-Schichten in Südwest-Afrika. *Paläontologische Zeitschrift*, **40,** 14-25.

Pisarevsky, S. A., J. B. Murphy, P. A. Cawood & A. S. Collins 2008: Late Neoproterozoic and Early Cambrian palaeogeography: models and problems. *In*: R. J. Pankhurst, R. A. J. Trouw, B. B. Brito Neves & M. J. De Wit (eds): *West Gondwana: Pre-*

Cenozoic correlations across the South Atlantic region, Geological Society, London, Special Publications, Vol. **294,** 9-31, London.

Porada, H. & E. H. Bouougri 2007: Wrinkle structures - a critical review. *Earth Science Reviews*, **81,** 199-215.

Porter, S. M. 2004: The fossil record of early eukaryote diversification. *In*: J. H. Lipps & B. M. Waggoner (eds): *Neoproterozoic - Cambrian Biological Revolutions*, The Paleontological Society Papers, Vol. **10,** 35-50, The Paleontological Society, New Haven, Connecticut.

—— 2006: The Proterozoic Fossil Record of Heterotrophic Eukaryotes. *In*: S. Xiao & A. J. Kaufman (eds): *Neoproterozoic Geobiology and Paleobiology,* Topics in Geobiology, Vol. **27,** 1-21, Springer, Dordrecht. 300 pp.

Porter, S. M., R. Meisterfeld & A. H. Knoll 2003: Vase-shaped microfossils from the Neoproterozoic Chuar Group, Grand Canyon: A classification guided by modern testate amoebae. *Journal of Paleontology*, **77,** 409-429.

Raff, E. C., K. L. Schollaert, D. E. Nelson, P. C. J. Donoghue, C.-W. Thomas, F. R. Turner, B. D. Stein, X. Dong, S. Bengtson, T. Huldtgren, M. Stampanoni, C. Yin & R. A. Raff 2008: Embryo fossilization is a biological process mediated by microbial biofilms. *Proceedings of the National Academy of Sciences, USA*, **105,** 19360-19365.

Retallack, G. J. 1994: Were the Ediacaran Fossils Lichens? *Paleobiology*, **20,** 523-544.

—— 2007: Growth, decay and burial compaction of *Dickinsonia*, an iconic Ediacaran fossil. *Alcheringa*, **31,** 215-240.

—— 2010: First evidence for locomotion in the Ediacara biota from the 565Ma Mistaken Point Formation, Newfoundland: Comment. *Geology*, **38,** e223.

Rosing, M. T. 1999: ^{13}C-depleted carbon microparticles in >3700-Ma sea-floor sedimentary rocks from West Greenland. *Science*, **283,** 674-676.

Rozhnov, S. V. 2010: From Vendian to Cambrian: the Beginning of Morphological Disparity of Modern Metazoan Phyla. *Russian Journal of Developmental Biology*, **41,** 357-368.

Salter, J. W. 1856: On fossil remains in the Cambrian rocks of the Longmynd and North Wales. *Quarterly Journal of the Geological Society*, **12,** 246-251.

—— 1857: On annelide burrows and surface markings from the Cambrian rocks of the Longmynd. *Quarterly Journal of the Geological Society*, **13,** 199-207.

Samson, S. D., R. S. D'Lemos, B. V. Miller & M. A. Hamilton 2005: Neoproterozoic palaeogeography of the Cadomia and Avalon terranes: constraints from detrital zircon U-Pb ages. *Journal of the Geological Society, London*, **162,** 65-71.

Sansom, R. S., S. E. Gabbott & M. A. Purnell 2010: Non-random decay of chordate characters causes bias in fossil interpretation. *Nature*, **463,** 797-800.

Schieber, J., P. K. Bose, P. G. Eriksson, S. Banerjee, S. Sarkar, W. Altermann & O. Catuneanu 2007: *Atlas of microbial mat features preserved within the siliciclastic rock record.* Atlases in Geoscience, 1st edition, Elsevier, Amsterdam. 324 pp.

Schopf, J. W. 1993: Microfossils of the Early Archean Apex Chert: New Evidence of the Antiquity of Life. *Science*, **260,** 640-646.

Schulz, H. N., B. B. Jørgensen, H. A. Fossing & N. B. Ramsing 1996: Community structure of filamentous, sheath-building Sulfur bacteria, *Thioploca* spp., off the coast of Chile. *Applied and Environmental Microbiology*, **62,** 1855-1862.

Scotese, C. R. 2009: Late Proterozoic plate tectonics and palaeogeography: a tale of two supercontinents, Rodinia and Pannotia. *In*: J. Craig, J. Thurow, B. Thusu, A. Whitham & Y. Abutarruma (eds): *Global Neoproterozoic Petroleum Systems: The Emerging Potential in North Africa*, Geological Society, London, Special Publications, Vol. **326,** 67-83, London.

Seilacher, A. 1989: Vendozoa: organismal construction in the Proterozoic biosphere. *Lethaia*, **22,** 229-239.

—— 1990: Paleozoic trace fossils. *In*: R. Said (ed): *The Geology of Egypt*, 649-670, Balkema, Rotterdam. 734 pp.

—— 1992: Vendobionta and Psammocorallia: lost constructions of Precambrian evolution. *Journal of the Geological Society, London*, **149,** 607-613.

—— 1999: Biomat-Related Lifestyles in the Precambrian. *Palaios*, **14,** 86-93.

Seilacher, A. & F. Pflüger 1994: From biomats to benthic agriculture: A biohistoric revolution. *In*: W. E. Krumbein, D. M. Peterson & L. J. Stal (eds): *Biostabilization of Sediments*, 97-105, Bibliotheks-und Informationssystem der Carl von Ossietzky Universitat Odenburg. 526 pp.

Seilacher, A., P. K. Bose & F. Pflüger 1998: Triploblastic animals more than 1 billion years ago: trace fossil evidence from India. *Science*, **282,** 80-83.

Seilacher, A., D. Grazhdankin & A. Legouta 2003: Ediacaran biota: The dawn of animal life in the shadow of giant protists. *Paleontological Research*, **7,** 43-54.

Seilacher, A., L. A. Buatois & M. G. Mángano 2005: Trace fossils in the Ediacaran-Cambrian transition: Behavioral diversification, ecological turnover and environmental shift. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **227,** 323-356.

Sepkoski, J. J. 1979: A kinetic model of Phanerozoic taxonomic diversity. II. Early Phanerozoic families and multiple equilibria. *Paleobiology,* **5,** 222-251.

Serezhnikova, E. A. 2007: Vendian *Hiemalora* from Arctic Siberia reinterpreted as holdfasts of benthic organisms. *In*: P. Vickers-Rich & P. Komarower (eds): *The Rise and Fall of the Ediacaran Biota*, Geological Society, London, Special Publications, Vol. **286,** 331-337, London.

Serezhnikova, E. A. & A. Y. Ivantsov 2007: *Fedomia mikhaili* - A new spicule-bearing organism of sponge grade from the Vendian (Ediacaran) of the White Sea, Russia. *Palaeoworld*, **16,** 319-324.

Sergeev, V. N. & J. W. Schopf 2010: Taxonomy, paleoecology and biostratigraphy of the late Neoproterozoic Chichkan microbiota of south Kazakhstan: the marine biosphere on the eve of metazoan radiation. *Journal of Paleontology*, **84,** 363-401.

Shannon, C. E. 1948: A mathematical theory of communication. *The Bell System Technical Journal*, **27,** 379-423 & 623-656.

Shapiro, R. S. 2004: Neoproterozoic-Cambrian microbialite record. *In*: J. H. Lipps & B. M. Waggoner (eds): *Neoproterozoic - Cambrian Biological Revolutions*, The Paleontological Society Papers, Vol. **10,** 5-15, The Paleontological Society, New Haven, Connecticut.

Shen, B., S. Xiao, L. Dong, C. Zhou & J. Liu 2007: Problematic macrofossils from Ediacaran successions in the North China and Chaidam blocks: Implications for their evolutionary roots and biostratigraphic significance. *Journal of Paleontology*, **81,** 1396-1411.

Shen, Y., T. Zhang & P. F. Hoffman 2008a: On the coevolution of Ediacaran oceans and animals. *Proceedings of the National Academy of Sciences, U.S.A.*, **105,** 7376-7381.

Shen, B., L. Dong, S. Xiao & M. Kowalewski 2008b: The Avalon Explosion: Evolution of Ediacara Morphospace. *Science*, **319,** 81-84.

Smith, A. B. & T. P. Crimes 1983: Trace fossils formed by heart urchins - a study of *Scolicia* and related traces. *Lethaia*, **16,** 79-92.

Sokolov, B. S. 1967: Drevneyshiye pogonofory [The oldest Pogonophora]. *Doklady Akademii Nauk SSSR*, **177,** 201-204 (English translation pages 252-255).

—— 1976: Precambrian metazoa and the Vendian-Cambrian boundary. *Paleontological Journal*, **10,** 1-13.

Sparrow Jr., F. K. 1936: Biological observations on the marine fungi of Woods Hole waters. *Biological Bulletin*, **70,** 236-263.

Sperling, E. A. & J. Vinther 2010: A placozoan affinity for *Dickinsonia* and the evolution of late Proterozoic metazoan feeding modes. *Evolution and Development*, **12,** 201-209.

Sperling, E. A., D. Pisani & K. J. Peterson 2007: Poriferan paraphyly and its implications for Precambrian palaeobiology. *In*: P. Vickers-Rich & P. Komarower (eds): *The Rise and Fall of the Ediacaran Biota,* Geological Society, London, Special Publications, Vol. **286,** 355-368, London.

Sperling, E. A., K. J. Peterson & D. Pisani 2009: Phylogenetic-Signal Dissection of Nuclear Housekeeping Genes Supports the Paraphyly of Sponges and the Monophyly of Eumetazoa. *Molecular Biology and Evolution*, **26,** 2261-2274.

Sperling, E. A., J. M. Robinson, D. Pisani & K. J. Peterson 2010: Where's the glass? Biomarkers, molecular clocks, and microRNAs suggest a 200-Myr missing Precambrian fossil record of siliceous sponge spicules. *Geobiology*, **8,** 24-36.

Sperling, E. A., K. J. Peterson & M. Laflamme 2011: Rangeomorphs, *Thectardis* (Porifera?) and dissolved organic carbon in the Ediacaran oceans. *Geobiology,* **9,** 24-33.

Sprigg, R. C. 1947: Early Cambrian (?) jellyfishes from the Flinders Ranges, South Australia. *Transactions of the Royal Society of South Australia*, **71,** 212-224.

Steiner, M. & J. Reitner 2001: Evidence of organic structures in Ediacara-type fossils and associated microbial mats. *Geology*, **29,** 1119-1122.

Steiner, M., M. Zhu, Y.-L. Zhao & B.-D. Erdtmann 2005: Lower Cambrian Burgess Shale-type fossil associations of South China. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **220,** 129-152.

Stolz, J. F. 2003: Structure of marine biofilms - flat laminated mats and modern marine stromatolites. *In*: W. E. Krumbein, D. M. Paterson & G. A. Zavarzin (eds): *Fossil and Recent Biofilms*, 65-76, Kluwer Academic Press, Dordrecht.

Stow, D. A. V. & D. J. W. Piper 1984: Deep-water fine-grained sediments: facies models. *Geological Society of London, Special Publications*, **15,** 611-646.

Summons, R. E., L. L. Jahnke, J. M. Hope & G. A. Logan 1999: 2-Methylhopanoids as biomarkers for cyanobacterial oxygenic photosynthesis. *Nature*, **400,** 554-557.

Sutton, M. D., D. E. G. Briggs, D. J. Siveter & D. J. Siveter 2001: Methodologies for the visualization and reconstruction of three-dimensional fossils from the Silurian Herefordshire lagerstatte. *Palaeontologia Electronica*, **4,** 1-17.

Tacker, R. C., A. J. Martin, P. G. Weaver & D. R. Lawver 2010: Trace fossils versus body fossils: *Oldhamia recta* revisited. *Precambrian Research*, **178,** 43-50.

Taylor, P. D. & M. A. Wilson 2003: Palaeoecology and evolution of marine hard substrate communities. *Earth-Science Reviews*, **62,** 1-103.

Teske, A. & D. C. Nelson 2006: The Genera *Beggiatoa* and *Thioploca*. *Prokaryotes*, **6,** 784-810.

Thompson, D. A. W. 1961: *On Growth and Form*. New edition (1992), Cambridge University Press, Cambridge. 346 pp.

Thompson, M. D., A. M. Grunow & J. Ramezani 2007: Late Neoproterozoic paleogeography of the Southeastern New England Avalon Zone: Insights from U-Pb geochronology and paleomagnetism. *Geological Society of America Bulletin*, **119,** 681-696.

Tomašových, A. & S. M. Kidwell 2010: Predicting the effects of increasing temporal scale on species composition, diversity, and rank-abundance distributions. *Paleobiology*, **36,** 672-695.

Toporski, J. K. W., A. Steele, F. Westall, K. L. Thomas-Keprta & D. S. McKay 2002: The simulated silicification of bacteria - new clues to the modes and timing of bacterial preservation and implications for the search for extraterrestrial microfossils. *Astrobiology*, **2,** 1-26.

Torsvik, T. H. 2003: The Rodinia Jigsaw Puzzle. *Science*, **300,** 1379-1381.

Urbanek, A. D. & G. Mierzejewska 1983: The fine structure of zooidal tubes in Sabelliditida and Pognophora. *In:* A. D. Urbanek & A. Y. Rozanov (eds): Upper Precambrian and Cambrian Palaeontology of the East-European Platform, 100-111, Publishing House Wydawnictwa Geologiczne, Warszawa. 158 pp. + XCIV Pls.

Van Kranendonk, M. J., J. G. Gehling & G. A. Shields 2008: Precambrian. *In*: J. G. Ogg, G. Ogg & F. M. Gradstein (eds): *The Concise Geologic Time Scale*, 23-36, Cambridge University Press, Cambridge.

Van Roy, P., P. J. Orr, J. P. Botting, L. A. Muir, J. Vinther, B. Lefebvre, K. el Hariri & D. E. G. Briggs 2010: Ordovician faunas of Burgess Shale type. *Nature*, **465,** 215-218.

Vidal, G. & M. Moczydlowska-Vidal 1997: Biodiversity, Speciation, and Extinction Trends of Proterozoic and Cambrian Phytoplankton. *Paleobiology*, **23,** 230-246.

Vishniac, H. S. 1956: On the ecology of the lower marine fungi. *Biological Bulletin*, **111,** 410-414.

Wacey, D. 2009: *Early Life on Earth: A Practical Guide*. Topics in Geobiology, Vol. **31,** Springer, Berlin. 274 pp.

—— 2010: Stromatolites in the ~3400 Ma Strelley Pool Formation, Western Australia: examining biogenicity from the macro- to the nano-scale. *Astrobiology*, **10,** 381-395.

Wade, M. 1968: Preservation of soft-bodied animals in Precambrian sandstones at Ediacara, South Australia. *Lethaia*, **1,** 238-267.

Waggoner, B. 2003: The Ediacaran Biotas in Space and Time. *Integrative and Comparative Biology*, **43,** 104-113.

Walter, M. R., R. Buick & J. S. R. Dunlop 1980: Stromatolites 3,400-3,500 Myr old from the North Pole area, Western Australia. *Nature*, **284,** 443-445.

Weaver, P. G., M. A. S. McMenamin & R. C. Tacker 2006: Paleoenvironmental and paleobiogeographic implications of a new Ediacaran body fossil from the Neoproterozoic Carolina Terrane, Stanly County, North Carolina. *Precambrian Research*, **150,** 123-135.

Wetzel, A. 1999: Tilting marks: a wave-produced tool mark resembling a trace fossil. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **145,** 251-254.

Whitehouse, M., J. S. Myers & C. M. Fedo 2009: The Akilia Controversy: field, structural and geochronological evidence questions interpretations of >3.8 Ga life in SW Greenland. *Journal of the Geological Society, London*, **166,** 335-348.

Wilby, P. R., J. N. Carney & M. P. A. Howe 2011: A rich Ediacaran assemblage from eastern Avalonia: Evidence of early widespread diversity in the deep ocean. *Geology*, **39,** 655-658.

Williams, H. & A. F. King 1979: *Trepassey Map Area, Newfoundland*. Geological Survey of Canada Memoir, Vol. **389,** 24 pp.

Wood, D. A., R. W. Dalrymple, G. M. Narbonne, J. G. Gehling & M. E. Clapham 2003: Paleoenvironmental analysis of the late Neoproterozoic Mistaken Point and Trepassey formations, southeastern Newfoundland. *Canadian Journal of Earth Sciences*, **40,** 1375-1391.

Xiao, S. & M. Laflamme 2009: On the eve of animal radiation: phylogeny, ecology and evolution of the Ediacara biota. *Trends in Ecology and Evolution*, **24,** 31-40.

Xiao, S., Y. Zhang & A. H. Knoll 1998: Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite. *Nature*, **391,** 553-558.

Xiao, S., X. Yuan, M. Steiner & A. H. Knoll 2002: Macroscopic carbonaceous compressions in a terminal Proterozoic shale: a systematic reassessment of the Miaohe biota, south China. *Journal of Paleontology*, **76,** 347-376.

Xiao, S., J. W. Hagadorn, C. Zhou & X. Yuan 2007: Rare helical spheroidal fossils from the Doushantuo Lagerstätte: Ediacaran animal embryos come of age? *Geology*, **35,** 115-118.

Xiao, S., M. Kowalewski, B. Shen, L. Dong & M. Laflamme 2010: The rise of bilaterians: a few closing comments. *Historical Biology*, **22,** 433-436.

Yin, L., M. Zhu, A. H. Knoll, X. Yuan, J. Zhang & J. Hu 2007: Doushantuo embryos preserved inside diapause egg cysts. *Nature*, **446,** 661-663.

Yochelson, E. L. & M. A. Fedonkin 1993: Paleobiology of *Climactichnites*, an enigmatic late Cambrian fossil. *Smithsonian Contributions to Paleobiology*, **74,** 1-84.

Yuan, X., S. Xiao & T. N. Taylor 2005: Lichen-like symbiosis 600 million years ago. *Science*, **308,** 1017-1020.

Yuan, X., Z. Chen, S. Xiao, C. Zhou & H. Hua 2011: An early Ediacaran assemblage of macroscopic and morphologically differentiated eukaryotes. *Nature*, **470,** 390-393.

Zhou, C., M. D. Brasier & Y. Xue 2001: Three-dimensional phosphatic preservation of giant acritarchs from the terminal Proterozoic Doushantuo Formation in Guizhou and Hubei Provinces, South China. *Palaeontology*, **44,** 1157-1178.

Zhou, C., G. Xie, K. A. McFadden, S. Xiao & X. Yuan 2007: The diversification and extinction of Doushantuo-Pertatataka acritarchs in South China: causes and biostratigraphic significance. *Geological Journal*, **42,** 229-262.

Zhu, M., J. Zhang & A. Yang 2007: Integrated Ediacaran (Sinian) chronostratigraphy of South China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **254,** 7-61.

Zhu, M., J. G. Gehling, S. Xiao, Y.-L. Zhao & M. L. Droser 2008: Eight-armed Ediacara fossil preserved in contrasting taphonomic windows from China and Australia. *Geology*, **36,** 867-870.

Zhuravlev, A. Y., J. A. Gámez Vintaned & A. Y. Ivantsov 2009: First finds of problematic Ediacaran fossil *Gaojiashania* in Siberia and its origin. *Geological Magazine*, **146,** 775-780.