Leicester's fossil celebrity: *Charnia* and the evolution of early life

Programme



Leicester Literary and Philosophical Society Section C (Geology) in conjunction with Dept of Geology, University of Leicester and Leicester Museums and Galleries

Saturday Seminar 10 March 2007 Bennett Building LT1, University of Leicester



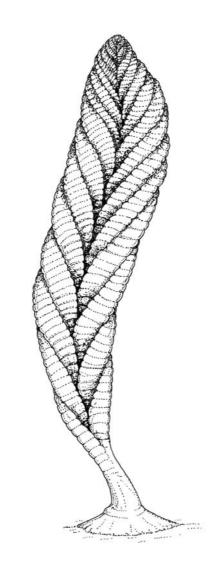












'Charnia: life restoration' by Mark Evans.

Introduction

The Leicester Literary and Philosophical Society Section C (Geology) in conjunction with the University of Leicester and Leicester Museums and Galleries would like to present a symposium on the Precambrian fossil biota preserved in Charnwood Forest and how its discovery is of major international significance. *Charnia* and *Charniodiscus* were the first 'Ediacarans' to be recognised as the macroscopic remains of Precambrian life, even before the significance of the famous Australian biota was realised. (Ediacarans are bizarre extinct multicellular organisms which may, or may not, be the first fossil animals). This symposium will highlight the global importance of the Ediacaran biota from Charnwood Forest.

2007 and 2008 mark the 50th anniversaries of the discovery and description of the biota, so it is an ideal time to celebrate *Charnia* and the Charnwood Ediacarans. The Charnwood fossils continue to generate controversy and debate, and the latest hi-tech methods are providing exciting new insights into their evolutionary significance. This and other exciting science will be presented during the symposium by distinguished speakers and researchers from Australia, Canada, Ireland, and the UK.

An exhibition of local and international Ediacaran fossils called 'Charni@50' will be held at Leicester's New Walk Museum and Art Gallery from 10 March – 15 April 2007. The exhibition will be opened at an evening reception which will commence directly after the close of the symposium. The reception, sponsored by the British Geological Survey, will also launch a new geological map of the Charnwood area. Light refreshments will be provided at the reception.

The symposium and exhibition is sponsored by the Geological Society's 'Local Heroes' Bicentennial celebrations and the Geologists' Association 150th Anniversary. The symposium is also part of National Science & Engineering Week.

The symposium and exhibition was organised by Mark Evans, Chairman of LLPS Geology Section and Senior Curator (Natural Sciences) at New Walk Museum and Art Gallery, Leicester; Dr. Joanne Norris, Vice-Chairman of LLPS Geology Section; Dr. Mark Purnell, Publicity Officer of LLPS Geology Section and Research Fellow at Leicester University, Prof. Richard Aldridge, LLPS Geology Section Committee Member and Professor at Leicester University; and Dr. Roy Clements, LLPS Geology Section Committee Member.

> Joanne Norris February 2007

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Saturday Seminar, 10 March 2007

Programme

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| Opening and Welcome |
| The discovery of <i>Charnia masoni</i> Prof. Roger Mason, China University of Geosciences, Wuhan, Hubei, China |
| The discovery and naming of <i>Charnia</i> and <i>Charniodiscus</i> Dr. Trevor Ford, Dept. of Geology, University of Leicester, UK |
| Further discoveries of Charnian fossils Dr. Helen Boynton, Leicester, UK |
| Geological setting, environment and age of the Charnwood biota Dr. John Carney and Dr. Steve Noble, British Geological Survey, Keyworth, UK |
| Break |
| Sequencing the Neoproterozoic Dr. Dan Condon, NERC Isotope Geoscience Laboratories, Keyworth, UK, and Prof. Sam Bowring, MIT, Cambridge, Ma, USA |
| The Great Divide: Life on Earth before and after the Ediacaran transition Dr. Nicholas Butterfield, University of Cambridge, UK |
| Lunch |
| The Ediacaran Diaspora: Diversity of the Ediacara Biota in South Australia Dr. James Gehling, South Australian Museum, Adelaide, Australia |
| Life after Snowball: The Mistaken Point Biota and the Origin of Animal Ecosystems Dr. Guy Narbonne, Queen's University, Kingston, Ontario, Canada |
| Break |
| The Charnwood Biota as seen from Arctic Russia – Ediacarans and their environments Dr. Dima Grahzdankin, University College Dublin, Ireland |
| Towards a new evolutionary framework for the Ediacaran biota Prof. Martin Brasier and Jonathan Antcliffe, University of Oxford, UK |
| Discussion and Concluding Remarks Close |
| |

18.00 **Reception and Exhibition Opening at New Walk Museum and Art Gallery** Refreshments will be available. (17.30 for 18.00 start, until 20.00)

ABSTRACTS

The discovery of Charnia masoni

Prof Roger Mason, China University of Geosciences, Wuhan, Hubei, China

Reginald Sprigg discovered the Ediacara fauna that includes frond-like forms of the genus Charnia in the Pound Quartzite of the Flinders Ranges north of Adelaide, Australia in 1946. Sprigg reported occurrences of strange fossils to his old university at Adelaide and published descriptions, but met with little interest. In April 1957, I went rock-climbing in Charnwood Forest with two friends, Richard Allen and Richard Blachford ('Blach'), fellow students at Wyggeston Grammar School, Leicester. I was already interested in geology and knew that the rocks of the Charnian Supergroup were Precambrian although I had not heard of the Australian fossils. Richard Allen and I agree that Blach (who died in the early 1960s) drew my attention to the leaf-like fossil holotype now on display in Leicester City Museum. I took a rubbing and showed it to my father, who was Minister of the Great Meeting Unitarian Chapel in East Bond Street, taught part-time at University College (soon to be Leicester University) and thus knew Trevor Ford. We took Trevor to visit the fossil site and convinced him that it was a genuine fossil. His publication of the discovery in the Journal of the Yorkshire Geological Society established the genus Charnia and aroused worldwide interest. Martin Glaessner's use of the genus name shows that Trevor's publication pre-dated his systematic description of the Australian Ediacara biota. I was able to report the discovery because of my father's encouragement and the enquiring approach fostered by my science teachers. Tina Negus saw the frond before I did but no one took her seriously. The study of the Ediacaran biota has never been one of the Earth Sciences' "hot" research topics but progresses steadily over the years, providing a counter example to the theory that science advances by a succession of publicised breakthroughs.

The discovery and naming of *Charnia* and *Charniodiscus*

Dr Trevor D. Ford, Dept. of Geology, University of Leicester, Leicester LE1 7RH

The events following Roger Mason and friends' discovery of *Charnia* will be outlined. I named the fossils after Charnwood Forest. With no described fossils to compare them with, I made a tentative assignment to Algae, but within months Martin Glaessner of Adelaide University published a note in *Nature* comparing *Charnia* with impressions found in the Ediacaran strata of South Australia. He referred them to the Pennatulacea, sea-pens, distant relations of corals. Though not proven this is still a widely held interpretation. Dating is still uncertain but most opinion places the *Charnia* horizon at about 550-570 Ma.

Further discoveries of Charnian fossils

Dr Helen Boynton, 7 The Fairway, Oadby, Leicester

After the initial discoveries of *Charnia masoni* and *Charniodiscus concentricus* between 1957 and 1963, the Precambrian story in Charnwood Forest of fossils didn't continue until 1975 when I took an Adult Education class on fieldwork. It was during that summer and the following five years we discovered the fauna at four further locations in Charnwood. By 1995 the main genera of the Charnian fauna had been named, i.e. *Bradgatia linfordensis, Charnia grandis, Blackbrookia oaksi, Ivesheadia lobata, Shepshedia palmata* and *Cyclomedusa cliffi.*

In the last ten years more fossils have been found, or reinvestigated, including those from the original *Charnia* quarry, where the fossils are now found on at least two bedding planes, and include a number of specimens of *B. linfordensis*, a large *B.* aff. *linfordensis* (about 1 metre long), several more discs (one is c. 19 cm in diameter) and worm-like trails of knotted stems.

From specimens and photographs in Leicester Museum, Leicestershire County Council and the authors' own collection from the old Cliffe Hill Quarry, reinvestigation has shown that most of the discs named *Cyclomedusa cliffi* and thought to be medusoids, are in actual fact holdfasts, some of which show emerging stems that bifurcate. These are actually discs of *Charnia*-like organisms. One specimen appears to be like *Charnia concentricus* with a disc and thick plaited stem which bears a mass of faint bush-like fronds. The bedding planes, on which these fossils were found, have probably long since been quarried away and it is now very difficult to gain close access to the remaining bedding planes in the quarry.

In 2003, an organism which can only be described as having affinities with *Blackbrookia oaksi* was discovered. It shows a disc with a small frond emerging and alongside a thicker branch bearing a number of lateral branches.

In conclusion it can be noted that each fossiliferous locality in the Precambrian of Charnwood Forest has its own particular suite of fossils.

Geological setting, environment and age of the Charnwood biota

Dr John Carney and Dr Steve Noble, British Geological Survey, Keyworth, Nottingham, NG12 5GG

At first glance, the total area of less than 40 km² occupied by the 'basement' rocks of Charnwood Forest seems trivial when compared to the extent of Precambrian terrains elsewhere in the World. Such considerations are, however, outweighed by the significance of the Charnian Supergroup for British Precambrian geology, and globally, for the evidence it continues to contribute towards deciphering the nature of the Ediacara biota. There is in fact a lot of 'geology' here, because the Charnian rocks have been compressed into a rather tight anticlinal fold, the hinge of which plunges to the south-east. Thus if one traversed from the oldest Precambrian rocks, exposed in the northern core of the anticline, to the youngest on the flanks and 'nose' of the structure, a thickness of some 3.5 kilometres of strata would be passed through.

Not surprisingly, the Charnian rocks have attracted the attention of eminent geologists and in his 1947 'swan song' volume on Charnwood Forest, Prof. W. W. Watts was able to summarise publications stretching back to 1790. A benchmark in this research must be the work of J. B. Jukes and his mentor, Prof. A. Sedgwick, who between 1833 and 1837 elucidated the anticlinal structure of the Charnian rocks and hinted at their volcanic origin. The naming of the Charnian units really started with Watts himself, while working with the British Geological Survey in the early 1900's. Many elements of his nomenclature were incorporated into the formal lithostratigraphy established in the 1979 thesis of John Moseley, and in a subsequent paper by the latter author and Trevor Ford in 1985.

The study of stratigraphy is basically about naming different rock units, helping to produce colourful geological maps, and informing about the vertical and lateral relationships of these units, but it does not say much about their environments or the processes that formed them. In Charnwood Forest this has been a problem, because the rocks present attributes are at first sight contradictory. For example, the well-developed stratification in many parts of the succession is typical of sedimentary rocks, whereas in virtually all microscope sections the examined grain constituents of mainly rock fragments and crystals, point to a wholly volcanic

origin. It is therefore accurate to say that the Charnian Supergroup is mostly a *volcaniclastic* succession. This is an 'umbrella' term for bracketing strata containing varying proportions of material derived directly from processes associated with explosive volcanism (pyroclastic in origin), as well as from processes that eroded pre-existing volcanic successions (epiclastic in origin).

To deduce the environmental setting of Charnian volcanism it is necessary to employ James Hutton's principle of uniformitarianism: the scientific law stating that the geological processes taking place in the present operated similarly in the past and can therefore be used to explain the origin of rock sequences. All of the Charnian rocks have chemical compositions that can be matched to rocks erupted from modern island arc systems, such as the Caribbean, which overlie a subduction zone. Moreover, the spectacular, boulder-rich rocks in the Maplewell Group of north-western Charnwood Forest (Figure 1) must have been erupted extremely violently perhaps as pyroclastic flows similar to those recently observed on the Caribbean island of Montserrat (Carney, 1999; Figure 2). Pursuing the analogy further, it is probable that the Charnian volcanoes were largely submerged, allowing fragmental material either eroded or erupted from them to be preserved as sedimentary layers on the surrounding sea floor.

The Charnian volcaniclastic strata can also reveal much about the water depths in which their Ediacaran fossils finally came to rest. Close examination of exposures shows a scarcity of features like cross-bedding or ripple marks, which generally indicate deposition in relatively shallow, wave or current-agitated conditions. Thus much of this succession, being unaffected even by storm-waves, was probably deposited at depths in excess of about 50 metres. Those sedimentary structures that do occur include: parallel bedding or lamination, normal grading, load structures and slump-induced disruption of bedding. They suggest the repeated action of submarine debris flows and turbidity currents that carried sediments down the slopes leading to their eventual sites of deposition on the sea floor.



Figure 1: Precambrian pyroclastic block flow exposed at the 'Bomb Rocks', NW Charnwood Forest.

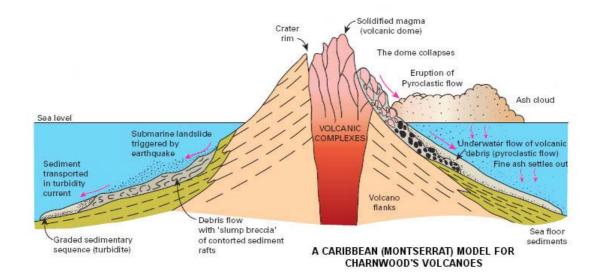


Figure 2: A Caribbean (Montserrat) model for Charnwood's volcanoes.

Some U-Pb radiometric age dates have been obtained for the upper part of the Maplewell Group, which contains the main Ediacaran fossil horizons. They indicate an age of 566-559 million years for this interval, which is in keeping with ages obtained for the Ediacaran biota worldwide. Work is now being undertaken to firm up these ages, and also to obtain more determinations from the lower c. 2000 metres of Charnian strata. It now seems possible that the Blackbrook Group, which is the oldest exposed Charnian unit, may date back to about 600 million years. There may be implications for Ediacaran evolution here, because rocks just above the exposed base of the Blackbrook Group reveal enigmatic, fossil-like impressions that could be precursors to some of the organisms represented within the main Ediacaran assemblages.

Carney, J. N. 1999. Revisiting the Charnian Supergroup: new advances in understanding old rocks. *Geology Today*, **15**, 221-229.

Sequencing the Neoproterozoic

Dr Dan Condon¹and S.A. Bowring² 1. NERC Isotope Geoscience Laboratories, Keyworth, NG12 5GG, UK 2. EAPS, MIT, 77 Massachusetts Avenue, Cambridge, Ma 02139, USA.

Understanding the links between environmental change and biological evolution during the Neoproterozoic center around our ability to precisely correlate and sequence disparate stratigraphic sections. Relative ages of events can be established within single sections or by regional correlation using litho-, chemo- and/or biostratigraphic markers. However such chronologies do not allow testing of the synchroneity of units, the validity of correlations or determining rates of change/duration of events. At present, a major limitation to our understanding of the Neoproterozoic is the dearth of accurate and high-precision dates. The recent increase in geochronological constraints suggests much progress remains to be made.

The determination of 'absolute' age constraints for Neoprotoerozoic successions can be achieved using a variety of geochronological techniques. These include U-Pb dating of either zircon from volcanic rocks (to directly date the horizon sampled) or detrital zircon (to constrain the maximum age of the horizon sampled) and whole rock approaches using Re-Os, Pb-Pb and Lu-Hf decay schemes. The database of geochronological constraints for the Neoproterozoic is growing but of variable quality and subject to multiple interpretations. For example, whole rock dates depend on the assumption that a suite of samples all have the same initial ratio and have evolved through time only as a function of different parent/daughter ratios and that the date reflects either precipitation of carbonate/phosphate (Pb-Pb, Lu-Hf) or enrichment of parent isotope during deposition/early diagenesis (Re-Os). These assumptions are often difficult to evaluate in many cases, however, Re-Os dating of black shales shows considerable promise. In addition, U-Pb geochronology data are derived from both isotope dilution thermal ionization mass-spectrometry (ID-TIMS) and sensitive high-resolution ion microprobe (SHRIMP), there are important differences between the techniques. While it is tempting to use all available geochronological data in compilations irrespective of decay scheme, accuracy and precision, this can result in misleading inferences.

Considerable progress has been made in the past decade on the calibration of Neoproterozoic time. Although the number, timing, duration and possible synchroneity of 'Cryogenian' glacial episodes still remains poorly constrained there is growing evidence for at least two glacial-cap carbonate sequences during the 760 to 700 Ma interval, one at ca. 635 Ma, and a final one at ca. 582 Ma. The base of the Ediacaran Period is formally defined at the base of the Nuccaleena (Marinoan) cap-carbonate as exposed in Enorama Creek, Flinders Ranges, South Australia. Correlation of its distinctive cap sequence coupled with high-precision U-Pb (zircon) ages from Namibia (within the glacial Ghaub Formation) and Southern China (within the cap-carbonate to the Nantuo tillite) indicate synchronous termination of the Marinoan glaciation at ca. 635 Ma. The top of the Ediacaran Period/base Cambrian Period is also not dated at its type locality. However U-Pb zircon dates on ash beds from Oman and Namibia constrain it to be ca. 542 Ma. During the Ediacaran Period the short-lived Gaskiers glaciation occurred ca. 582 Ma and the oldest known Ediacaran fossils, (Charnia-type fronds from the Drook Formation which have strong affinities with assemblages from Charnwood Forest in the Avalon zone of central England) first appear within 4 Ma of deglaciation. When all well-dated sequences containing Ediacaran fossils are considered in the context of global chemostratigraphic correlation schemes, a number of major conclusions can be drawn. At ca. 570-551 Ma, the global carbon cycle underwent a major reorganization consistent with progressive oxidation and remineralization of the organic reservoir. At about the same time, and suggestive of a link, the first complex trace fossils as well as the stem group mollusc Kimberella are found in White Sea sections. Weakly calcified metazoans, such as Cloudina and Namacalathus appear ca. 548 and continue to the Ediacaran/Cambrian boundary where they are inferred to have become extinct. It is clear that our understanding of the relationships/feedback loops between biology, the carbon cycle, and climate will require a much more highly calibrated record.

Outstanding issues centre on the number, synchroneity and durations of glacial deposits, the exact age of the oldest metazoan fossils, the relationship of non-cap carbonate δ^{13} C excursions to evolutionary change, and the validity of molecular clock estimates for the timing of animal evolution, and the global significance of the Gaskiers glacial event and the first appearance of megascopic Ediacaran fossils. Future work will focus on using the highly calibrated record to understand developmental and environmental controls on evolution that preceded the Cambrian explosion, including a precise and accurate temporal framework for the period from ca. 1000-750 Ma in order to integrate proxy records (isotopic, lithostratigraphic and palaeomagnetic) to evaluated causal relationships and rate-dependent effects responsible for the transition into the Cryogenian.

The Great Divide: Life on Earth before and after the Ediacaran transition

Dr Nicholas J. Butterfield, University of Cambridge, Cambridge, CB2 3EQ, UK

The Earth has supported an active biosphere for at least the past 3500 million years, but the obvious fossil record is limited to just the last ca. 530 Ma. This Phanerozoic record documents a wealth of large scale (macro)evolutionary patterns, such as mass extinction and adaptive radiation, and sheds important light on the functioning and potential fate of the modern biosphere: not only is the present the key to the past, but the past can be the key to the present. In this seemingly uniformitarian light, the macroecological and macroevolutionary "rules" of the Phanerozoic have commonly been extrapolated uncritically into the much deeper, pre-Cambrian record.

Study of the pre-Cambrian fossil record over the past few decades has yielded an abundance of prokaryotic and eukaryotic fossils, but the emerging patterns differ fundamentally from those of the Phanerozoic. Prior to ca. 630 Ma, not only were all organisms effectively microscopic, but diversity appears to have been fundamentally lower and evolutionary turnover fundamentally slower than at any subsequent time. The principal signature is of profound evolutionary stasis and no measurable extinction, over hundreds of millions of years.

All this changed with the onset of the Ediacaran, which begins with the first measurable radiation in the whole of the fossil record, followed closely by the appearance and relatively rapid turnover of Ediacaran macrofossils, the first sedimentary trace fossils and the first biomineralized macrofossils. Thus, the Ediacaran marks a fundamental shift towards macroevolutionary patterns typical of the Phanerozoic.

There is no shortage of hypotheses to explain the shift of evolutionary dynamics at the beginning of the Ediacaran, but most of these (e.g., Snowball Earth, meteorite impact, global oxygen increase) fail to provide a proximal explanation for the observed phenomena. I will argue here that the key innovation was the evolution of Eumetazoa – i.e., diploblastic and triploblastic animals with a differentiated gut and nervous system – and their unique impact on ecology and evolution. Unlike all other types of organisms, eumetazoans are capable of building multi-tiered trophic structures, and driving the morphology-based co-evolutionary arms races that give the Phanerozoic biosphere its peculiar character – not least large organismal size, complex behaviour, biomineralization, high diversity, high standing biomass, rapid evolutionary turnover, dynamic (in)stability, mass extinction, biogeographic partitioning, and eukaryote-dominated primary productivity. As such, the history of life on Earth can be divided into two, more-or-less mutually exclusive phases, separated by the (newly ratified) Ediacaran Period (Figure 3). It was during this critical, 100 million-year transition that animal-based ecosystems were developed, along with the peculiarly uniformitarian rules of Phanerozoic macroecology and macroevolution.

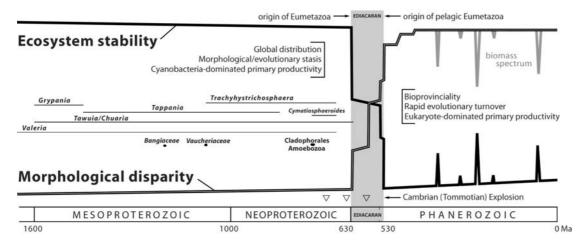


Figure 3: A conceptual view of the macroecological differences between the pre-Ediacaran and post-Ediacaran marine biospheres, and the transitional Ediacaran. The disparity curve is derived from acritarch data and estimated number of intra-organismal cell-types, and ecosystem stability from estimated rates of evolutionary turnover. The spikes in ecosystem stability following Phanerozoic mass extinctions are inferred from observed and modelled recovery times. Biomass spectrum very broadly tracks disparity through this interval except during mass extinctions, which are characterized by the loss of large organisms but not cell-types. Also shown are the occurrences/age ranges of pre-Ediacaran eukaryotes, and the Cryogenian and Ediacaran glaciations (triangles). Note that the Ediacaran/Cambrian boundary as depicted here (at ca. 530 Ma) differs from the IUGS-ratified position (at ca. 542 Ma).

The Ediacaran Diaspora: Diversity of the Ediacara Biota in South Australia

Dr James G. Gehling, Nature Sciences, South Australian Museum, North Terrace, Adelaide, South Australia 5000. [gehling.jim@saugov.sa.gov.au].

Did animals evolve on deep seafloors only to emerge onto continental shelves in the late Ediacaran? The newly defined and named Ediacaran Period acknowledges the global distribution of fossil assemblages of the unique Ediacara biota. Confined to the late Ediacaran, about 575-542 Ma (million years before the present), fossil associations of the Ediacara biota can be considered to represent an evolutionary succession that was curtailed but not entirely extinguished at the base of the Cambrian (Figure 4). Recent discoveries in South Australia, Newfoundland, Russia and China suggest that characteristic Ediacara fossils had long time ranges and global distributions for which there is little equivalence in the younger fossil record.

The Global Stratotype Section and Point or "golden spike" for the base of the newly defined Ediacaran Period was designated at the base of the Nuccaleena Formation in the Flinders Ranges National Park, South Australia (Knoll et al., 2006). This carbonate formation of apparent global distribution, that "caps" the so-called Marinoan tillites, represents the melt-down of the last "snowball earth" event in the Neoproterozoic Era (see Hoffman et al., 1998). The end of "snowball" set in train environmental changes leading to the evolution of large, multicellular life forms on Earth. The 4 km thick Ediacaran succession in South Australia is succeeded by 2-3 km of Early to Middle Cambrian sediment in the Flinders Ranges and Mount Lofty Ranges of South Australia. Fossils are apparently absent from the lower half of the Ediacaran succession in this region. A marker horizon, produced by the local Acraman impact ejecta blanket, defines the mid-Ediacaran level in this succession, above which large spinose organic-walled microfossils first appeared (Grey, 2005), and finally the first animal fossils. The Ediacara fossil assemblage in the Flinders Ranges, while dominated by shallow marine benthic communities, also includes some of the classic Ediacara forms from the Charnwood and Mistaken Point assemblages of the Avalon Province, as well as forms

previously known only from the Nama assemblage of southern Namibia (Gehling et al., 2006). In South Australia, the Ediacara biota is first encountered as an assemblage in prodelta sediment at the top of the Wonoka Formation (Haines, 1998). The better-known and most diverse assemblage is 500 m up section, in the Ediacara Member of the Rawnsley Quartzite. Up to 500 m of barren sandstones of the Rawnsley Quartzite separate these Ediacara assemblages from the base of the Cambrian in South Australia (Gehling, 2000).

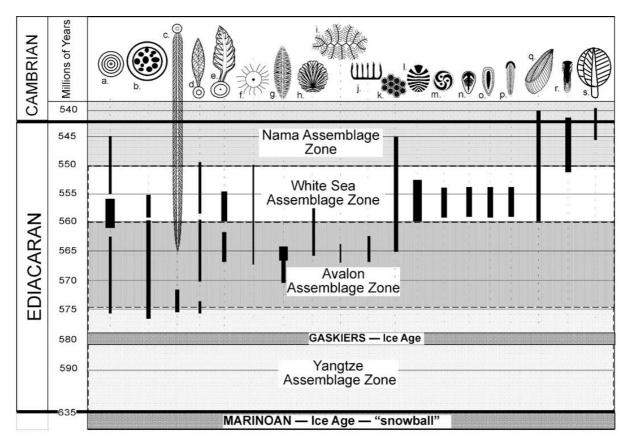


Figure 4: Fossil associations of the Ediacara biota with approximate ranges of representative taxa: a. *Aspidella*; b. *Ivesheadia*; c. *Charnia wardi*; d. *Charnia masoni*; e. *Charniodiscus*; f. *Hiemalora*; g. spindle form; h. *Bradgatia*; i. network form; j. pectinate form; k. *Beltanelliformis;* I. *Dickinsonia*; m. *Tribrachidium*; n. *Parvancorina*; o. *Kimberella*; p. *Spriggina*; q. *Pteridinium*; r. *Cloudina*; s. *Swartpuntia*.

At a new site on the western margins of the Flinders Ranges, my colleague Mary Droser and I, with the help of many volunteers, have been excavating serial fossiliferous surfaces in strata deposited near wave base (Droser et al., 2006). These reveal remarkable changes in composition from bed to bed, that reflect both ecological differences and modification by the burial events. In deeper water environments, at the heads of incised submarine canyons, event beds preserve assemblages dominated by single species but also include previously unknown taxa (Gehling et al., 2006). Large organisms stripped by storms from shallow marine environments were preserved as three-dimensional moulds and casts in massive sand flows swept down into these canyons. Fossils include giant fronds, discs, fractal and sack-shaped organisms of unknown affinities, some of which are closely related to the older fossils of the Avalon Province, while others were previously known only from the younger Namibian assemblage.

It appears that the Ediacara biota had its origins in deep water settings of the Avalon Province before expanding into shallow marine settings as oxygen levels rose to critical levels around 560 million years ago (Canfield et al., 2006). In the younger parts of Ediacaran successions (from 560–542 Ma), in Russia, western Canada and the USA, Namibia, China and Australia, we see the emergence of small motile organisms that began to leave their

marks as traces in seafloor microbial mats while coexisting with the more archaic discs, fronds, vanes and mat-like Ediacara organisms that had been around since 575 Ma (Narbonne, 2005). The affinities of the enchanting Avalon organisms of the Charnwood and Mistaken Point assemblages may forever remain obscure due to the apparent extinction of most of these forms by the end of the Ediacaran. The sheer diversity of body plans in the Early Cambrian fossil record suggests the existence of Ediacaran stem groups to animal phyla. If we wish to understand animal evolution, attention should be focused on the concurrent appearance of Ediacara trace fossils with body fossils that were probably animals from the ancestral lines of arthropod, mollusc, lophophore and worm-like forms, including some with the earliest mineral skeletons.

Although it is the giant Ediacara forms that have transfixed us, the key innovations are to be found in the small bilateral, conical and tubular forms, and the traces of their activities, in the latest part of the Ediacaran (Jensen et al., 2005). Just as small Cretaceous mammals diversified in the Cainozoic, the progenitors of the Cambrian explosion were likely the small, bilateral Ediacara forms that have remained all but unnoticed amongst fractal, frondose and mat-like giants.

A key to our new discoveries has been a change of field-work methodology. Instead of making collecting forays, we are excavating and re-assembling beds for the purposes of palaeoecological study. The results have been spectacular in demonstrating a marked increase in diversity of Ediacara taxa, evidence of unexpected bed-by bed heterogeneity, an un-appreciated dominance by simple tubular and serial forms, and the existence of contrasting taphonomic windows preserving remarkable new three-dimensional fossils. The cooperation of local landholders, indigenous elders, tourism operators, and teams of dedicated volunteers have made our continued study possible, and enabled us to conserve field sites for continuing research. Recent Heritage Listing of Ediacara fossils at Nilpena has come with funding from the Australian Commonwealth Government for putting security systems in place, and for ongoing management and interpretation of the site for the benefit of future researchers and the regional economy. In the long run, nature-based tourism will replace traditional dry-land farming as the more sustainable industry in outback Australia.

While fate has offered a handful of palaeontologists the unique experience of realizing the earliest known impressions of animal communities on Earth, posterity will judge how well we conserve these relics in their natural context for future appreciation, rather than the wisdom of our current interpretations.

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Life after Snowball:

The Mistaken Point Biota and the Origin of Animal Ecosystems

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The first formal description of Ediacaran fossils was Billings' (1872) naming of *Aspidella terranovica* from Newfoundland, but these simple discs were pronounced as inorganic by Walcott and were forgotten until their resurrection as the attachment discs of Ediacaran fronds more than a century later. Ten years after the seminal discoveries at Charnwood Forest, a diverse assemblage of complex Ediacaran fossils was discovered at Mistaken Point in the Avalon Peninsula of Newfoundland. Like Charnwood Forest, Mistaken Point represents a deep-water turbiditic assemblage with the fossils preserved on upper bedding surfaces beneath beds of volcanic ash. All of the major taxa in Charnwood Forest – the fronds *Charnia* and *Charniodiscus*, the bush *Bradgatia*, and the discs *Ivesheadia*, *Blackbrookia*, and *Aspidella* – are present at the genus or even species level. Mistaken Point is unique in exhibiting numerous surfaces littered with hundreds to thousands of complete fossil specimens, including at least 10 taxa that are not known from Charnwood.

Ediacaran fossils in Newfoundland occur above the glacial tillites of the Gaskiers Formation, which is dated at 580 Ma and probably represents the last of the Neoproterozoic "snowball" glaciations. The world's oldest Ediacaran fossils, indeed the oldest large and architecturally complex eukaryotes known anywhere, are fronds of *Charnia* up to 2 m in length that postdate the Gaskiers glaciation by less than 5 million years. Recent geochemical studies of iron speciation by Don Canfield and his colleagues indicate that the end of the Gaskiers glaciation was marked by a sudden infusion of oxygen into the world's oceans, perhaps because the melting glaciers produced nutrients that caused blooms of photosynthesizing micro-organisms. It seems likely that this increase in oxygen levels was the trigger that permitted life to get big, and that ultimately resulted in the animal-dominated ecosystems of our modern world.

Due to tectonism, the quality of preservation at Mistaken Point is not normally quite as good as in Charnwood Forest. A marked exception to this occurs near Spaniard's Bay, where undeformed, three-dimensional fronds in mudstone exhibit a resolution of features less than 0.03 mm. These fossils exhibit complex fractal branching patterns and a modular construction that typify the rangeomorphs, a failed experiment in the Neoproterozoic evolution of multicellular life. More than 75% of all species and individuals of Mistaken Point fossils are rangeomorphs.

Mistaken Point fossils were preserved in place as "census populations" that provide a unique opportunity to study the ecology of rangeomorph communities. Ecological studies at Mistaken Point show that rangeomorphs exhibited tiering patterns and spatial distributions remarkably similar to those of modern and Phanerozoic filter-feeding animals. There is no evidence of potentially mobile bilaterians in the fossil assemblage or of any bioturbation in the sediments, implying that these assemblages consisted entirely of sessile organisms. Nor is there any evidence of macropredation, scavenging, or herbivory among any of the organisms. These ecological innovations would have to await the later evolution of skeletons and brains that culminated in the Cambrian "explosion" of animal life.

The Charnwood Biota as seen from Arctic Russia – Ediacarans and their environments

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The earliest known communities of large organisms are represented by the extinct Ediacaratype animals exceptionally preserved in rocks of late Precambrian age (580-535 million years). Within this range there is a clustering of three distinct fossil assemblages: the Avalon, Ediacaran and Nama biotas. The Avalon biota of Newfoundland consists of closely related problematic fusiform, frondose and plumose organisms characterized by their diagnostic fractal quilting. The Ediacaran biota is best known from the classic localities in the Flinders Ranges of Australia. It is also the most diverse assemblage characterized by segmented and non-segmented fossils with bilateral and trilateral symmetry. The Nama biota of Namibia comprises an assemblage of forms, the most exotic to mainstream biology, dominated by serially quilted body plans. The Avalon, Ediacaran and Nama biotas have been interpreted either as a direct fingerprint of evolution, as the product of geographic provinciality, or as an artefact of selective preservation.

In fact, careful analysis of sedimentary rocks and distribution of associated Ediacara-type fossils in remote localities of Arctic Russia clearly demonstrates that the Avalon, Ediacaran and Nama biotas were globally distributed and coexisted in different environments. These biotas represent ecological guilds on a global scale, with Avalon-type biotas distributed in deep marine habitats, Ediacaran-type biotas inhabiting microbial substrates in shallow marine prodeltaic settings, and Nama-type biotas found in river-mouth bar shoals (Figure 5). This in turn reveals a marked degree of environmental sensitivity and ecological specialization in first communities of large-size organisms, which rapidly explored various environments, ranging from shallow-water deltas to deep-water shelf, and maintained this ecological disparity, with limited overall change, for more than 30 million years.

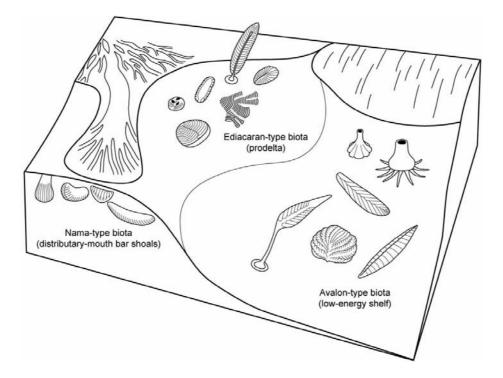


Figure 5: Schematic diagram of ecological distribution of Ediacaran organisms.

How were the Ediacaran communities structured and how did they function? Were they like modern communities or different? Fossil evidence suggests that Ediacaran ecosystems operated on a different type of infrastructure which is not typical for modern animal communities. First, the overall diversity of Ediacaran-type organisms, with an estimated 110 species, appears to be strikingly low when compared to modern ecosystems, but the Ediacaran community structure nevertheless exhibits a marked degree of stability and integrity. Second, in modern ecosystems larger areas normally contain more species than smaller, however this major ecological rule of species-area relationship does not apply to Ediacaran communities. Because structural stability of modern marine communities is thought to be maintained by high species richness, the mechanisms responsible for maintaining the integrity of the Ediacaran biota are, therefore, puzzling. The answer probably lies in extreme heterogeneity and patchiness of Ediacaran communities: the number of species, as well as population densities in Ediacaran communities vary considerably between different sites. This could be a result of intense competition, although low-diversity low-biomass communities could be a result of inhabiting harsh environments.

Where does the Charnwood biota fit in this scheme? The Charnwood Forest fossil assemblage consists of 5 identifiable taxa: *Charniodiscus concentricum* Ford, 1958; *Charnia masoni* Ford, 1958 (*=Charnia grandis* Boynton and Ford, 1995); *Bradgatia linfordensis* Boynton and Ford, 1995; *Ivesheadia lobata* Boynton and Ford, 1995 and *Cyclomedusa davidi* Sprigg, 1947. The specimens described as *Pseudovendia* Boynton and Ford, 1979, *Shepshedia* Boynton, 1999 and *Blackbrookia* Boynton, 1999 are pseudofossils. The species *Charniodiscus concentricum* is represented by a single deformed specimen which was uprooted by current action and transported to the place of final burial. Therefore, it is not characteristic of the Charnwood Forest community. *Charnia masoni* was unusual among Ediacaran organisms in being a generalist species with broad ecological tolerance. Both *Bradgatia linfordensis* and *Ivesheadia lobata* are typical species of low-diversity communities in deep-water shelf environments, as are the discoidal fossils *Cyclomedusa davidi* representing microbial colonies. Accordingly, the Charnwood Forest fossil assemblage should be reconstructed as an Avalon-type low-diversity low-biomass Ediacaran community.

Towards a new evolutionary framework for the Ediacaran biota

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Fifty years have now passed since the providential discovery of *Charnia masoni* and *Charniodiscus concentricus* in Charnwood Forest by Roger Mason and their prompt description by Trevor Ford in 1958. But what exactly is *Charnia*? And just how was it related, if at all, to the great explosion of animal fossils at the base of the Cambrian? Do these fossils represent ancestors of the great animal phyla, as Martin Glaessner and the Australian school have for long argued? If so, there would seem to have been at least some kind of long fuse to the radiation of invertebrates in the Cambrian that followed. Or were the Ediacaran fronds actually members of an extinct grade of organization, as Dolf Seilacher and the European school now maintain? That could mean that the Cambrian explosion was very abrupt indeed.

Our group at Oxford has been studying the growth and evolution of the Ediacara biota as part of a larger project on the nature of the Animal Ancestors in the fossil record. We have found that two new tools are useful in helping us to understand how these strange creatures lived and grew (e.g., Antcliffe and Brasier, 2007). The first approach involves getting the maximum amount of information out of the fossils themselves using new photographic and laser scanning techniques. This allows us to build a virtual map of each major fossil type, that can then be viewed and rotated in three dimensions. The second approach involves using these new data to pick out the different growth stages and work out the nature of the generative zones (growth tips) and, if possible, the life cycle. We have now applied these new techniques to bedding planes in Charnwood Forest and to key Ediacaran fossils from Charnwood, Newfoundland, Australia, the White Sea and Namibia, including *Ivesheadia*, pizza discs, rangeomorphs, spindle animals, *Charnia, Charniodiscus, Bradgatia, Dickinsonia, Swartpuntia* and related forms.

Laser-based conservation of key fossil sites in England and Newfoundland is now being planned.

We will show how laser scanning of fossils is now able to test, critically, various hypotheses put forward for modes of growth, feeding strategy, and levels of oxygen uptake on the seafloor in late Precambrian times.

We will use these data to explore major changes in the position and number of the generative zones through ontogeny and phylogeny (Brasier and Antcliffe, 2004) and to test models for the evolution of the Ediacara biota and the origins of the animal phyla. These studies are now well advanced.

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

Brasier, M.D. and Antcliffe, J. 2004. Decoding the Ediacaran Enigma. *Science*, **305**: 1115-1117.