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Patterns in Palaeontology — The earliest skeletons

by [Amelia Penney](#)^{*1}

Introduction and background

The ability to build and maintain a skeleton is one of the major innovations in the history of life. During the [Cambrian explosion](#), which began around 540 million years ago, diverse animal (metazoan) skeletons appeared suddenly in the fossil record. This is also when we first see evidence for predation, the ability to move around and most of the animal body plans we would recognize today. The ability to grow a resistant skeleton was a major factor in the evolutionary arms races of the [Phanerozoic eon](#) — the time since the Cambrian explosion — and it made possible the dizzying variety of shells, bones and teeth scattered throughout the Phanerozoic fossil record. But the origin of skeletons has a much deeper root, in the Proterozoic eon (2,500 million years ago to 540 million years ago), and that is what I would like to explore here.

Organisms control the growth of minerals such as calcite, aragonite, apatite and silica through a process called biomineralization. Not all skeletons are biomineralized (think of the exoskeletons of many insects, for example), but skeletons made of minerals are especially interesting for several reasons. Not only are they a crucial biological innovation, but they also link life to biogeochemical cycles such as the carbon cycle, and allow organisms to leave a lasting trace on their environment after they die.

Most of the limestone on Earth today originally came from the skeletons of marine animals that settled onto the seafloor and were compressed into rock. The store of carbon locked up in carbonate rocks is estimated to be more than 60 million billion tonnes, by far the largest store of carbon in the Earth system, and much larger than the 4,130 billion tonnes of carbon in the world's fossil-fuel reserves. Today, the growth of carbonate skeletons is one of the main ways in which carbon is removed from the oceans, particularly in tropical reefs, which have been estimated to have the highest rate of calcium carbonate production in the world.

There are more than 60 different biominerals, but animals use only a few of these to build skeletons: mostly calcium phosphate, calcium carbonate or silica. Although there are many different ways to build a skeleton, the basic molecular toolkit required seems to be surprisingly uniform — so much so, in fact, that the mother-of-pearl inside an oyster shell can be used to encourage growth in vertebrate bone, because the organic molecules that the oyster uses to biomineralize are so similar to those used by vertebrates. Given that molluscs and vertebrates are quite distantly related, this is remarkable — but it fits the pattern found in the fossil record. Many animal groups evolved mineralized skeletons independently during the Cambrian period (541 million years ago to 485 million years ago), suggesting that they might have co-opted the same set of genes.

The earliest skeletons

The earliest skeletons were not built by animals at all, but by microorganisms. The oldest fossil skeletons found so far date back more than 700 million years. These tiny skeletons range from bottle-shaped structures to intricate scales with delicate spines and perforations, which probably coated the outside of a

single-celled organism like a suit of chainmail. These skeletons were built by protists, single-celled [eukaryotes](#) (creatures from the same domain of life as us) — although nobody is yet sure why. Even by ~700 million years ago, several species of these pioneering little skeleton-builders had evolved, suggesting that their strategy had been around for some time. [Molecular clocks](#) and sponge biomarkers (molecules produced by sponges) both suggest that sponges had also evolved by this time, and many modern sponges construct skeletons from silica or calcium carbonate, but so far, there are no universally accepted sponge fossils of this age.

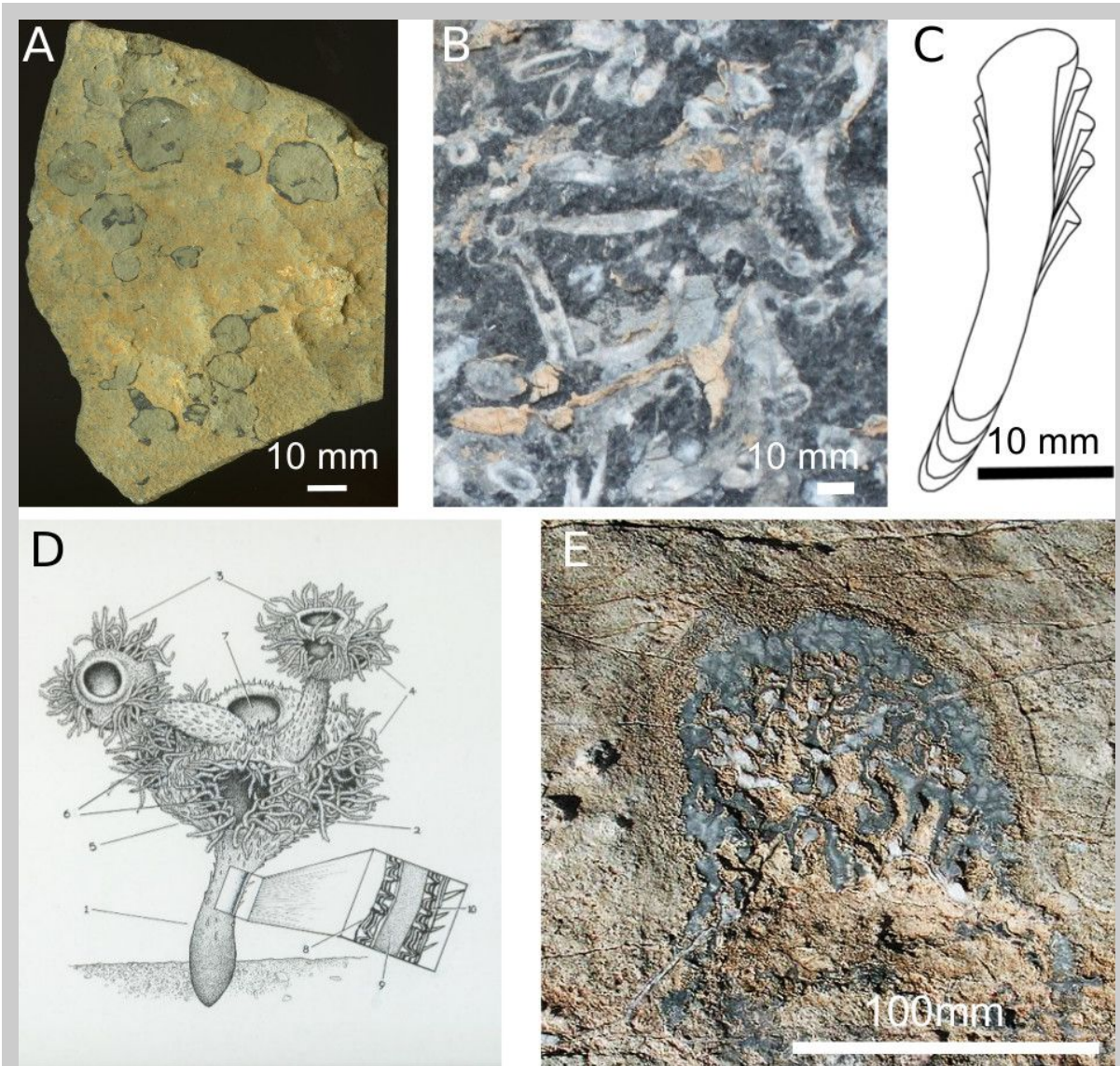


Figure 1 — Ediacaran skeletal metazoans. A – *Spreroceras* from the Nama Group, Namibia. B – *Dickinsonia* from the Nama Group, Namibia. C – Reconstruction of *Dickinsonia* showing the structure of its skeleton, a stack of cones nested one inside the next. Redrawn from Grant (1990). D – *Spreroceras*, reconstructed as a lophophorate. Image copyright John Sibbick, first published in Zhuravlev et al. (2015). E – *Spreroceras* from the Nama Group, Namibia. Image from Wood et al. (2002).

It took another 150 million years for multicellular life to adopt skeleton-building, but when it did, the results were striking. Around 550 million years ago, mysterious fossils with calcium carbonate skeletons appeared in limestones all over the world: in China, Spain, Paraguay, Uruguay, Argentina, Brazil, Namibia, Canada and the United States, like a foreshadowing of the Cambrian explosion. The tube-shaped groups, or [genera](#), called *Ujif* and *Xb M* grew together in the microbial slime of the sea floor during the Ediacaran period (635 million years ago to 541 million years ago), and *Xb M* participated in reef-building (Fig. 1). *Ma/y*, a stalked, spiny, symmetrical creature shaped like a wine glass or goblet (Fig. 1), began to colonize the sea floor in areas as far-flung as present-day Canada, Paraguay and Namibia, taking its chances with oxygen-poor environments in deeper waters. And *Nb*, a lumpen creature interpreted as a large sponge, quietly developed a preference for the dark crevices in reefs that were still dominated by masses of microbes (Fig. 1, 2).

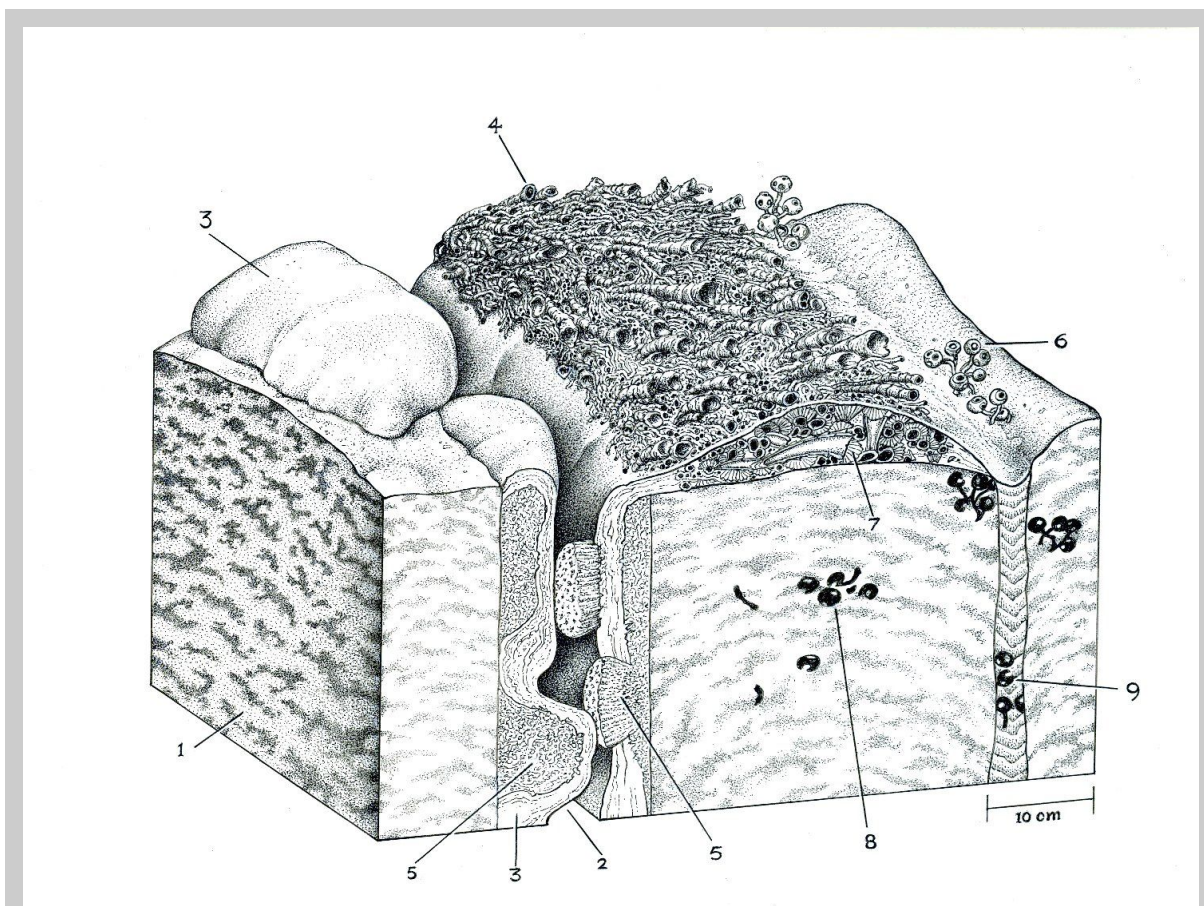
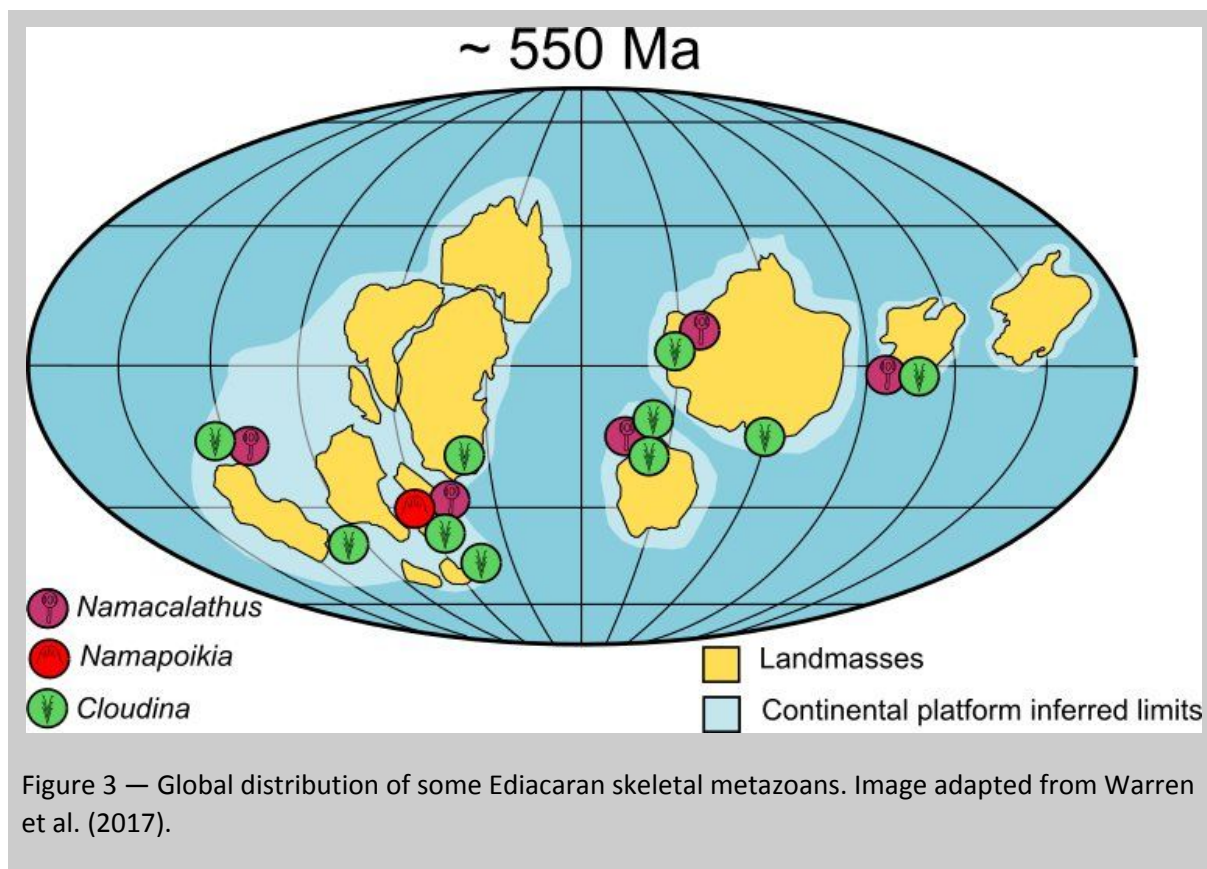


Figure 2 — An Ediacaran reef community based on fossils from southern Namibia. Reconstruction copyright John Sibbick, first published in Penny et al. (2014). 1 – Clotted microbial sediment (thrombolite). 2 – Reef fissure. 3 – Stomatolites encrusting the walls of the reef fissure. 4 – *Xb M* constructing reefs on open reef surfaces. 5 – *Ma/y* growing on the walls of the reef fissure. 6 – *Ma/y* growing between mounds of microbial sediment. 7 – Aragonite crystals forming from seawater, and growing on *Xb M* skeletons. 8 – *Ma/y* skeletons buried under microbial mats. 9 – *Ma/y* skeletons accumulating in the gaps between microbial mounds.

These animals were not especially diverse, compared with the unmineralized fossils of the [Ediacaran](#); there were only around 15 species, although this number is not settled. Nor were they particularly long-lived, in geological terms — they thrived for around 10 million years, before vanishing as mysteriously as they had appeared, at some time in the latest Ediacaran or earliest Cambrian. Compared to the 200-million-year reign of the dinosaurs, this is nothing. But although they might be regarded as brief, failed prototypes of modern animal groups, the skeletal animals of the late Ediacaran represent the early stages of some very fundamental processes of large-scale life on Earth: skeleton building, ecological specialization and ecosystem engineering.

Life as an Ediacaran skeletal animal

Given their importance in the history of life, it is surprising how little we know about the first skeletal-animal communities. The animals were all sessile, spending their lives attached to the sea floor and probably filter-feeding on small food particles in the seawater around them, much like modern corals, sponges and clams. Beyond that, work on their ecology — their environmental preferences, how they reproduced and spread across the oceans, and how they interacted with their environments — is in its early stages. But these unassuming early skeleton-builders were, briefly, an evolutionary success, colonizing shallow ocean settings around the world. *Dickinsonia* was especially successful in this regard, and its fossils are abundant in certain locations on five continents (Fig. 3).



It is challenging to decide how Ediacaran skeletal animals relate to modern animal groups, because their shapes are generally very simple, without many characteristics that could be used to classify them. For now, *Dickinsonia* has been interpreted as a possible annelid worm or cnidarian, related to sea anemones or jellyfish. The goblet-shaped animal *Dickinsonia* has been suggested to be a cnidarian-grade animal, or possibly a

relative of the lophophorates, a group of animals that all have a feeding structure called a lophophore. It has been suggested that *Tribrachium* was a total-group sponge, meaning that it has some sponge-like characteristics that indicate it is more similar to sponges than to any other group, but we can't be sure where it fits exactly. Ediacaran organisms are notoriously difficult to place in modern groups, and in some cases this might be because they represent the early stages in the evolution of those groups.

Although there are only a few genera of Ediacaran skeletal metazoans, they are not especially similar in shape; their skeletons are built from two different calcium carbonate minerals (high-magnesium calcite and aragonite), and they are interpreted to have belonged to distinct groups. This means that these animals probably did not inherit their ability to build skeletons from a common ancestor: it is more likely that they converged on skeleton-building in response to ecological or environmental pressure that they all faced. It has been estimated that carbonate skeletons evolved independently 28 times in eukaryotes, including 20 times in animals. This being the case, the big question is why — what is it about the late Ediacaran that made skeleton building suddenly so important?

Building a skeleton costs energy: a great deal of energy, if the skeleton is large, or composed of a mineral that does not easily precipitate from its environment. There has to be an evolutionary advantage to building a skeleton, for so many groups to adopt it at the same time. But the dominant driver for the Ediacaran boom in skeletal animals is not yet well understood. Most theories involve a combination of ecological and environmental factors, interacting to create the conditions in which forming the first large skeleton was worth the cost.

Ecological drivers for skeleton building

In modern ecosystems, hard skeletons often act as armour. The thick, heavily mineralized shells of some bivalves, for instance, give protection from predators trying to get at the soft, edible tissue inside. This dynamic has been suggested as a cause of the evolution of skeleton building in both protists and metazoans, the theory being that on the evolution of a new predator, prey species will grow increasingly robust skeletons for defence. This forces predators to become more efficient at getting through those skeletons, and so on, creating an evolutionary arms race that feeds rapid evolutionary diversification.

This was probably a major driving force for the rapid diversification of skeletal metazoans in the Cambrian, when predation became a major ecological pressure in marine ecosystems, but there is less compelling evidence that the first skeletal organisms had predators. Predators can get around their prey's armour in a number of ways — for instance, by crushing the skeleton, prising parts of it apart or drilling a hole through it. Drilling is a common style of predation in modern invertebrate predators, and is useful to palaeontologists because it can leave clear traces in the fossil record. Tiny borings in vase-shaped microfossils in Arizona have been plausibly interpreted as evidence of single-celled predators as early as 742 million years ago. Larger-scale inferred predatory borings in *Tribrachium* fossils have been reported from China (Fig. 4). This is intriguing — if the earliest fossil skeletons show traces of predators, then perhaps the first skeletons were a response to the threat of being eaten.

As usual, it might not be that simple. The theory that predation was a principal driver of biomineralization in late-Ediacaran metazoans leaves some important questions unanswered. For instance, why have borings been found in *Tribrachium* but not in the skeletal animals *Dickinsonia*, which have been found in the same places, or in *Dickinsonia*? More importantly, how can we be sure that the coincidence between the origins of biomineralization and metazoan predation is not due to one common, environmental cause?

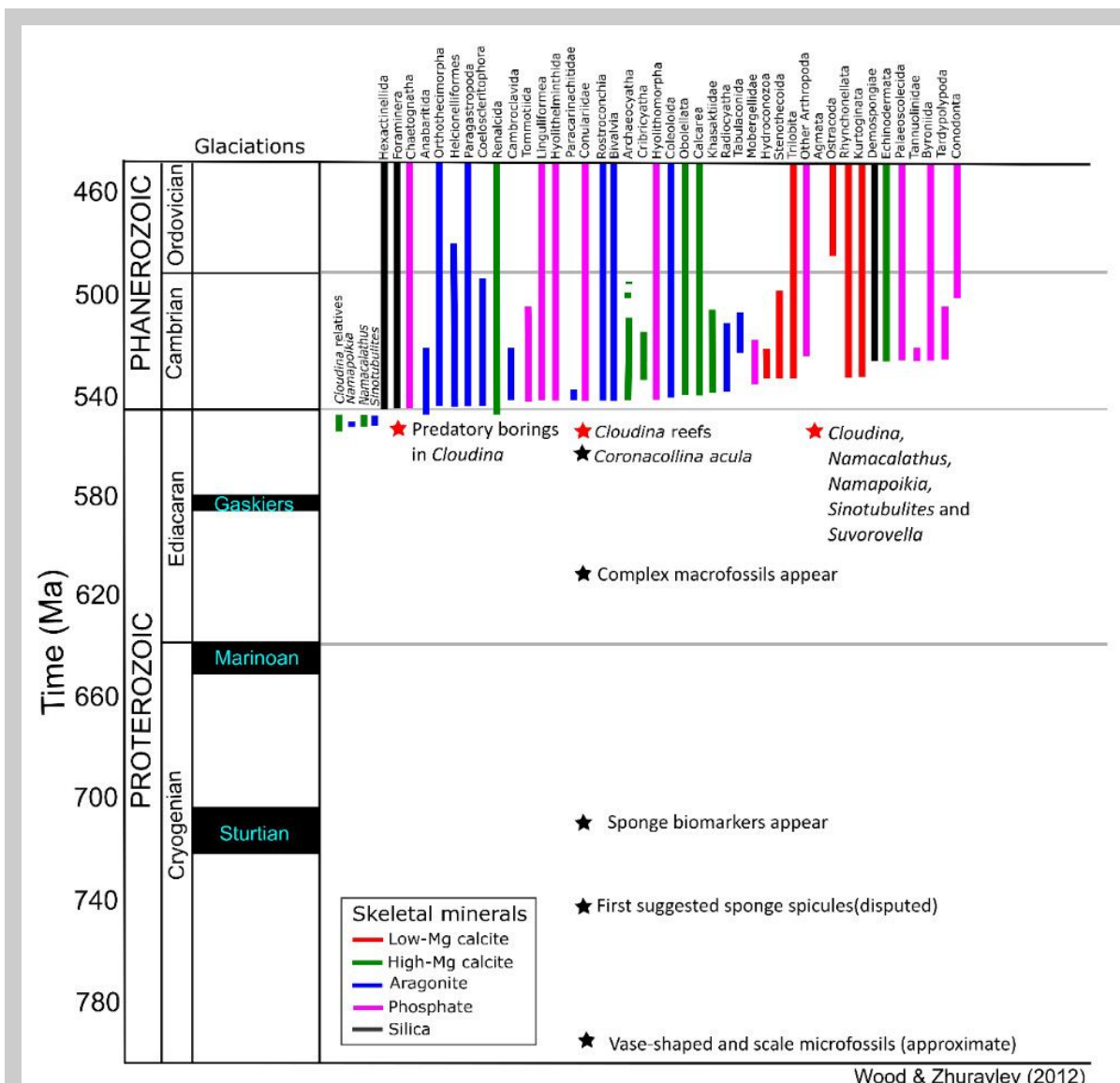


Figure 4 — Major biological events in the Proterozoic and early Phanerozoic, with the diversification of metazoan skeletons in the early Cambrian. Image redrawn from Wood & Zhuravlev (2012).

Environmental drivers for skeleton building

The independent acquisition of carbonate skeletons by metazoans all over the world, at around the same time, might suggest that ocean chemistry had an important part to play. One theory suggests that the earliest large skeletons evolved as a way for animals to dispose of excess calcium from sea water. More recently, the theory has developed that a fall in the ratio of magnesium to calcium ions in seawater was important. This produced a switch from conditions in which the less biologically useful mineral dolomite would form alongside aragonite, to conditions called aragonite seas, where large aragonite crystals could form directly from sea water. This implies that producing an aragonite skeleton at this time could have

been quite easy, and that Ediacaran animals, already equipped with thin, flexible organic coatings, might have been able to produce skeletons passively, under only loose biological control.

Some evidence for this comes from the Ediacaran rocks of the Yudoma Group in Siberia, and the Dengying Formation of south China. Recently, researchers observed that unmineralized tubular and disc-shaped fossils have very similar-looking mineralized 'twins' in carbonate rocks. This suggests that in the late Ediacaran, skeletal mineralogy and skeleton formation was largely the result of local environmental conditions. Primitive metazoans would have had an organic, carbon-based coating on which skeletal minerals could grow when conditions were favourable.

The amount of oxygen in the environment was probably highly important too. The Ediacaran atmosphere was probably lower in oxygen than today's, and the oceans were generally different from our own, with relatively high oxygen levels in shallow waters and little or no oxygen deeper down. As a result, Ediacaran life had to tolerate low or fluctuating levels of oxygen, a challenge for any animal, but particularly for one undergoing the oxygen-intensive process of building a mineralized skeleton. In modern marine basins, skeletal metazoans seem to show higher minimum oxygen requirements than non-skeletal ones. So it is possible that, although ocean carbonate chemistry helped the process along, the biologically controlled biomineralization needed to build a skeleton was possible only in the small areas of Ediacaran oceans where oxygen levels were relatively high. Studies of late Ediacaran and early Cambrian rocks in China and Namibia have shown that large, skeletal metazoans are generally present only in environments that carry chemical traces of oxygenation — implying that environmental oxygenation also had a role in the evolution of metazoan skeletons.

Metazoan skeletons and the making of the modern oceans

The evolution of metazoan skeletons in the Ediacaran marked a fundamental change in marine ecology and marine environments. Masses of skeletons from these early skeletal metazoans began to appear, contributing new types of substrate to the sea floor. Ediacaran skeletal metazoans *Dickinsonia* and *Spriggina* aggregated together, changing the landscape of their local environments. Carbonate skeletons can persist in the environment for hundreds of years after the organism that produced them has died, providing new kinds of substrates and resources for future generations. The evolution of mineralized skeletons meant that organisms could modify their environments over long time scales, with future generations inheriting environments partially made of the skeletons of their predecessors. This is the principle of ecosystem engineering, still a major force in marine ecosystems today.

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