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Fossil Focus: The Ediacaran Biota

by Frances S. Dunn*[1] and Alex G. Liu[2]

Introduction:

The Ediacaran period, from 635 million to 541 million years ago, was a time of immense geological and evolutionary change. It witnessed the transition out of an ice-house climate, the break–up of one supercontinent (Rodinia) and the assembly of another (Gondwana), a major meteorite impact (the Acraman event) and unprecedented shifts in global ocean chemistry that included a significant rise in oxygen concentrations (Fig. 1A). Rocks from the Ediacaran also record the appearance of a diverse (species-rich) group of large, morphologically complex lifeforms: the Ediacaran biota. These organisms were globally abundant from about 571 million to 541 million years ago. To our modern eyes, many Ediacaran fossils look strange and unfamiliar, and they have puzzled palaeontologists for decades. Determining the position of these organisms in the tree of life is one of the biggest unresolved challenges in palaeobiology.

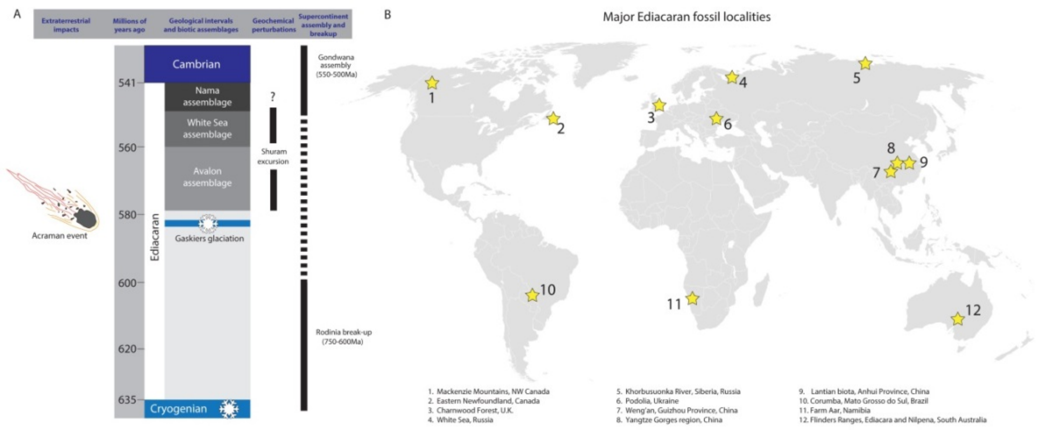

Figure 1 — Major events during the Ediacaran period, and the main palaeontological Ediacaran field localities. A, Key tectonic, geochemical and extraterrestrial events during the Ediacaran period (635 million to 541 million years ago), and the approximate ranges of the Avalon, White Sea and Nama biotic assemblages of soft-bodied Ediacaran macrofossils. The Shuram excursion is the largest recorded change in the carbon-isotope record in Earth history, and indicates a substantial shift in the global carbon cycle. However, the precise timing of this event is unclear. B, Notable Ediacaran fossil localities. All are macrofossil sites, except Weng'an, which houses the well-known Doushantuo microfossil assemblages. Credit: F. Dunn and A. Liu.

For many years, evidence from the fossil record seemed to indicate that animals appeared suddenly (geologically speaking) in an event termed the Cambrian explosion. Small shelly fossils, exotic soft-bodied invertebrates, trilobites and abundant burrows all have their first appearances in layers of rock from the Cambrian period, suggesting that animal life evolved and rapidly diversified between 540 million and 520 million years ago. However, although events in the early Cambrian are undoubtedly relevant to our understanding of the diversification of the animal groups, major discoveries relating to their origins are being made further back in time, in the Ediacaran period. The Ediacaran contains evidence for a number of important evolutionary milestones, including fossils thought to represent evidence of the first animal movement, biomineralization (the formation of hard shells or spicules), predation and reefs. Perhaps the most infamous Ediacaran fossils, however, are those of the Ediacaran biota.

Fossils of the Ediacaran biota preserve a record of large (up to 2 metres), biologically complex, mostly soft-bodied organisms, and are most commonly found as impressions of their external surfaces. The study of Ediacaran fossils has had a relatively brief history. It was only in the 1950s that they were confirmed to be older than the Cambrian, and the Ediacaran System to which they are now assigned was formally defined only in 2004. Importantly, their often unusual body plans mean that even very basic questions, such as 'what were the Ediacaran biota?', are still controversial. We need to answer such questions if we are to understand the early evolution of animals and, more broadly, the diversification and development of multicellular life. This article will briefly describe what we mean by the Ediacaran biota; look at previous suggestions of what they are likely to have been; and summarize the most recent thinking on how their appearance and (apparent) disappearance in the fossil record may relate to geological events.

Introducing the Ediacaran macrobiota:

Between the 1840s and 1870s, interesting impressions were found in England and Newfoundland, Canada, on bedding planes that pre-dated known Cambrian fossils (Fig. 2B–C). It was not clear to their discoverers whether these often circular structures were truly the remains of living organisms, or were the result of unrelated sedimentary processes. The widely held opinion at the time was that there was no life before the Cambrian; older rocks were called Azoic, meaning 'without life', and the known fossil record strongly suggested that life exploded from nowhere into an astounding diversity of forms during the Early Cambrian, around 520 million years ago. This paradigm discouraged the early discoverers from seriously considering that their impressions could have been biological in origin, but contradicted the long ancestry of complex life predicted by Darwin's theory of evolution by natural selection. In the 1930s and 1940s, a range of more complex impressions were found in Russia, Namibia and South Australia. Although it was clear that these fossils recorded biological remains, their actual age could not be determined. The Russian material lay in sediments that had previously been mapped as dating from the Devonian period (419 million to 359 million years ago), whereas in Australia, the possibility that the fossils belonged to the lowest Cambrian could not be ruled out.

The situation changed in 1957 with the discovery and publication of a fern-like fossil named *Charnia masoni* (Fig. 2A), which was found on a bedding plane in England that was demonstrably older than the Cambrian. The similarities between *Charnia* and some Australian and Russian fossils (particularly other fern-like forms) enabled palaeontologists to recognize that globally distributed communities of soft-bodied organisms had existed, and thrived, well before the famous Cambrian explosion, vindicating Darwin's predictions. The organisms were collectively termed the Ediacara biota, after the Ediacara Hills in South Australia, from which some of the specimens had been discovered.

Since those early discoveries, members of the Ediacara biota have been found all over the world (Fig. 1B). They have been joined by a variety of other late Ediacaran fossils that are not found at the original Ediacara site, and do not represent the remains of originally soft-bodied organisms.

Figure 2 — Fossils discovered between 1840 and 1957 in rocks of 'Azoic' age. A, *Charnia masoni*, discovered by schoolchildren in Charnwood Forest, Leicestershire, UK, in the 1950s. This specimen is the holotype (type specimen) of *Charnia masoni*, and is housed at the New Walk Museum, Leicester. B, *Aspidella terranovica*, from St John's in Newfoundland, Canada. C, 'Ring fossils' from the 'ring pit', Charnwood Forest, first documented in the 1840s. These disc-shaped fossils are now recognized to be the anchoring holdfasts of frond-like organisms. Scale bars, 10 mm (A–B) and 50 mm (C). Credit: F. Dunn and A. Liu.

As a result, 'Ediacara biota' has become a less clear-cut term, and in this article we use 'Ediacaran macrobiota' to refer to all large fossils of late Ediacaran age, soft-bodied or otherwise. Further confusion has arisen because different research groups have previously used different systems to categorize rocks of Ediacaran age (for example, the Sinian System in China and the Russian Vendian System). These systems did not precisely correlate with one another, but the decision in 2004 to use the Ediacaran System as the internationally agreed system has mostly resolved this issue.

Before concentrating on Ediacaran macrofossils, we emphasize that life had already achieved considerable diversity well before their appearance. In addition to a Precambrian record of microbes (including stromatolites, thrombolites, and microbial mats) spanning around 3 billion years, fossils from the Cryogenian period (720 million to 635 million years ago) and Tonian period (~1 billion to 720 million years ago) suggest that groups including foraminifera, amoebae and red algae were present from around 700 million to 800 million years ago. There are eukaryotic embryos from the Doushantuo Formation of China some 600 million years ago (which some researchers claim to be animal), alongside microfossils of acritarchs and algae. In short, the Ediacaran macro-organisms would have shared the oceans with a host of other lifeforms, and represent only one component of a diverse and complex biosphere.

The oldest Ediacaran macrofossils may belong to the Lantian biota of China. Here, groups of large algae a few centimetres long are joined by conical organisms with 'tentacle-like' structures (such as *Lantianella*, Fig. 3), which have been compared to cnidarian polyps. The Lantian fossils could be as old as 600 million years, but their age is yet to be precisely pinpointed, and they might have been younger. As a result, fossils of what is known as the Avalonian biota, from the United Kingdom and Newfoundland, are often said to document the oldest communities of diverse macroscopic (big enough to be seen without a microscope) complex organisms, appearing in the fossil record around 571 million years ago. The vast majority of the Avalonian organisms were soft-bodied, frond-like in shape, and lived stationary lives anchored to the sea floor (Fig. 4). They lived in darkness in deep-marine environments, either reclining on the sediment or elevated into the water column. The frond-like forms, including *Charnia* and *Fractofusus* (Figs 2A, 4D), dominate Ediacaran fossil assemblages spanning almost 20 million years, with only a few non-frond-like groups for company (including the triangular form *Thectardis*, Fig. 4A). No Ediacaran fronds have yet been convincingly identified as animals, but rare trace fossils (Fig. 5A) and impressions of non-frond-like organisms (for example, *Haootia*, Fig. 4C) may hint at the presence of early animals.

Figure 3 — Macrofossils from the Lantian biota, Anhui Province, China. Specimens are housed in the collections of the Nanjing Institute of Geology and Palaeontology. A, *Lantianella laevis* (at left; NIGP163377), and a larger conical form. B, *Lantianella annularis*, NIGP163384. Scale bars, 10 mm. Credit: F. Dunn and A. Liu.

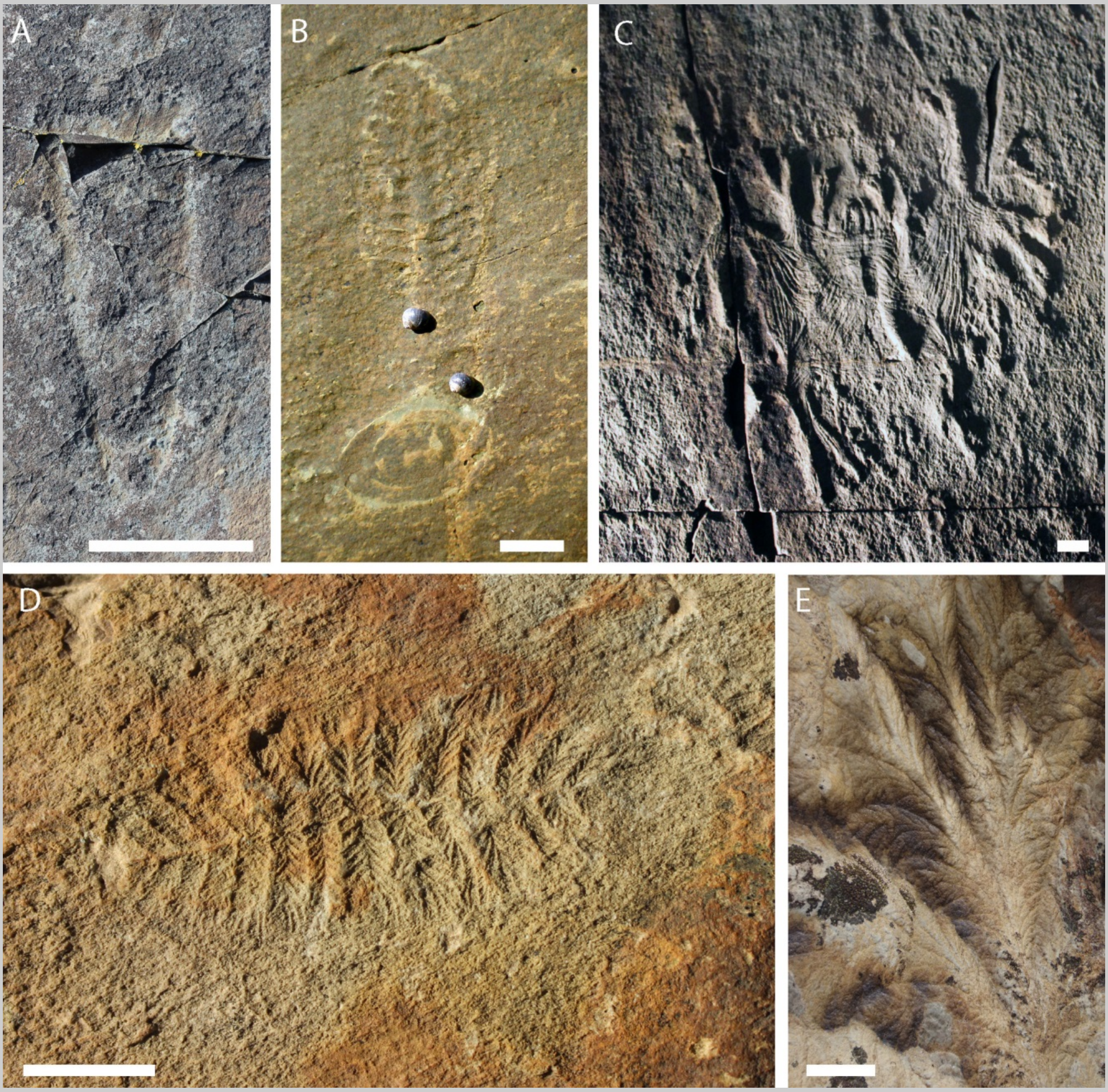

Figure 4 — Avalonian taxa from Newfoundland, Canada. A, *Thectardis*, Drook Formation. B, *Charniodiscus*, a frondose fossil from the Mistaken Point Formation. C, *Haootia*, a possible muscle-bearing cnidarian from the Fermeuse Formation. This holotype specimen is housed at The Rooms Provincial Museum, St. John's. D, *Fractofusus*, a frondose fossil from the Briscal Formation, Mistaken Point Ecological Reserve World Heritage Site. E, Partial *Bradgatia*, a rangeomorph from the Trepassey Formation of the Bonavista Peninsula. All specimens except C remain in the field. Scale bars, 50 mm (A) and 10 mm (B–E). Credit: F. Dunn and A. Liu.

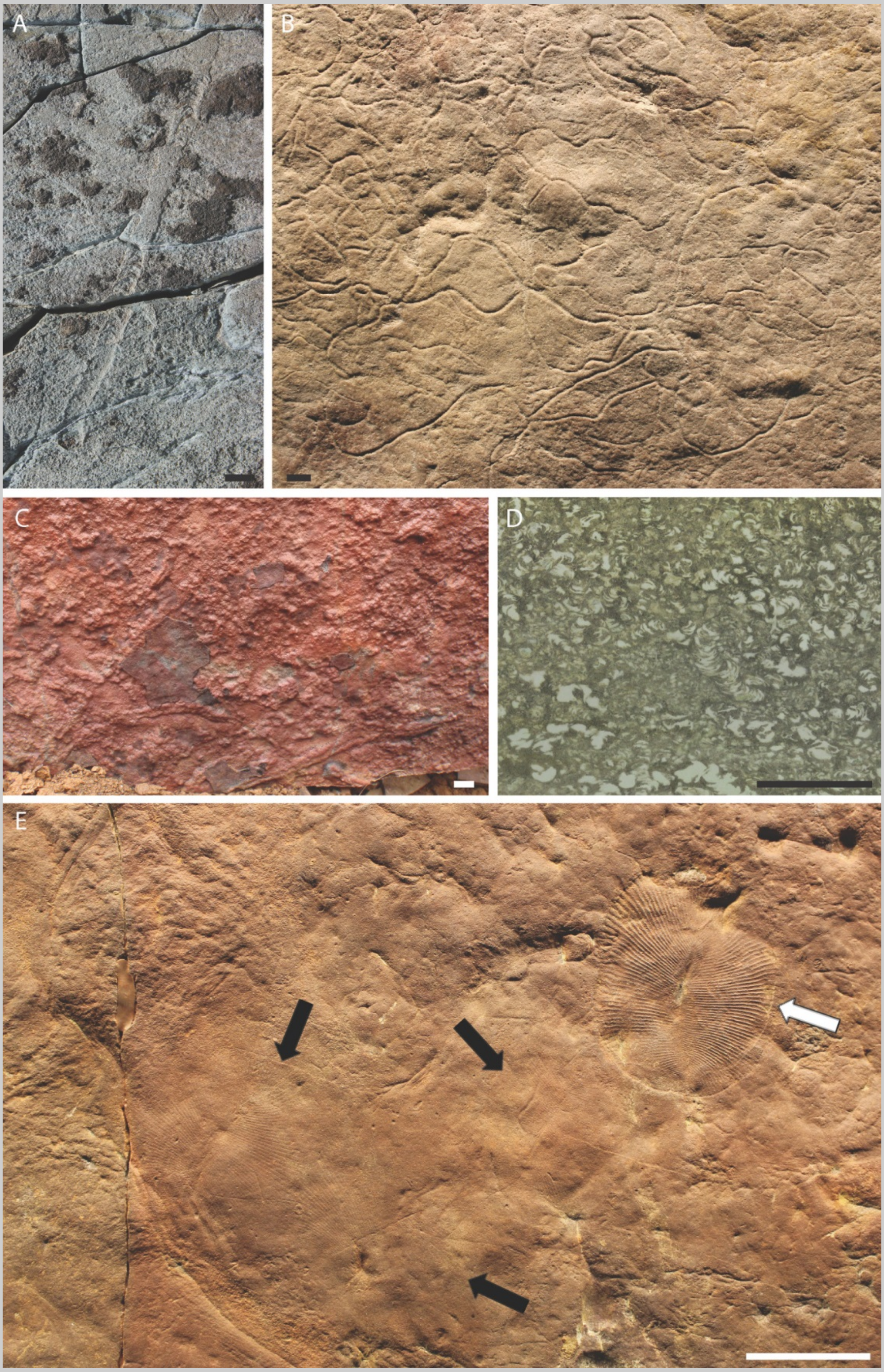

Figure 5 — Trace fossils from the upper Ediacaran period. A, Surface horizontal trace, Mistaken Point Formation (about 565 million years old), Newfoundland. B, *Helminthoidichnites* trace fossils made beneath a microbial mat, Ediacara Member, South Australia (around 560 million years old), South Australia Museum specimen SAM P42142. C, Bi-lobed traces considered to have been made by bilaterian animals, Shibantan Member, South China (about 555 million years old). D, Potential bioturbation in the Khatyspyt Formation, Arctic Siberia (about 553 million years old). E, *Epibaion* impressions (black arrows) associated with *Dickinsonia costata* (white arrow, SAM P49377) and interpreted as evidence for active movement by *Dickinsonia*. Ediacara Member, South Australia. Scale bars, 10mm (A–D) and 50 mm (E). Credit: F. Dunn and A. Liu.

Around 560 million years ago, we see a sharp increase in the apparent diversity of Ediacaran macrofossils worldwide. The fronds become less diverse, but are joined by a variety of new forms, including teardrop-shaped organisms such as *Parvancorina* (Fig. 6B), 'segmented' forms such as *Spriggina* (Fig. 6C) and circular forms such as the tri-radial *Tribrachidium* (Fig. 7B). These organisms lived in shallow seas, and today are found most abundantly in South Australia and the White Sea of Russia. They include a number of groups that have previously been interpreted (with varying degrees of confidence) as early animals, such as *Arkarua* (echinoderms), *Eoandromeda* (ctenophores) and the tongue-twisting *Palaeophragmodictya* (compared to sponges; Fig. 7C). Importantly, some of these organisms, like *Dickinsonia* (Figs 6A, 8A) and *Kimberella* (Figs 6D, 8C), are often found close to trace fossils possibly created by movement and feeding (Fig. 5E), which are two key animal characteristics. Other trace fossils of a similar age document the movement of small organisms beneath microbial mats (Fig. 5B), and potentially (from Siberia) even vertical burrowing and sediment mixing (Fig. 5D). Macroalgae (such as *Flabellophyton*; Fig. 9A) are also present in these shallow marine settings, together with a variety of large tubular organisms, often composed of ring-like segments, some of which might have reproduced sexually (for example *Funisia*; Fig. 7A).

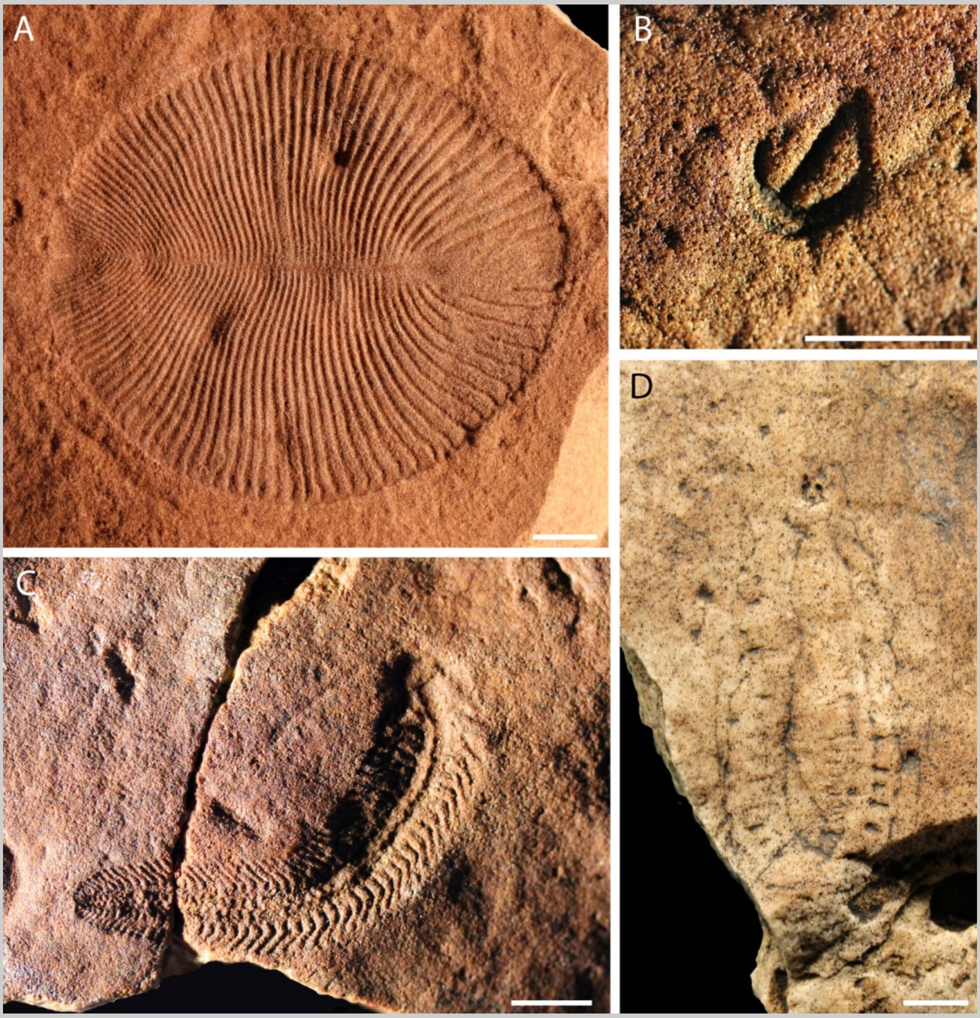

Figure 6 — Ediacaran fossils from the Ediacara Member, South Australia. All specimens reside at the South Australia Museum. A, *Dickinsonia*, SAM P40135. B, *Parvancorina*, SAM P40695. C, Two specimens of *Spriggina*, SAM P29802 and P29803. D, *Kimberella*, SAM P48935. Scale bars, 10 mm. Credit: F. Dunn and A. Liu.

Figure 7 — Further soft-bodied Ediacaran organisms from the Ediacara Member, South Australia. All specimens reside at the South Australia Museum. A, *Funisia*, SAM P40726. B, *Tribrachidium*, SAM P12898 (holotype). C, *Palaeophragmodictya*, SAM P48140. D, *Eoandromeda*, SAM P44349. E, Arkarua, SAM P49266. F, *Palaeopascichnus*, SAM P36854d. G, *Nemiana*, SAM P49342. Scale bars, 10 mm. Credit: F. Dunn and A. Liu.

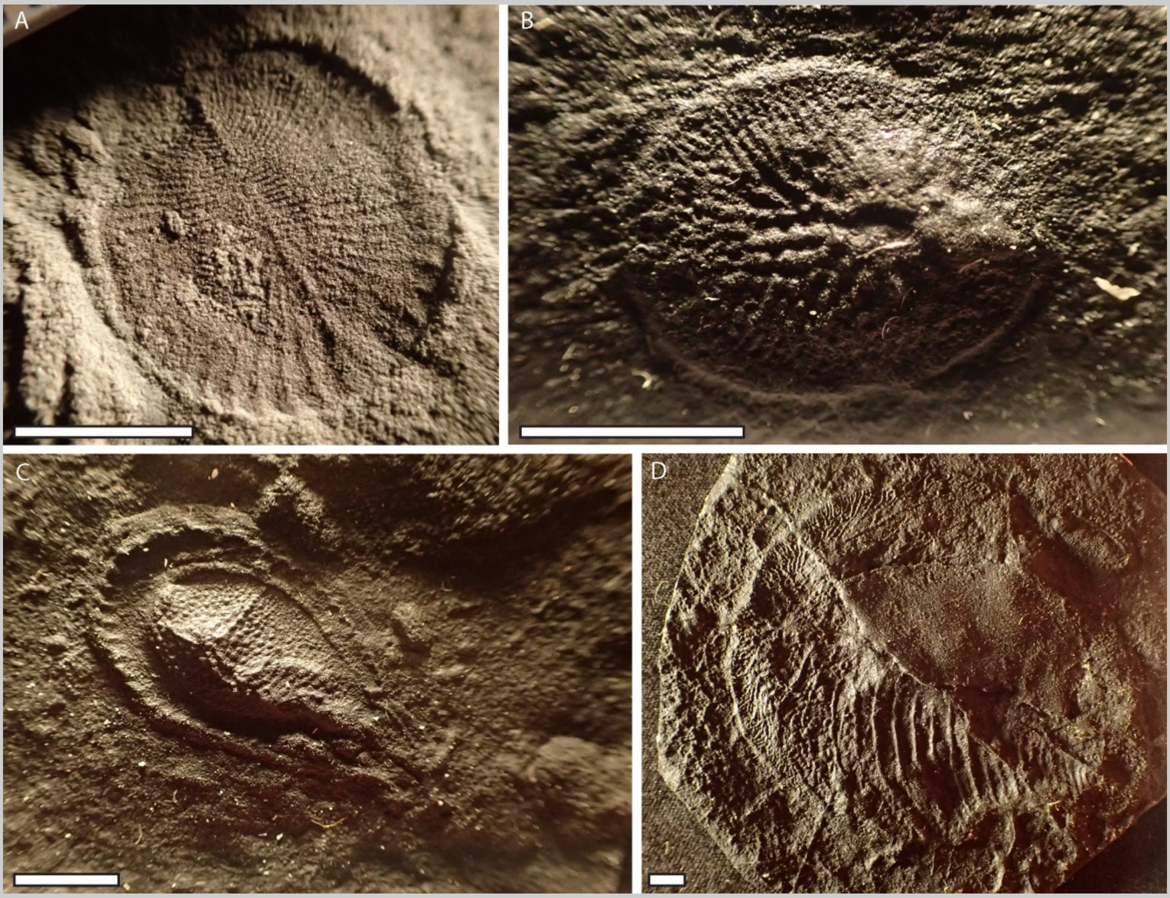

Figure 8 — Casts of soft-bodied Ediacaran organisms from the White Sea of Russia. All photographed specimens reside at the Royal Ontario Museum. A, *Dickinsonia*, ROM 54231. B, *Solza*, ROM 62397. C, *Kimberella*, ROM 62392. D, *Yorgia*, ROM 62387. Scale bars, 5 mm. Credit: F. Dunn and A. Liu.

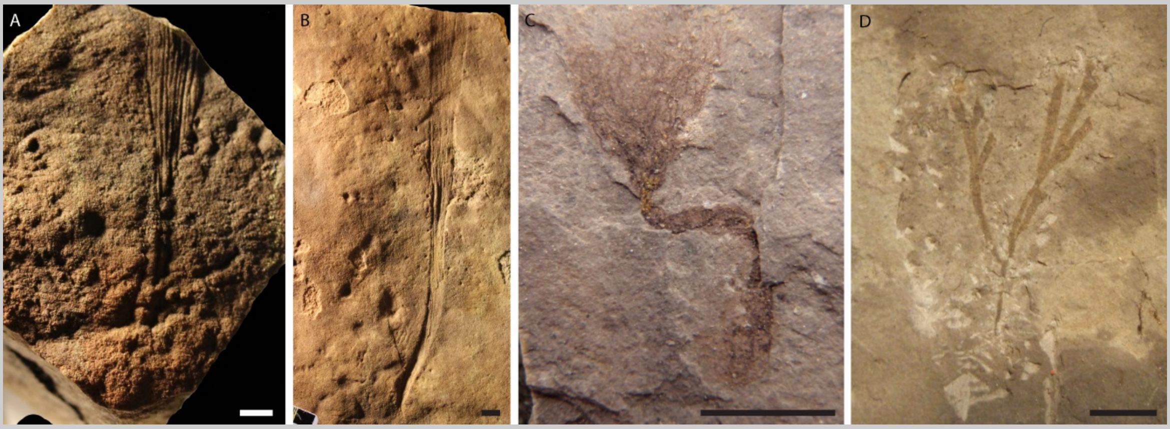

Figure 9 — Macroalgal taxa in the late Ediacaran period. A, *Flabellophyton*, Ediacara Member, South Australia, SAM P35701. B, *Liulingjitaenia*, South Australia, SAM P48771. C, *Longifuniculum*, field specimen, Miaohe Member, South China. D, *Konglingiphyton*, Miaohe Member, South China. Scale bars, 10 mm (A–B) and 5 mm (C–D). Credit: F. Dunn and A. Liu.

The White Sea/Australian biota persisted until about 550 million years ago, and represent the pinnacle of Ediacaran macroscopic diversity. After this, the number of soft-bodied groups declines in Ediacaran assemblages worldwide. Bag-shaped organisms that seem to have lived within the sediment of the sea floor, such as *Pteridinium* and *Ernietta*, become the most common soft-bodied groups, but these bizarre organisms had very unusual body plans, being composed of aligned tubes that may have been filled with sand during life (Fig. 10). Tubular fossils remained common (such as *Wutubus* and *Corumbella*; Fig. 11). Perhaps the most striking new arrivals were biomineralizing organisms with calcium carbonate skeletons, such as *Cloudina* (Fig. 11B) and *Namacalathus*. These organisms constructed the earliest reefs. Some *Cloudina* have also been found with holes in their shells, possibly indicating that they were being preyed upon.

Taken together, the Ediacaran macrofossil record suggests that by the start of the Cambrian, many important ecological and physiological innovations that would shape ecosystems in the Phanerozoic eon (from 541 million years ago to the present), such as predation, movement, reef-building and perhaps even bioturbation, had already evolved. Although we are hampered by the limitations of the fossil record, and by insufficient understanding of the age of many Ediacaran fossil localities, researchers are making progress in tackling questions about the patterns and processes that governed the distribution of Ediacaran organisms in time and space. However, a more fundamental question remains: what sort of organisms were the Ediacaran macrobiota?

Figure 10 — Ediacaran macrofossils from the Nama Group, Namibia, around 545 million years old. A, *Pteridinium*. B, *Ernietta*. C, *Swartpuntia*. Scale bar in C, 10 mm. Credit: M. Laflamme (A–B) and J. Hoyal Cuthill (C).

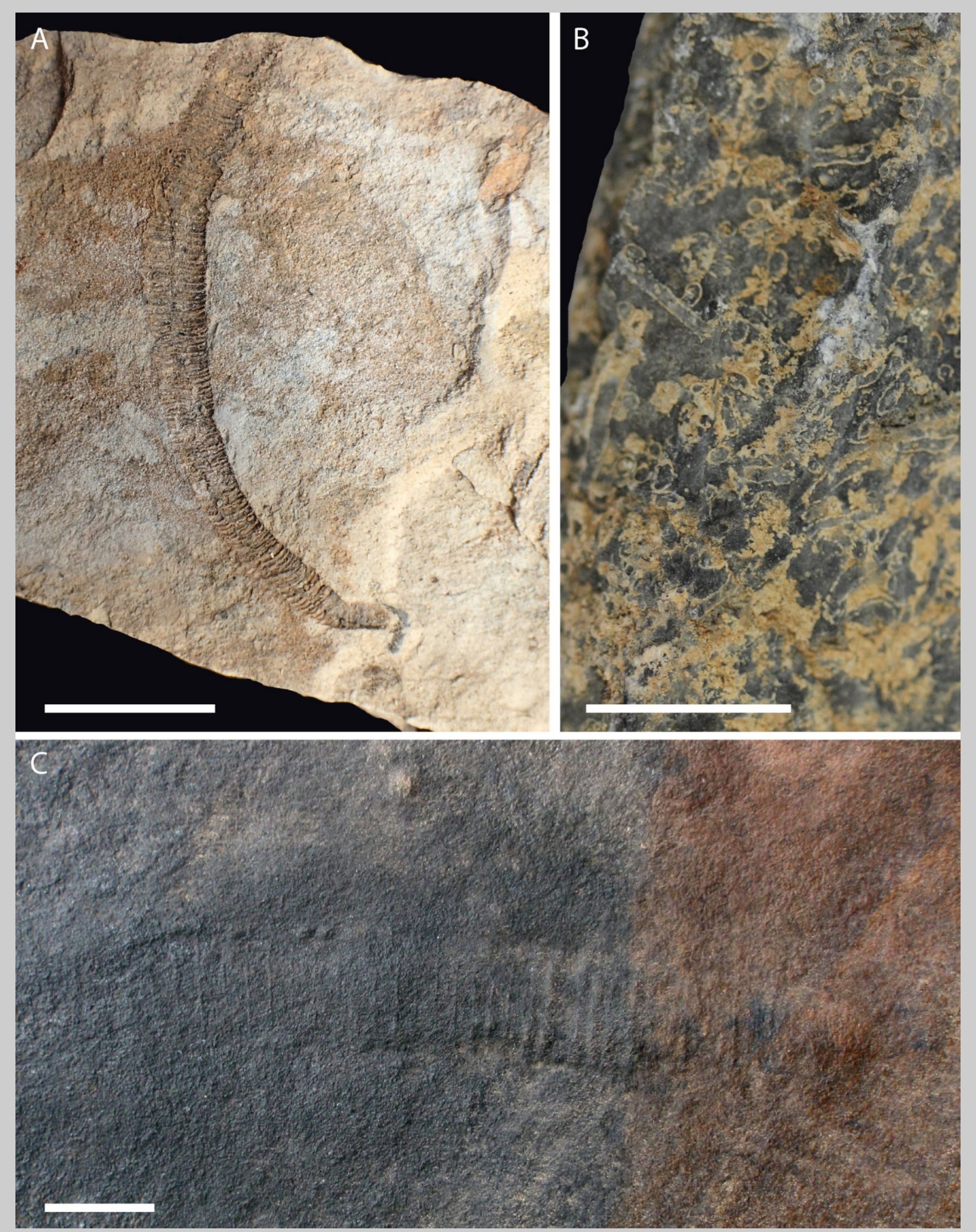

Figure 11 — Tubular taxa of the latest Ediacaran period. A, The possible cnidarian *Corumbella*, field specimen from the Tamengo Formation, Brazil. Corumbella has a seemingly flexible organic exoskeleton. B, *Cloudina*, from the Nama Group, Namibia, with a calcium carbonate cone-in-cone construction. C, *Wutubus*, field specimen from the Shibantan Member, South China. *Wutubus* was a seemingly soft-bodied, non-mineralized organism. Scale bars, 10 mm. Credit: F. Dunn and A. Liu.

Resolving the biological affinities of the Ediacaran macrobiota:

When first described in the 1960s and 1970s, members of the original Ediacara biota were largely considered to be ancient animals. Many frond-like groups were compared to sea-pens (a form of soft coral). *Dickinsonia* and *Spriggina* were thought to be annelid worms, and a variety of circular impressions (now recognized to be anchoring structures that attached Ediacaran fronds to the sediment) were interpreted as jellyfish. Those views culminated in Martin Glaessner's 1985 book *The Dawn of Animal Life*. However, palaeontologists such as Hans Pflug, Mikhail Fedonkin and Dolf Seilacher had already begun to question whether Ediacaran fossils really recorded the impressions of creatures belonging to extant animal groups in the 1970s and 1980s. They suggested that many members of the soft-bodied Ediacaran macrobiota may have been more closely related to each other than to any groups of organisms alive today. Seilacher took this argument furthest, reconstructing organisms such as *Charnia*, *Dickinsonia* and *Tribrachidium* as being made up of modular, self-repeating units, and placing them in their own extinct clade, the Vendozoa. This idea stimulated interest in the fossils, and led to a wide range of other suggestions, including that the organisms might have been fungi, protists, bacterial colonies or (most dubiously) lichens, rather than animals or vendozoans. As a result, to a non-specialist the discussion of Ediacaran fossils can seem extremely confusing and discordant, but since the turn of the millennium there has been a growing acceptance that the soft-bodied Ediacaran macrobiota should not be treated as a single monophyletic entity, all descended from one common ancestor. Instead, the biota reflect a diverse group of organisms that include crown- and stem-group members of several kingdoms and phyla (see Box 1), including early animals.

New technologies and approaches to studying these organisms are rapidly improving our knowledge of individual groups. These techniques include tomographic scanning, topographic analysis, and laser scanning for better visualization of morphological features (see Video 1), as well as modern ecological and geochemical methods.

Perhaps the fossils most likely to record Ediacaran animals are the mollusc-like organism *Kimberella* (Figs 6D, 8C), and *Dickinsonia* (although its precise position in the animal tree is unclear, with suggestions that it could be a placozoan, ctenophore, cnidarian or a bilaterian all proposed; Figs 6A, 8A). Several tubular fossils, such as *Corumbella*, have been compared to cnidarians, and some of the oldest candidate animal fossils include: the possible staurozoan *Haootia* at around 560 million years ago; the potentially older fossils *Lantianella* and *Xiuningella* from the Lantian biota; and the considerably more ancient putative sponge *Eocyathispongia* at 600 million years ago. Trace fossils likely to have been formed by animals (Fig. 5), probable sponge biomarkers, and predictions from modern DNA analysis (molecular clocks) all support the idea that animals existed before the Cambrian, and it should therefore not be surprising if many of the Ediacaran macrobiota do turn out to be animals. However, considerable work remains to confirm the validity of animal and other interpretations, and as palaeontologists we need to provide positive and robust evidence in order to determine the biological affinities of these fossils.

Box 1: Crown group or stem group?

Evolutionary relationships between organisms, both living and extinct, are studied as part of a discipline called phylogenetics. Phylogenetics attempts to identify related biological groups and construct a tree of life, using the assumption that closely related organisms should be more similar to each other than to more distantly related groups, or taxa. Organisms with common features, or characters, are assigned to groups called clades. For example, wolves and donkeys are both covered in fur and have mammary glands (characters that are shared by all mammals), and so are more closely related to each other than either is to, for example, a snail. But follow the tree back, and wolves, donkeys and snails will eventually share common characters, and can be assigned to the same clade (in this case, the Animalia).

We use specific terminology to describe the relationship between a fossil taxon and living organisms:

- The ‘crown group’ is made up of the last common ancestor of all extant (living) members of a group, and all of its descendants (many of which will be extinct).
- The ‘stem group’ consists of extinct lineages that fall outside the crown group, but are considered to be more closely related to that group than to any others.
- If we combine both of these groups, we have the ‘total group’: all the living members of the group and all fossil organisms considered to be more closely related to that group than to any other.

These terms help palaeontologists to relate long-dead organisms to extant groups. Where we place a fossil in a group depends on the combination of characters it shows. To lie in the crown group, an organism typically must possess all characters found in that group, or have been known to have once had them, and then lost them (‘lost them secondarily’). Where an organism has some but not all of the characters of a group, it might be more likely to belong in the stem. The term total group is particularly useful if we know that a fossil belongs to a particular clade, but we don’t know the relationships between extant groups well enough to be able to say whether the fossil belongs in the crown or stem group (Fig. 12).

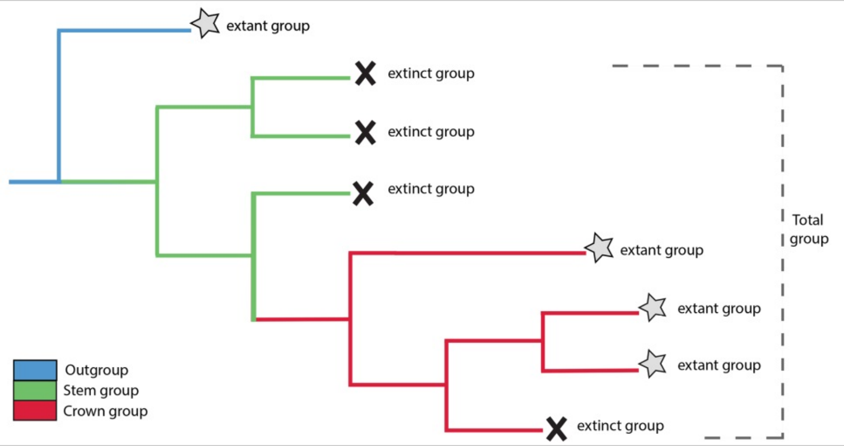

Figure 12 — An illustration of the concepts of total, stem and crown groups. An outgroup is an organism to which the group of interest is closely related to. Credit: F. Dunn and A. Liu.

Determining where the Ediacaran macro-organisms lie in the tree of life is difficult, because they have few preserved characters that could help us to assign them to any particular clade. Recent studies have suggested that many Ediacaran macrofossils may have been stem-group members of various animal phyla, or even stem-group animals.

Why did the Ediacaran macrobiota appear in the latest Precambrian?

Even if we can positively identify the Ediacaran macrobiota, questions remain about how the organisms lived, their relationships to one another, their interactions within their ecosystems and their impact on the wider biosphere. One broader question with implications for the wider Earth system is why did they appear in the fossil record at around 571 million years ago? The rock record reveals a short-lived glacial episode, the Gaskiers glaciation, only a few million years before the earliest Ediacaran macrobiota show up in the fossil record (Fig. 1A), but this may not have been a global event. Researchers have speculated that a release from ice-house conditions would have melted icecaps and released vast quantities of nutrients into the oceans, supporting blooms of microbes called cyanobacteria and triggering an increase in atmospheric oxygen levels. Oxygenation of the oceans may have let animals thrive and diversify, but several researchers dispute this. Some doubt that the timing of the oxygen rise correlates with the appearance of the earliest animals, and others have suggested that the presence of animals may itself have oxygenated the planet. Current research suggests that stability in oxygen levels may have been more important in creating suitable conditions for the evolution of complex life than how much oxygen there actually was. An alternative, biological, explanation for the appearance of the Ediacaran macrobiota is an explosion in genetic diversity, not necessarily because the genes themselves diversified, but because animals evolved new genetic 'machinery' that controlled how genes acted. Unravelling these factors is difficult, but will be essential if we are to determine what led the Ediacaran macrobiota to appear when they did.

Equally notable is the apparent disappearance of the Ediacaran macrobiota from the rock record at the start of the Cambrian, with only a handful of Ediacaran 'survivors' having been described from Cambrian rocks. Possible explanations for this disappearance have included: an extinction event caused by the appearance and diversification of the first predators; the removal of unique conditions that favoured the fossilization of soft-bodied organisms; and out-competition by better-adapted organisms. The latter scenario has been heavily influenced by the idea of ecosystem engineering — the alteration of an environment through the activities of organisms, such as burrowing or recycling nutrients — which may have resulted in the removal of microbial mats (a source of food and sediment stability for some of the Ediacaran macro-organisms). This ecosystem-engineering model has recently been supported by large scale analyses of multiple Ediacaran localities and their fossils.

Summary:

Ediacaran fossils undoubtedly record important steps in eukaryotic evolution, and together with the Cambrian fossil record they reveal an interval of biological innovation and diversification on a scale unparalleled in Earth history. Although the precise identities of many Ediacaran forms remain elusive, our understanding of both individual organisms and wider ecosystems is improving at a remarkable rate. New and exciting fossils are being discovered every year, and many more are yet to be formally described and studied. Continued expansion of research to consider the full range of Ediacaran organisms (rather than only a handful of iconic groups), and to use new techniques and data sets from other geological and biological disciplines, offers our best hope of understanding the true place of these remarkable fossils in the evolutionary history of our planet.

Suggestions for further reading:

Budd, G. E. & Jensen S. A critical reappraisal of the fossil record of the bilaterian phyla. *Biological Reviews* **75**, 253–295 (2000). DOI: 10.1111/j.1469-185X.1999.tb00046.x

Erwin, D. H. *et al*. The Cambrian conundrum: early divergence and later ecological success in the early history of animals. *Science* **334**, 1091–1097 (2011). DOI: 10.1126/science.1206375

Fedonkin, M. A. *The Rise of Animals: Evolution and Diversification of the Kingdom Animalia*. (Johns Hopkins University Press, 2007).

Glaessner, M. F. *The Dawn of Animal Life: A Biohistorical Study*. (Cambridge University Press, 1985).

Laflamme, M., Darroch, S. A. F., Tweedt, S. M., Peterson, K. J. & Erwin D. H. The end of the Ediacara biota: Extinction, biotic replacement, or Cheshire Cat? *Gondwana Research* **23**, 558–573 (2013). DOI: 10.1016/j.gr.2012.11.004

Liu, A. G. Framboidal pyrite shroud confirms the 'death mask' model for moldic preservation of Ediacaran soft-bodied organisms. *PALAIOS* **31**, 259–274 (2016). DOI: 10.2110/palo.2015.095

Narbonne, G. M., Xiao, S. & Shields, G. The Ediacaran Period. In: *The Geologic Timescale*. (eds Gradstein, F. M., Ogg, J. G., Schmitz, M. & Ogg, G.) 413–435 (2012).

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