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The Cambrian explosion

Derek E.G. Briggs

The sudden appearance of fossils that marks the so-called ‘Cambrian explosion’ has intrigued and exercised biologists since Darwin’s time. In *On the Origin of Species*, Darwin made it clear that he believed that ancestral forms ‘lived long before’ their first fossil representatives. While he considered such an invisible record necessary to explain the level of complexity already seen in the fossils of early trilobites, Darwin was at a loss to explain why there were no corresponding fossils of these earlier forms. In chapter 9 of the *Origin*, entitled ‘*On the imperfection of the geological record*’, he emphasized the ‘poorness of our palaeontological collections’ and stated categorically that ‘no organism wholly soft can be preserved’. Fortunately much has been discovered in the last 150 years, not least multiple examples of Cambrian and Precambrian soft-bodied fossils. We now know that the sudden appearance of fossils in the Cambrian (541–485 million years ago) is real and not an artefact of an imperfect fossil record: rapid diversification of animals coincided with the evolution of biomineralized shells. And although fossils in earlier rocks are rare, they are not absent: their rarity reflects the low diversity of life at this time, as well as the low preservation potential of Precambrian organisms (see Primer by Butterfield, in this issue).

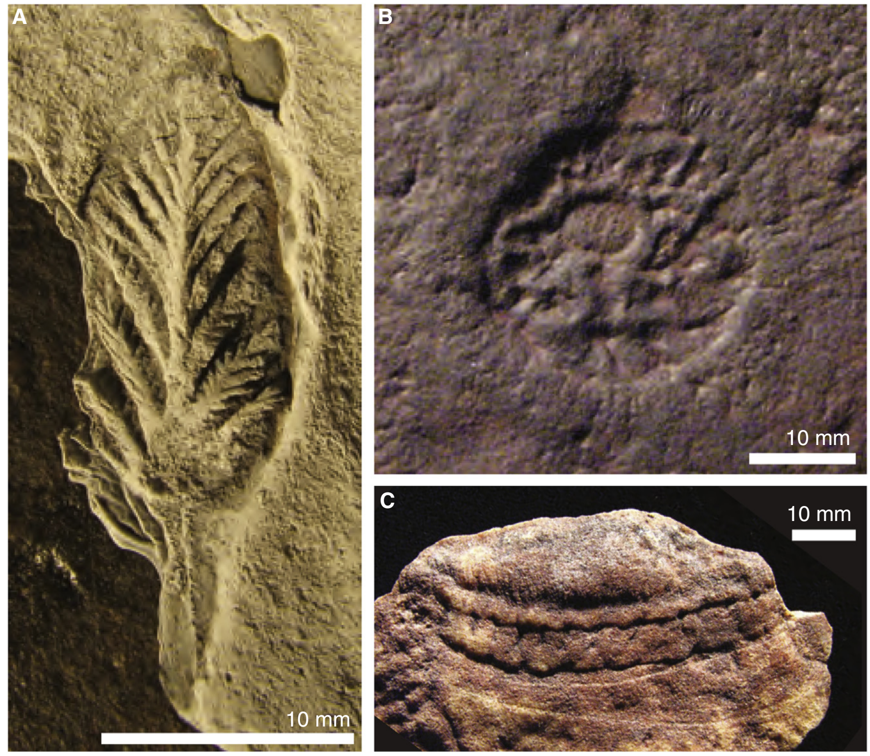

Figure 1. The first large organisms, from the Ediacaran period.
(A) Rangeomorph vendobiont *Avalofractus abaculus* from Spaniard’s Bay, Newfoundland (Newfoundland Museum NFM F-754). (B) Sponge *Palaeophragmodictya reticulata* from Flinders Ranges, South Australia (South Australian Museum P32352). (C) Mollusc *Kimberella quadrata* from Flinders Ranges, South Australia (South Australian Museum P23532). Photos: Marc Laflamme.

Evidence of Cambrian diversity

in the 1970s, Jack Sepkoski painstakingly tabulated the ranges of different taxonomic groups through the fossil record, revealing patterns of diversity through geological time. He used the theory of island biogeography, formulated by Robert MacArthur and E.O. Wilson in their 1967 book, to explain the Cambrian explosion. He predicted that global diversity would rise exponentially following the origin of animals until it reached a constant equilibrium. Sepkoski’s plot of the fossil record of taxonomic orders of marine animals strongly mimicked the predicted trajectory, but the rise of families is more complex and Sepkoski explained the pattern as a product of the radiation of separate ‘evolutionary faunas’. The Cambrian fauna was dominated by families of ecological generalists, such as trilobites, brachiopods and stem echinoderms. The succeeding Paleozoic fauna was characterized by more specialized groups — echinoderms, graptolites, ostracod crustaceans and corals — and reached a much higher maximum diversity in the Ordovician. In effect, the major body plans or phyla were established during the Cambrian explosion and marine animal diversity reached a ‘plateau’ in the Ordovician, a steady state which was impacted by extinctions but only seriously disrupted by the enormous mass extinction at the end of the Permian, which defines the end of the Paleozoic. Although later compilations of diversity through time have refined this picture, the general pattern of rapid diversification in the Cambrian and Ordovician remains valid.

The Ediacaran Period

Darwin’s dilemma regarding the absence of Precambrian fossils was not resolved until the 1940s when a diversity of large animals of Ediacaran age (635–541 million years ago) was discovered in South Australia, providing spectacular evidence of life prior to the appearance of the first shells. The fossils were first thought to be Cambrian — the presence of large organisms earlier was not considered plausible. More than 100 Ediacaran genera are now known from sites all over the world, on every continent except Antarctica (Figure 1).

Most of the classic Ediacaran fossils are preserved in fine sandstones and silts. Microbial mats covered the sea floor in Ediacaran times and sealed the sediment surface. The fossils survived as impressions where the sediment immediately adjacent to a carcass became cemented by rapid precipitation of minerals. This type of preservation, together with their unfamiliar morphology, makes it difficult to compare the Ediacaran creatures to living organisms or Cambrian fossils. Molecular clock dates indicate that the ancestors of most modern marine phyla had evolved by the Ediacaran, but identifying their representatives, even among the remarkable range of Ediacaran forms, is not straightforward. Some Ediacaran creatures lack apparent organ systems and consist of modules in an essentially two-dimensional, fractal-like arrangement. These organisms were among those named vendobionts by Dolf Seilacher. Vendobionts are thought to have lived by absorbing nutrients through the body wall. However, a number of Ediacaran fossils are interpreted with reasonable certainty as early offshoots (stem taxa) of lineages leading to modern groups — including sponges (*Palaeophragmodictya*), cnidarians, and bilaterians such as molluscs (*Kimberella*) and possibly arthropods. The presence of other unknown bilaterian animals is evidenced by shallow horizontal burrows in the sediment. During the Ediacaran Period the ancestors of modern marine animals lived alongside vendobionts until the latter went extinct.

Creatures of the Cambrian

Our picture of marine diversity through geologic time is based mainly on the relatively continuous fossil record of animals with shells. However, some 19 (~60%) of the ~33 phyla recognized today lack readily preserved hard parts and are soft-bodied. Exceptionally preserved Cambrian fossil deposits, such as the famous Burgess Shale, yield examples of 14 of the 19 soft-bodied phyla. If today's representatives provide a reliable guide, the small size and fragile nature of members of the other five mitigated against preservation, except in unlikely contexts, and explain why they appear much later in the fossil record: the earliest examples of rotifers and platyhelminthes, for example, are found in amber. Shelly fossils reveal the steep rise in diversity that is the Cambrian explosion, but the full cast of characters is seen only in settings that preserve evidence of soft-parts.

Cambrian marine communities were dominated by arthropods, including trilobites, and by sponges, which together accounted for more than half the species. Other invertebrates included annelids (polychaetes), brachiopods, hemichordates and priapulids; rare chordates were also present, including some interpreted as fish. This Cambrian world has become familiar through reconstructions of sea floor communities fossilized in the middle Cambrian Burgess Shale of Canada and the early Cambrian Chengjiang localities in China. In his book *Wonderful Life,* Stephen Jay Gould referred to *Wiwaxia*, *Hallucigenia*, *Opabinia* and *Anomalocaris* (Figure 2) as 'weird wonders', visual evidence of the rapid morphological evolution (disparity as opposed to diversity) that took place during the Cambrian explosion. Disparity certainly increased at a rapid rate, but estimates have shown that the volume of morphospace — based on character distributions plotted in multidimensional space — filled by the explosion was not very different to that occupied by marine life today. It appears that evolution during the Cambrian rapidly exploited the potential range of form, and subsequent diversification was subject to similar limitations as today. The affinities of some of the Cambrian creatures that were dubbed 'weird wonders' are still debated but phylogenetic analyses have shown that most of them are much less weird than first thought — they do not represent extinct higher taxa, but are early offshoots of the lineages leading to modern groups. *Hallucigenia*, *Opabinia*, and *Anomalocaris*, for example, lie on the stem leading to modern arthropods.

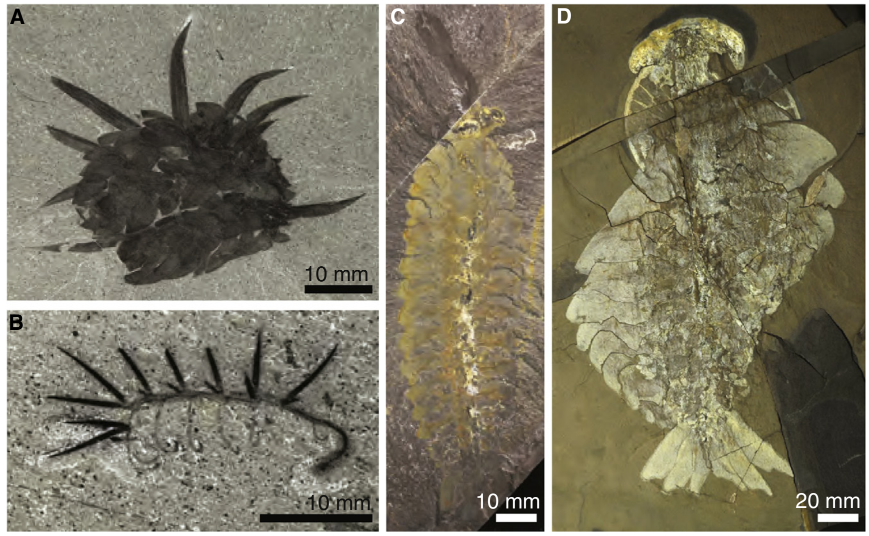

Figure 2. Animals from the Cambrian Burgess Shale of British Columbia.
(A) *Wiwaxia corrugata* (Royal Ontario Museum ROM 56950). (B) *Hallucigenia sparsa* (ROM 61513). (C) *Opabinia regalis* (Yale Peabody Museum YPM 5809). Photo: Jessica Utrup. (D) *Anomalocaris canadensis* (ROM 51211). (A,B,D from http://burgess-shale.rom.on.ca/en/)

Fossilization during the Cambrian

The Cambrian is remarkable compared to younger geological periods for the large number of marine deposits that yield soft-bodied fossils — there are more than 50 exceptional preservations (*Konservat-Lagerstätten*, conservation deposits) similar to the Burgess Shale. This fortunate circumstance means that we have an unusually complete window on the marine forms that evolved at this critical juncture in the history of animal life — during the Cambrian explosion. The abundance of exceptional preservations was a conundrum until investigations of the chemistry of the associated sedimentary rocks provided a possible explanation. Sulfate concentrations may have been low in the Cambrian oceans, suppressing decay bacteria in sediments. More importantly, perhaps, Cambrian sea water was unusually high in alkalis, which promoted early consolidation of the sediment, sealing off buried carcasses. The chemistry of the Cambrian oceans apparently favored exceptional preservation across the globe.

Various arthropods from the Cambrian of China have recently been shown to preserve evidence of the brain and nervous system, which

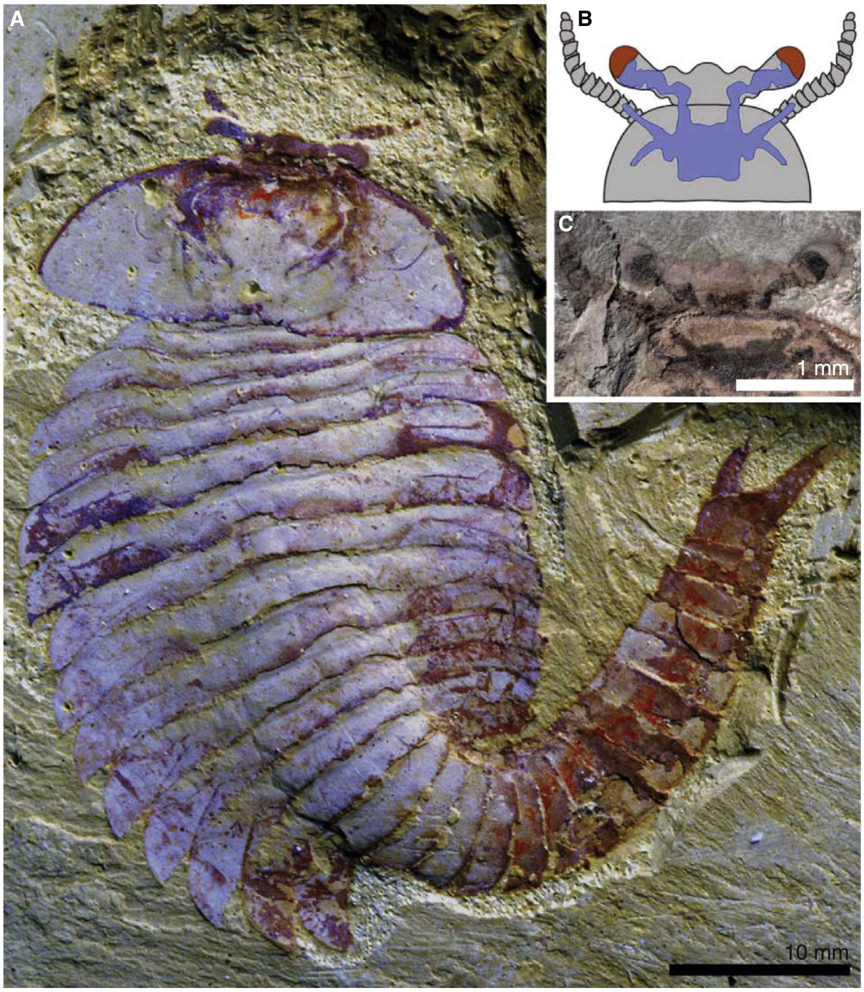

Figure 3. Arthropod *Fuxianhuia protensa* from the Cambrian Chengjiang fauna of Yunnan Province, China.
(A) A complete specimen (Yunnan Key Laboratory for Palaeontology, Yunnan University, Kunming, YKLP 11321). (B) Reconstruction of head showing nerve tracts connecting the brain to the eyes and antennae (image courtesy of Nick Strausfeld). (C) Head showing preserved outline of brain and nervous tissue (YKLP 15006). (A,C: Reprinted by permission from Macmillan Publishers Ltd: Nature (Ma., 2012), copyright 2012).

were fossilized in rapidly precipitating minerals (Figure 3). But while Cambrian soft-bodied fossils may preserve remarkable details, fossils are rarely pristine versions of the original animal. Simple decay experiments documenting how features are degraded and lost have proved very instructive in interpreting fossil specimens. Robert Sansom's observations on chordates revealed a sequence of decay stages that is perfectly echoed by fossils of early chordates from the Cambrian of China. Fossilization is a race between decay and preservation: just as in forensics, a carcass can appear very different depending on the length of time and progress of decay between death and fossilization. Unfortunately the more derived attributes of chordates, mainly features of the head, tend to be lost first so that the resultant fossils look more primitive in appearance and end up lower down on the cladogram. This kind of 'stemward slippage' explains why the phylogenetic position of some of the chordates from the Chengjiang biota, which lie low on the stem leading to modern vertebrates including ourselves, has proved controversial. It also emphasizes the importance of understanding the impact of decay when interpreting soft-bodied fossils.

Insights from fossils and genes

Unraveling the mysteries of the Cambrian explosion used to be the exclusive domain of paleontologists. Fossils provided a time scale, including evidence of the first appearance of the various animals in the fossil record. And through Cambrian soft-bodied fossils paleontologists had the makings of a metazoan menagerie that might provide clues to relationships between the major animal groups. But the relationships between phyla remained elusive — not surprisingly perhaps, given that phylum status was assigned where there was no evidence of close affinity with another major group. A renewed interest in phylogenetics among biologists, fueled by affordable gene sequencing, has provided an additional basis for generating phylogenies (see review by Telford *et al*. in this issue). Of course, sequences are not available for fossils, but extinct forms are important in revealing lost morphologies that may be intermediates between living taxa and fundamental to determining their relationships. Fossils are also critical to calibrating the age of branching events in a phylogeny and, by extrapolation, to computing a molecular clock (see review by Lee and Palci in this issue). A recent metazoan phylogeny generated by Kevin Peterson and colleagues, combined with a molecular clock (Figure 4), allows the age of branching points to be estimated and provides clear evidence of the Cambrian explosion.

Although the fossil record is silent on mechanisms to explain how morphology could have evolved so rapidly, developmental biology investigates how genetic mechanisms affect body plans. Evolutionary developmental biology (evo-devo) may provide clues to how such a remarkable range of morphology evolved so quickly, at least in organisms amenable to experimental manipulation.

Where is the Cryogenian record?

The fossil record is incomplete, particularly among taxa without biomineralized 'hard' parts. However, ages based on the molecular clock (Figure 4) closely match those of the earliest fossil representatives, providing independent confirmation of a rapid metazoan radiation. But the molecular clock yields dates for basal branching events in metazoan phylogeny that significantly predate the earliest fossils — the origin of sponges and cnidarians, as well as the ancestral bilaterian, plunge into the Cryogenian (850–635 million years ago), more than 650 million years ago, around the time of the global glaciation known as the Sturtian. While these three animal groups are represented in the Ediacaran, convincing examples have yet to be discovered in older rocks, yielding a gap of ~100 million years. These earliest metazoans are likely to have been rare, small and soft bodied. Sponges might be expected to yield fossils of their spicules, but they might not have had a biomineralized skeleton until the early Cambrian, when most other metazoans evolved hard skeletons. There is, however, evidence of sponges, at least, in older rocks: the biomarker 24-isopropylcholestane (known as 24-ipc), which occurs only in demosponges, is abundant in rocks more than 700 million years old and body fossils of sponge-like forms have recently been reported from China (600 million years old) and Australia (>635 million years ago).

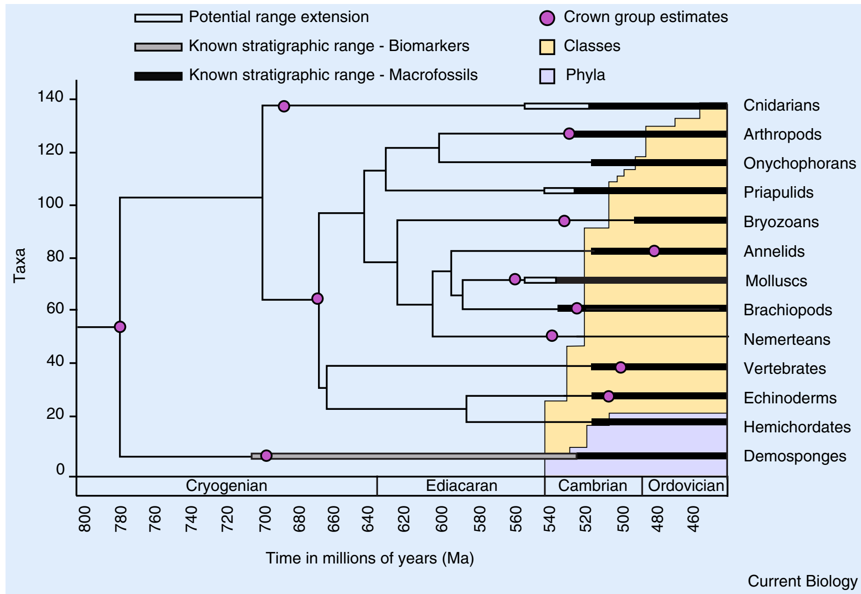

Figure 4. The Cambrian explosion — ranges and relationships.
Fossil evidence for the diversification of major animal groups based on first appearances of taxa during the Cambrian explosion, overlain by a metazoan phylogeny with branch lengths calibrated using a molecular clock approach (after Erwin *et al*. 2011).

Setting off the explosion

The drivers behind the Cambrian explosion were varied and complex, and there is no simple explanation of either the timing or ecological mechanism involved. The rise of oxygen levels in the earth's atmosphere and oceans has often been implicated in initiating rapid diversification. A recent study of polychaete feeding strategies in modern environments suggests that there may be a direct link between critical oxygen thresholds, the rise of larger carnivores, and the evolution of complex food webs. The abundance and diversity of carnivorous polychaetes today is greater where oxygen levels are higher. The rise of carnivorous predators in the Cambrian may have promoted new defense strategies with a consequent elaboration of food webs. Rapid biodiversification was no doubt also boosted by the animals themselves and their impact on the environment, in a kind of ecosystem engineering. The disappearance of the microbial mats that covered the Ediacaran sea floor was associated with the rise of grazing invertebrates, which opened up the sediment to burrowers. This invasion of the sediment introduced oxygen to the substrate which was then colonized by a diversity of infaunal animals. The rise of zooplankton allowed particles to sink to the sea floor as fecal material which significantly augmented the nutrient supply. Such increases in environmental complexity during the Cambrian may well have resulted in a proliferation of diverse ecological strategies that were not present earlier.

Until recently many of the unusual life forms of the Cambrian were assumed to have been lost long before the end of that period (485 million years ago). Recent discoveries of exceptionally preserved fossils near Zagora in Morocco, however, have provided dramatic evidence that a number of iconic Cambrian animals, such as anomalocaridids (Figure 5), persisted into the Ordovician (485–444 million years ago). Conditions in part of the sedimentary sequence known as the Fezouata formations clearly favored the preservation of soft-bodied fossils. Not only are creatures, such as marrellomorphs, present that would look perfectly at home in a Cambrian assemblage, so too are animals such as horseshoe crabs that were previously thought to appear only much later. Deposits like the Fezouata formations, which preserve soft-bodied fossils, are important to understanding the great Ordovician biodiversification event, the rapid diversification within the major animal groups that followed the Cambrian explosion and heralded the origins of elements of the modern fauna.

Conclusion

The Cambrian fossil record shows that the major body plans which are familiar today were established early. But deposits, such as the Burgess Shale, also preserve animals that appear alien to our eyes. Such extinct forms are a critical component of phylogenetic analyses that explore the early evolution of major groups. They are complemented today by analyses of gene sequences from living animals. In this way, understanding the Cambrian explosion has become an interdisciplinary endeavor. Phylogenies calibrated by fossil occurrences allow molecular clocks to estimate the timing of branching even where fossil evidence is wanting. And in due course, experiments on the role of control genes in the development of animals from embryo to adult may provide clues to how all the major animal groups evolved in a relatively short time during the Cambrian explosion.

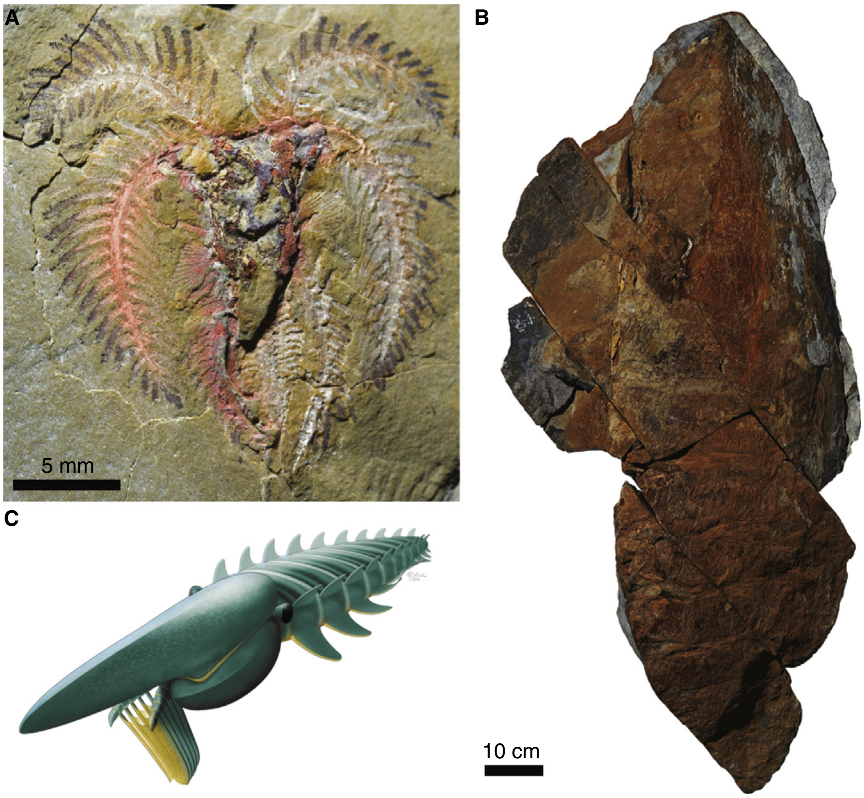

Figure 5. Animals from the early Ordovician Fezouata formations of Morocco.
(A) The marrellomorph arthropod *Furca* (Natural History Museum of Toulouse, France, MHNT. PAL.2007.39.80.1). (B) A concretion preserving the giant filter feeding anomalocaridid *Aegirocassis benmoulai* (Yale Peabody Museum YPM 237172). (C) Reconstruction of *Aegirocassis benmoulai* © Marianne Collins. (Images reprinted by permission from Macmillan Publishers Ltd: Nature (Van Roy *et al*., 2010 and 2015), copyright 2010 and 2015.)

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Insect evolution

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It goes without saying that insects epitomize diversity, and with over a million documented species they stand out as one of the most remarkable lineages in the 3.5-billion-year history of life on earth (Figure 1). This reality is passé to even the layperson and is taken for granted in the same way none of us think much of our breathing as we go about our day, and yet insects are just as vital to our existence. Insects are simultaneously familiar and foreign to us, and while a small fraction are beloved or reviled, most are simply ignored. These inexorable evolutionary overachievers outnumber us all, their segmented body plan is remarkably labile, they combine a capacity for high rates of speciation with low levels of natural extinction, and their history of successes eclipses those of the more familiar ages of dinosaurs and mammals alike. It is their evolution — persisting over vast expanses of geological time and inextricably implicated in the diversification of other lineages — that stands as one of the most expansive subjects in biology.

Insects comprise the more diverse of two classes united together as the arthropod subphylum Hexapoda, the other being the Entognatha, consisting of the orders Diplura, Protura, and Collembola (springtails). While it is often easy to recognize an insect and even a hexapod, identifying the closest relatives of Hexapoda has been a pernicious problem. Interestingly, while much has improved regarding arthropod phylogeny and the placement of hexapods, today we are somewhat less certain of a precise culprit for the hexapodan sister group. This uncertainty highlights the challenges in reconstructing relationships among major groups of Arthropoda and of interpreting broad patterns in the evolution of the phylum.

Hexapoda and the origin of insects

Relationships among Arthropoda have long been a matter of debate, and even monophyly of the phylum was once called into question. The door to arthropod polyphyly has been closed, however, and with the recognition of the relationship of Cycloneuralia to

