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Patterns in Palaeontology: The Cambrian explosion – Paradoxes and possible worlds

by Janathan B. Antcliffe [*1]

Introduction:

The transition between the Precambrian and the Cambrian period (about 550 million to 500 million years ago) records one of the most important patterns of fossils in all the geological record. Complex animals with a suite of shells, intricate body plans and associated movement traces appeared for the first time, suddenly and unambiguously, in sequences all over the world during this interval. This 'Cambrian explosion' remains one of the most controversial areas of research in all of the history of life, and one of the most exciting. Palaeontological data like this is definitive in its support for evolutionary theory, the relative sequence of first appearances in the fossil record over the past several billion years ties very closely with what we would expect from evolutionary theory. Bacteria appear first, followed by simple nucleated cells, then simple animals, plants and fungi, followed by more advanced organisms. Without palaeontological data, we have no way of looking at the biology of extinct organisms, which represent more than 99% of everything that have ever lived. We wouldn't know about anomalocaridids, dinosaurs or giant sloths, and we would be much the poorer for that. Furthermore, without palaeontological data we wouldn't know about the great events in the history of life, such as the mass extinction of dinosaurs. In contrast to that event, the Cambrian explosion is a mass origination: a time when the pattern of fossils suggests that animals appeared during a relatively short interval of time. To understand what happened at that time, we must understand what a 'pattern' of fossils is. How do we recognize patterns of fossils? Is the observed pattern reliable, or are we in some way being misled by the fossil record? What process formed the pattern?

Paradoxes:

These questions are really all the same question, although at first they look very different. The problem all comes down to what is known as the pattern and process paradox. Once you understand the existence of this paradox, it changes how you look at the history of life. A fossil pattern is the information gained when you classify organisms that are observed in sequences of rocks. Some fossils appear before others, some occur later. Classifying them into different biological groupings produces a pattern of appearances of these groups in the fossil record. The natural processes that generate such a pattern of fossils can be of many different types, such as the evolutionary processes that cause creatures to change from generation to generation, or the process of fossilization itself. At first, this all seems fine. There are two distinct things that it is reasonable to be interested in: fossil patterns and evolutionary processes. That is how many biologists and palaeontologists treat them. If you learn something about the fossil pattern, then you can work out the evolutionary processes. If you discover some new process of evolution, then that would help to explain fossil patterns.

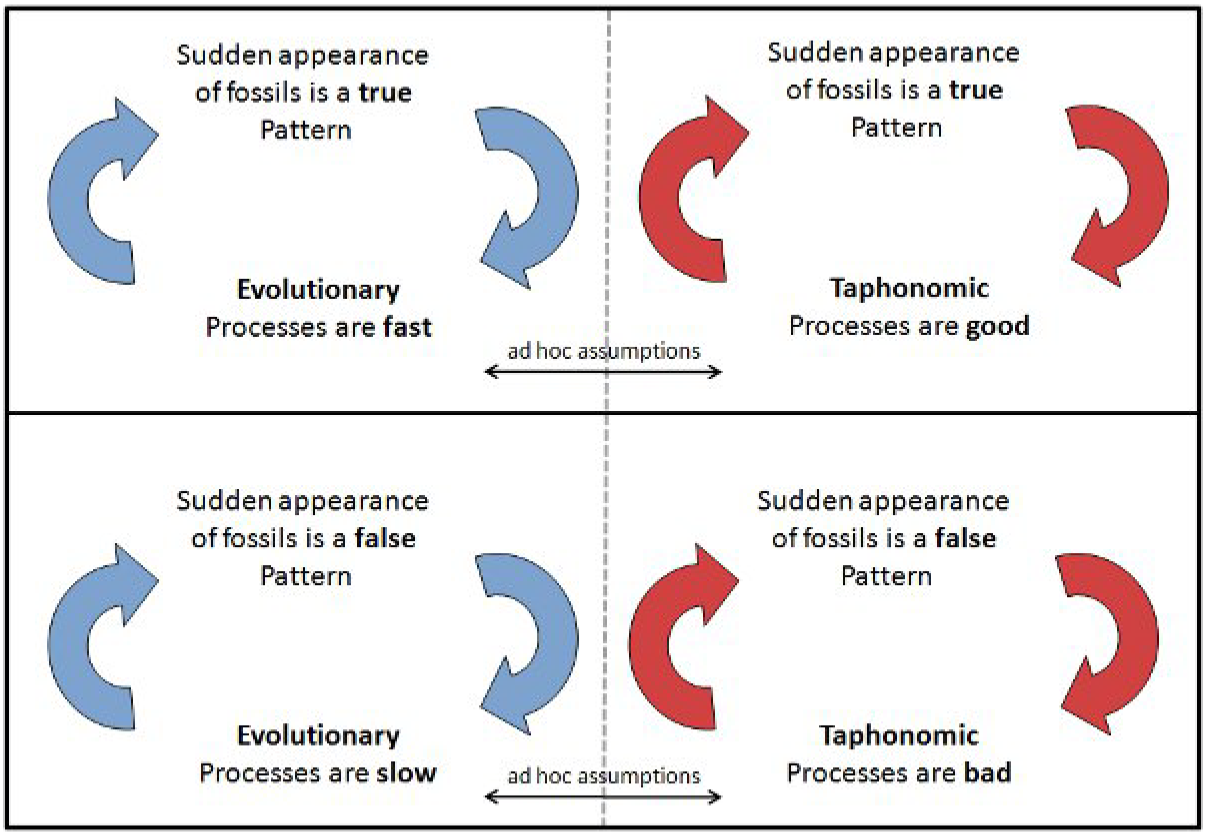

FIGURE 1 — SCHEMATIC OF THE PATTERN AND PROCESS PARADOX.

Unfortunately, it is much more difficult than that (see Fig. 1). Fossil patterns and evolutionary processes are not separate sets of data. The fossil pattern that you see is based on how you have classified your fossils, and that in turn is based on two things. First, what evolutionary process do you think best explains how the organisms should be classified? Should you classify fossils based on overall similarity to each other, or overall difference? Should some characters have priority over others (for example, is mode of reproduction more important than length of arm), or should all characters be treated equally? If characters are to be treated differently, then *how* should they be treated differently?

Second, how does preservation affect the fossil pattern that you see? Are the characters present in the fossil just the ones that preserve well, or are they a reliable witness to evolutionary history? Are characters that are absent from the fossil absent because they do not preserve well or because they hadn't evolved yet in the group that the fossil represents? For example, soft tissue doesn't preserve as readily as biominerals, such as shells and bone, so we expect to see more hard-bodied animals preserved in the fossil record and fewer soft-bodied animals. These sorts of bias in the preservation processes affect the pattern of fossils we see. So in merely recognizing a fossil pattern, you have already had to make a great many assumptions about the evolutionary and preservation processes that produced it.

The situation is similar for understanding evolutionary processes from the fossil record. There are many evolutionary processes that are well documented and well understood from studies of modern organisms: gradual evolution by natural selection, for example; symbiogenesis (when two organisms merge and start living and reproducing as one organism — found only in very simple creatures such as bacteria); or even major alterations owing to large or significant mutations. These processes are very useful for understanding vast amounts about biodiversity on Earth. But are there other processes that act over longer time periods, which we can't observe in the modern world because they are too slow? What evolutionary processes operate during the evolution of major new groups of animals? Are they the same as or different from those that cause small changes in living animal groups? To answer such exciting questions about long-term evolutionary processes, we must look at the patterns that we see in the fossil record.

When examining what we think may be a rational idea about evolutionary processes, we must refer to the evidence from fossil patterns — but the evidence from fossil patterns is already full of assumptions about evolutionary processes. The only reason we could form a fossil pattern is because we have ideas about evolutionary process that we think are reasonable that allow that pattern to form. The fossil pattern and evolutionary process are a circular paradox from which there is seemingly no escape.

Possible Worlds:

Attempts to understand the Cambrian explosion provide some of the most interesting examples of the pattern and process paradox. Before the Cambrian explosion, the fossil record contains no shells or bones — only soft-bodied fossils. During the Cambrian explosion, biomineralized animals appear for the first time, as does unambiguous evidence for almost all the major modern groups of animals. But what should we make of all the fossils that are older than this? Does the appearance of biomineralized animals mark roughly the origin of animals, or did animals evolve earlier and only later add biominerals to their bodies? Some scientists base their views concerning the origin of animals on evidence from evolutionary processes, whereas others base their views on patterns of fossils. There are five basic models concerning the origin of animals and how this relates to the pattern of fossils at the base of the Cambrian (see Fig. 2).

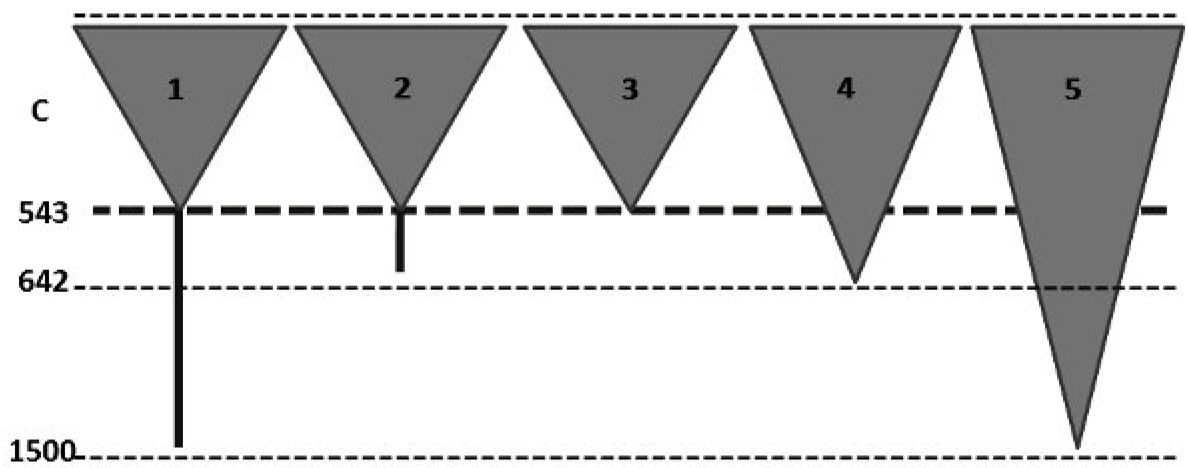

FIGURE 2 — DIFFERENT MODELS FOR THE ORIGIN AND DIVERSIFICATION OF ANIMALS AND THE CAMBRIAN EXPLOSION. NUMBERS, TIME BEFORE PRESENT (MILLIONS OF YEARS); C, CAMBRIAN PERIOD.

Model 1: The slow-burning fuse

The fossil pattern suggests that the major diversification of animals started at the beginning of the Cambrian period (about 543 million years ago). Evidence for this includes the gradual assembly in the fossil record of the major modern animal groups as they acquire the important characters that allow us to distinguish them in the modern world. The pattern of the fossils in this regard is generally accepted to be true, which is important evidence that something significant and interesting took place at this time.

However, many scientists have argued that some very primitive animals existed a long way back in to the Precambrian. Evidence for this comes from controversial genetic data from 'molecular clocks'. The molecular clock works more or less on the principle that speed = distance/time. If you can take genes from two different animals, and you know in general how quickly genes evolve (speed) and how different two particular genes are from each other (distance), then you can calculate how long it must have been since they were the same gene: that is, when the ancestor containing the genes must have lived. In the calculation, the speed of evolution is worked out using fossils that everyone can agree on, known as calibration points. These allow you to say that certain animal groups must have evolved by a particular time, because we have some very convincing fossils of them by then (usually from the Cambrian or younger sediments). When you do this calculation to work out when the first animals lived you invariably get an origin time well into the Precambrian: the earliest molecular clocks (which were very methodologically flawed) all made predictions of very ancient divergences. In this way, calculations based on an understanding of processes can lead people to form very strong views about what the pattern of the fossil record should look like. People who believe this molecular-clock data expect to find animal fossils one billion years old, and they sometimes accept evidence to support this even when that evidence isn't very good.

The slow-burning-fuse model suffers from over-reliance on evidence from molecular clocks. Molecular clocks are like trying to draw a dot-to-dot picture, with fossil calibration points as dots and lines based on inferences from genetic data. Unfortunately, you don't really know for certain where the dots are and you can complete the picture only because you have an idea of how you ***should*** draw lines. Ultimately such analysis becomes an argument about the reliability of the dots (have the fossil calibration points been correctly interpreted?). In fact, it is even worse that this makes it seem. Imagine you had a dot-to-dot picture of a bear, and from what you could see it wasn't wearing a hat. Now, imagine that you started to draw a hat on the bear not because you have any reason to put it there (there are no dots), but because you think it should be there. Using molecular clocks to learn about the origin of animals is like inventing new bits of the picture, having gone way past the parts of the picture that did have reliable dots.

Some fossils, such as the Stirling Biota from Western Australia — centimetre-scale fossils from around 2 billion years ago — have been controversially interpreted to support the slow-burning-fuse model, but these are not considered by most palaeontologists to be good evidence for early animals, because they show no characteristics that are unique to animals. Many other things could have made them, some of which may not even be biological.

In summary: animals originated perhaps a billion or more years ago but didn't really get going until around the Cambrian when they diversified dramatically.

FIGURE 3 — DICKINSONIA COSTATA FROM THE FLINDERS RANGES, SOUTH AUSTRALIA. ONE OF THE MOST ICONIC FOSSILS OF THE LATE PRECAMBRIAN, DATING TO AROUND 555 MILLION YEARS AGO.

Model 2: The shallow fuse

Perhaps more mainstream than the first model, this view also supports the idea that animal groups diversified during the Cambrian, but it places the origin of animals later: at the end of the Precambrian (Ediacaran period, about 635 million to 542 million years ago). A number of molecular-clock models have made predictions that have supported animal origins in this interval; these models, including the most recent ones, seem to have overcome some of the methodological flaws of earlier efforts. Unfortunately, we have few ways to judge molecular-clock estimates apart from against the pattern of the fossil record. We have a tendency to think that molecular clocks are more reliable when the estimates they give are closer to the evidence from the fossil record. However, that doesn't mean that anything is analytically better about the molecular clocks that give an estimate of 600 million years for the origin of animals as opposed to the clocks that give estimates of 700 or 800 million years, they still suffer from the problem of drawing lines in a dot-to-dot picture that lacks the necessary dots.

There are many Ediacaran fossils that have been interpreted as evidence for the earliest animals. Here, the fossil record is regarded mostly as a reliable witness to early evolution, with preservation processes having fossilized soft-bodied organisms. The Ediacaran biota are a group of highly enigmatic soft-bodied fossils (lacking shells, bones, and teeth) that are preserved globally from roughly 580 million to 545 million years ago. These and related fossils have received much attention for their basic morphological similarity to many different modern animal groups (see Figs 3 and 4).

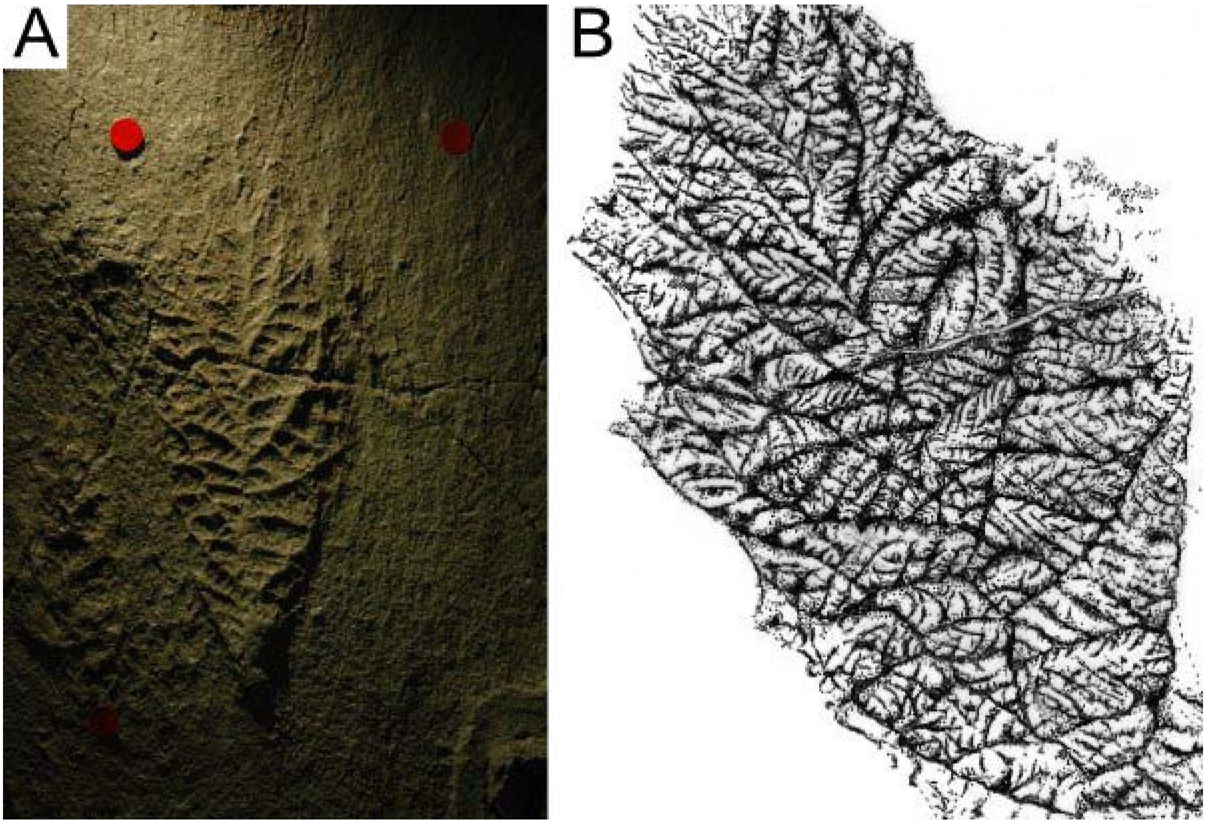

FIGURE 4 — PHOTOGRAPH (A) AND DRAWING (B) OF THE HOLOTYPE OF BEOTHUKIS MISTAKENSIS. THIS FOSSIL IS IMPORTANT BECAUSE IT HELPS TO DECODE HOW EDIACARAN FOSSIL ARE CONSTRUCTED. (BRASIER, M. D. & ANTCLIFFE, J. B. 2009. EVOLUTIONARY RELATIONSHIPS WITHIN THE AVALONIAN EDIACARA BIOTA: NEW INSIGHTS FROM LASER ANALYSIS. JOURNAL OF THE GEOLOGICAL SOCIETY 166, 363–384. (DOI:10.1144/0016-76492008-011))

But it is important to remember that there is no such thing as an unambiguously interpreted Precambrian animal fossil: if there were, there would be no debate. When you look at the Ediacaran fossils in detail, they are difficult to match directly with modern animal groups — they lack definitive characters and they seem to grow in completely different ways to modern animals groups (Fig. 5). Similarly, fossils once thought to be animal embryos from the Doushantuo Formation of China (about 555 million years old) no longer convince the community at large that they are animals or embryos, let alone both. We must also ask, why should good animal fossils not be preserved for so long? How did they evade the fossil record, when there are so many examples of amazing preservation of fossil algae and other soft-bodied forms in the late Precambrian? It doesn't seem to be because the fossil record at this time was a hopeless record of what was living.

Overall, this remains a fairly mainstream view that has much to recommend it — not least the logic that if the first animal fossils appear at 543 million years ago then animals must have evolved before they left fossils. That does not mean that they had to evolve 90 or 100 million years earlier; perhaps it was just a few million years. The shallow fuse could be very shallow indeed. In that case, this model becomes similar to model 3.

In summary: Origin of animals somewhere in the Ediacaran, major diversification in the Cambrian.

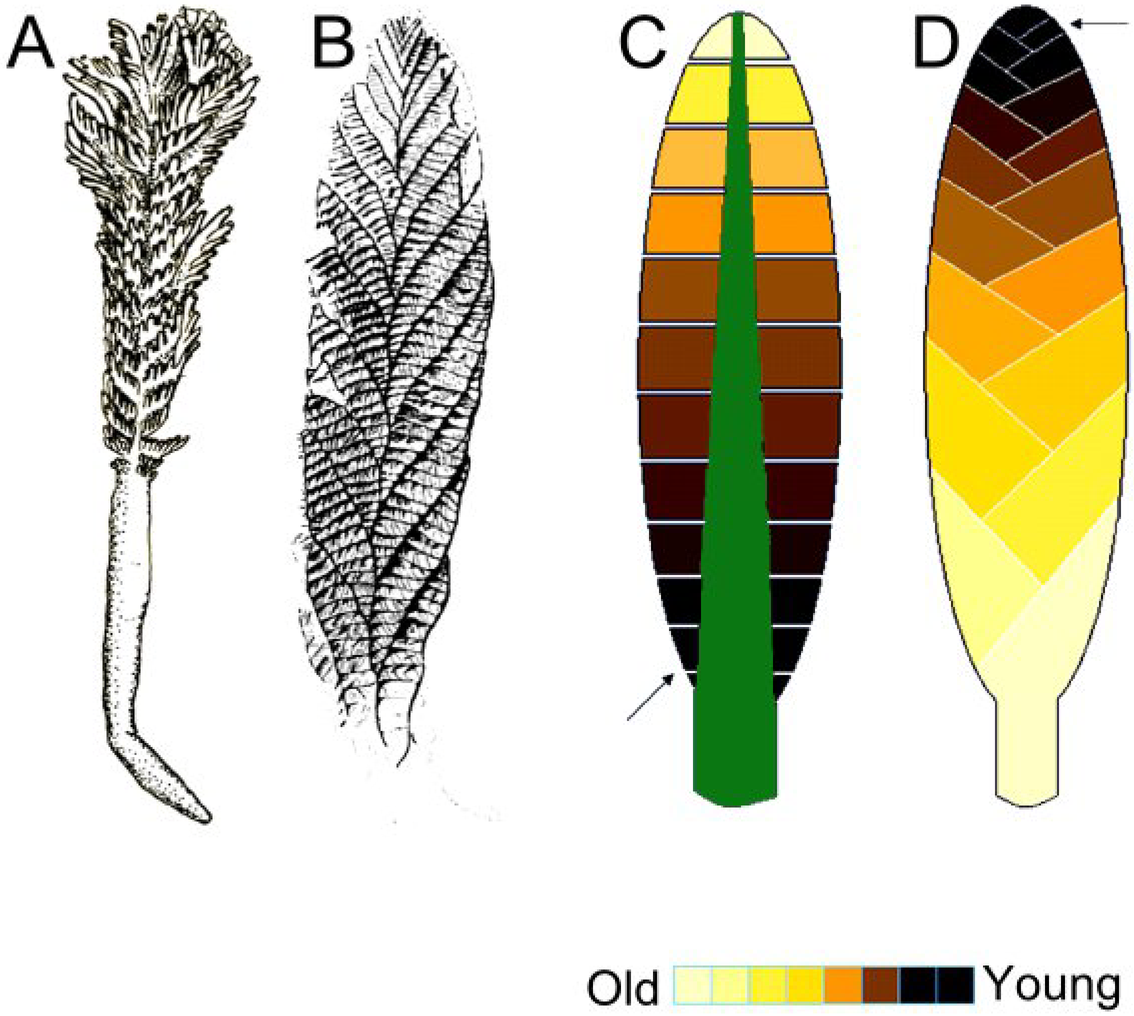

Figure 5 — A comparison of the growth dynamics of a modern sea pen and an Ediacaran fossil. (A) A drawing of Pennatula phosphorea, a species of sea pen from the modern ocean. (B) A drawing of Charnia masoni, an Ediacaran fossil. Growth schematics show that for the Pennatulacea (C) insertion of new elements occurs at the base of the frond, in contrast to the Ediacaran fossils (D), where insertion of new elements occurs at the apex of the frond. (Antcliffe and Brasier (2008))

Model 3: Evolutionary Big Bang

The pattern of the Cambrian record is profoundly impressive. In geological sections all over the world, dated independently using different methods that all give the same answer, a simple suite of animal burrows and shells appears in a regular pattern from about 543 million to 510 million years ago. It includes the origin of biominerals, the first complex animal burrows, the first animal reefs (see Fig. 6), the gradual assembly of recognizable animal body plans, the first zooplankton (microscopic animals) and the first animal predators. The third model differs little from the previous two, except that here, the fossil pattern of the Cambrian explosion is thought to mark not just the major diversification of animals, but also their actual origin. Many opponents of this view point out the controversially interpreted Ediacaran fossils and the data from molecular clocks that imply a much older origin of animals. Furthermore, the origin of biominerals at the base of the Cambrian greatly increased fossilization potential; many argue that this means that the Cambrian fossil pattern is an artefact of better preservation. But the major strength of this model in comparison to the first two is that it does not require some unknown and speculative mechanism to prevent the diversification of animals once they have originated. In this model, once animals evolved they could immediately diversify; there is no need for a long time to pass with a few animals but not all, as in the previous models. It also means that animals do not need to avoid leaving convincing fossils in the record for hundreds of millions of years before the Cambrian. So mechanistically, this model is probably the best understood and probably requires fewest assumptions regarding the nature of the Precambrian fossil record, which on the whole seems to preserve a lot of high-quality fossils that are simply not definitively animal.

In summary: Animals originated and diversified at or around the base of the Cambrian.

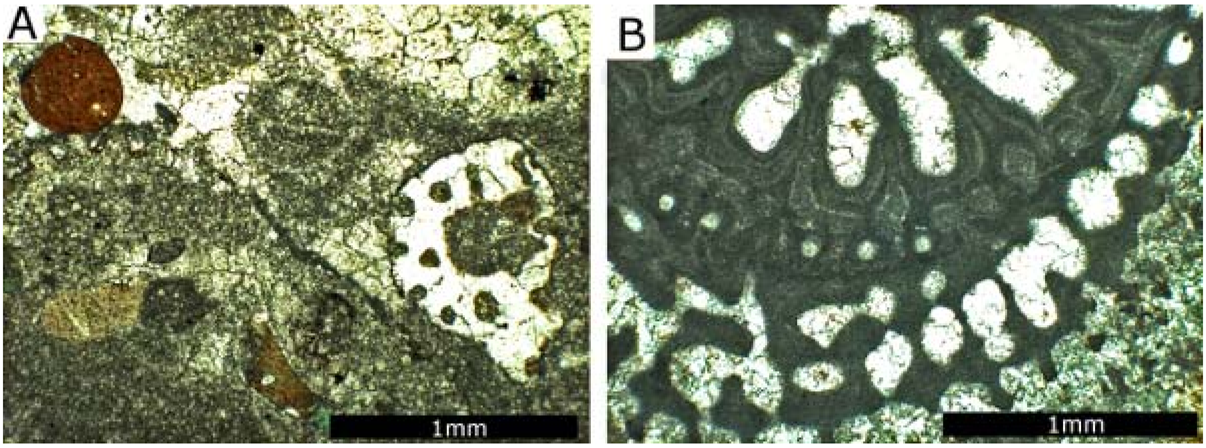

FIGURE 6 — A COMPARISON OF THE EARLY AND LATE MORPHOLOGY OF ARCHAEOCYATHAN (AN EXTINCT GROUP OF SPONGES) BODY WALLS DURING THE LOWER CAMBRIAN. (A) A THIN SECTION OF A BASAL CAMBRIAN PRIMITIVE SINGLE-WALLED ARCHAEOCYATHAN SPONGE CALLED ARCHAEOLYNTHUS POLARIS (PRESERVED IN PALE CALCITE), ALONGSIDE PHOSPHATIZED SMALL SHELLY FOSSILS. (B) A THIN SECTION OF AN ARCHAEOCYATHAN FROM A LATER STAGE IN THE CAMBRIAN, SHOWING THE GRANULAR, LAYERED, ASPICULAR SKELETON (DARK GREY CALCITE, WITH LATER WHITE CALCITE INFILLING INTERNAL PORE SPACES).

Models 4 and 5: The shallow missing record and the deep missing record

The only book written by a geologist that most biologists have read is ***On The Origin of Species*** (1859) by Charles Darwin. This great work had one unfortunate side effect: it convinced a great number of biologists that the fossil record was so incomplete that it was essentially not worth their attention. This view is still common among biologists, who, despite being exceptionally well versed in modern biological data, are often roughly 150 years out of date when it comes to palaeontological data. The Precambrian is no longer considered a wasteland barren of fossils, as it was during the nineteenth century. Still, many scientists propose that because molecular clocks predict that animals originated and diversified in the Precambrian, this is what must have taken place, and the fossil record is too incomplete to provide meaningful constraints. This is rather interesting because molecular clocks have to be calibrated against fossils (the dots in the dot-to-dot picture); otherwise there is little idea of the picture of early animal evolution.

Advocates of the shallow missing record model and the deep missing record model usually argue that the Cambrian explosion is simply an artefact of fossil preservation, and not at all related to evolutionary process and events. However, this doesn't account for the great number of exceptionally preserved soft-bodied fossils now known from the Precambrian, or for the astounding absence of even a single uncontroversial animal among them. The only real difference between these models is how far into the Precambrian the molecular clock predicts diversification.

In summary: Animals originated and diversified somewhere in the Precambrian; the Cambrian explosion is an artefact of fossil preservation.

Discussion (and my opinion):

Exploring the origin of animals and the Cambrian explosion produces a pattern and process paradox, and a doubly difficult one because the evolutionary process is not the only type of process involved. We must also concern ourselves with the preservation processes that were in play between about 550 million and 500 million years ago. Much work over the past few decades has focused on the context and the time frame of Cambrian explosion fossils, which has allowed more recent work to speculate on the evolutionary processes that operated during this time. It is now crucial in this field to appreciate the subtle inter-relations of fossil pattern and evolutionary process, particularly when making inferences from one to the other. To make matters worse, at this interval events are confounded by the changes in preservation process that also interact with the fossil pattern, forming a second inference paradox. When these things are considered independently, the situation seems hopeless and beyond obvious resolution. However, when taken together, models of large-scale evolutionary processes and large-scale preservation processes shed light on each other and produce a coherent and predictive model for the origin of animals.

Ultimately, the debate would be settled by a well preserved animal fossil from the Precambrian. It is not really plausible that animals, if they existed then, could have evaded fossilization for hundreds of millions of years in the Precambrian. The Ediacaran period was a time of prodigious fossilization potential, shown by the global preservation of soft-bodied fossils such as the Ediacaran biota; by geological data showing that sediment turned to rock quickly and early in the sediment cycle, resulting in fossils forming before bacteria had time to decay tissue; by crystal deposits that show that the oceans were not dissolving cements, and so were helping rock to form quickly; and by the chemical profiles of the sediments that show that oxygen levels were low, so bacterial decay would have been hindered.

These conditions were destroyed towards the start of the Cambrian, when animals started to dig vertical burrows that let air defuse into the sediment, allowing bacteria to use oxygen to help them to decay tissue. The burrows also help to break up buried bodies, because the predatory animals making the burrows would eat organisms in the sediment. The evolution of bones and teeth depleted the oceans of all the chemicals that were making early cements in the Precambrian, so decay processes had longer to act before sediment turned to rock and organism turned to fossil. Thus the preservation of soft tissue became substantially less likely at around the same time that animals acquired biominerals for the first time, and the 'shelly' fossil record began. This leads to the astounding but apparently real conclusion that the quality of the fossil record actually improves as you go back into deep time. Animals, with their shells and burrowing behaviour, didn't improve the fossil record (except in terms of bulk abundance of shells and burrows), but actually went a long way to destroying the possible preservation mechanisms of soft tissue (see Fig. 7).

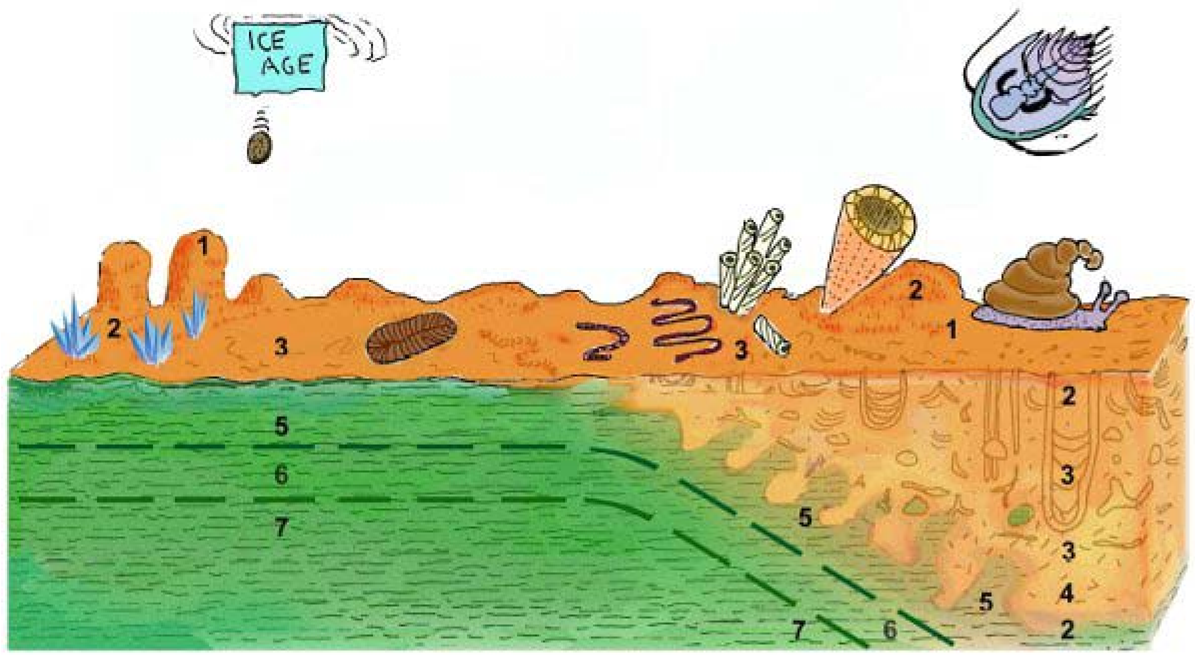

FIGURE 7 — MODEL SHOWING HOW THE BIOSPHERE REVOLUTION FROM EDIACARAN (AT LEFT) TO CAMBRIAN TIMES AND LATER (AT RIGHT) SHIFTED THE POSITION OF IMPORTANT GEOCHEMICAL BOUNDARIES IN THE SEDIMENT AND HENCE THE QUALITY OF FOSSIL PRESERVATION (AFTER BRASIER ET AL. 2010). IN THE EDIACARAN PERIOD, HIGH LEVELS OF MINERALS COULD BUILD UP NEAR THE SEDIMENT–WATER INTERFACE, SO SEDIMENT TURNED TO ROCK QUICKLY AND OFTEN ENTOMBED REMAINS BEFORE ORGANISMS COULD DECAY. THE NUMBERED METABOLIC PROCESSES ARE: (1) OXYGENIC PHOTOSYNTHESIS; (2) CALCIUM CARBONATE PRECIPITATION; (3) AEROBIC RESPIRATION, INCLUDING METAZOANS; (4) CALCIUM CARBONATE DISSOLUTION; (5) CALCIUM PHOSPHATE PRECIPITATION; (6) ANAEROBIC RESPIRATION BY SULPHATE-REDUCING BACTERIA; (7) ANAEROBIC RESPIRATION BY METHANOGENIC MICROOGRGANISMS.

What caused the Cambrian events can be explained either by the origin of animals and their subsequent natural selection causing diversification, or by a much earlier origin followed by a long gap of uncertain cause before something else triggers the radiation of animals during the Cambrian. Such triggers always fall into the pattern and process paradox: there is no independent or cohesive evidence for the extraordinarily slow evolutionary processes that would be required for deep Precambrian origins and then later Cambrian diversification. By contrast, there is a great deal of evidence from the Cambrian fossil pattern that indicates that the Cambrian explosion saw both the origin of the animal kingdom and the diversification of animal body plans with the origin of biomineralization, the origin of animal burrowing, the origin of the predator–prey system, the evolution of the first metazoan reefs and the evolution of zooplankton.

The Precambrian is full of interesting and controversial fossils, and not enough people are working on them. You should come and join us. Now is the time for detailed palaeontology on these fossils to understand their anatomy, compare suites of similar fossils worldwide and study their preservation.

I think that this field has the most exciting questions in palaeontology, and it doesn't look as if the scientific community is going to settle on 'the answers' any time soon. There is still so much to do.

Suggestions for further reading:

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