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# Patterns in Palaeontology: Environments of the Cambrian explosion

by Thomas W. Hearing\*1

# Introduction:

Shimmering curtains of sunlight stream down through the waters of a shallow sea that has been advancing landwards for several million years. This transgression has formed wide areas of shallow continental shelf seas. The sea bed teems with life — some of it familiar, some much less so. The oddities begin on the floor of this tropical sea: a reef built not of corals, but by carbonate-producing microbes and the strange <u>archaeocyathan</u> sponges, alongside creatures that look more conventionally sponge-like but probably aren't. Streams of seaweed drift on the currents; closer examination reveals small, snail-like shelled <u>molluscs</u> on some of the tendrils. A <u>trilobite</u> scuttles for cover, startled by the flickering shadow passing overhead, and narrowly avoids a stab by the inverting mouthparts of a pouncing <u>priapulid</u> worm. The shadow-casting terror glides off in search of slower prey.

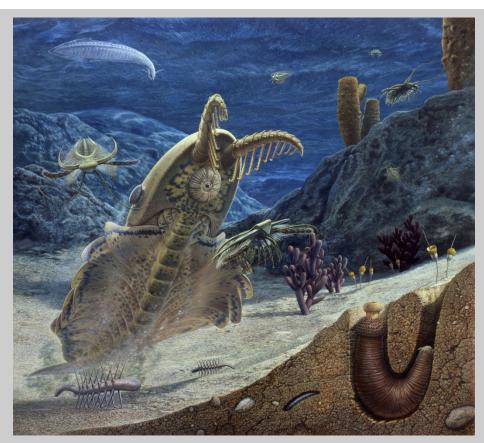


Figure 1 — Reconstruction of the Burgess Shale ecosystem: a priapulid (*Ottoia*) burrows in the foreground as *Anomalocaris* hunts overhead. Illustration: John Sibbick.

This is what life might have been like 508 million years ago on what is now the middle Cambrian Cathedral Escarpment, a rock deposit in the Rocky Mountains of British Columbia, Canada (Fig. 1, Video 1). The fossils found there are classic examples of Cambrian explosion taxa: a multitude of animal body and trace fossils in the layers overlying Precambrian rocks that seem to contain no large, complex lifeforms. The sudden appearance of these fossils was a profound concern for Charles Darwin when he was formulating his thoughts on evolution. More than 150 years later, through the discoveries of several famous Konservat-Lagerstätten, we now have a much clearer understanding of the biological changes that occurred during the Cambrian explosion. The 'shadow-casting terror' (Fig. 1) could be Anomalocaris — it's name meaning 'strange shrimp', owing to the appearance of its frontal appendages — which now seems like a weird evolutionary experiment. But others like the priapulid worms can still be found in their seafloor burrows today, living much as Ottoia (Fig. 1) did 508 million years ago; their generalist diet, for example, is different only because the surrounding animals on which they prey have changed. However, there remain many questions to answer — particularly concerning the environments in which these early animals evolved.

The causes of the Cambrian explosion have been debated at length, and it may have been influenced by both 'intrinsic' (biological) and 'extrinsic' (environmental) factors. The Cambrian explosion was followed by the even bigger <u>Great Ordovician Biodiversification Event</u> (GOBE), which lasted from 485.4 million to 443.8 million years ago and has been linked to declining global temperatures and the establishment of a stronger <u>latitudinal biodiversity gradient</u> – where biodiversity is different between the poles and the tropics. Two ice ages bracket the Cambrian and Ordovician periods: the Ediacaran Gaskiers glaciation and the Late Ordovician Hirnantian glaciations (Fig. 2). The Cambrian explosion has also been linked to the development of the <u>'Great Unconformity'</u>, a gap in the geological record across North America that formed as seas flooded global coastlines in the late Ediacaran and early to middle Cambrian periods.

Researchers have suggested a variety of hypotheses about how environmental conditions might explain the Cambrian explosion, but to test these ideas we need to collect evidence about ancient environments at this time. Gathering and interpreting these palaeoenvironmental data is far from straightforward, and requires the synthesis of many different analytical approaches.

# **Reconstructing past environments and climates:**

"It is important to note that the Quaternary is not a climatically average time interval" – (Boucot et al., 2013)

The climate and environmental patterns that we see on Earth at the moment do not cover the full range of conditions that have existed throughout Earth's history, and neither do they reflect a 'normal' climate state for the <a href="Phanerozoic">Phanerozoic</a> Eon, which covers the last half a billion years. For instance, over the Phanerozoic Eon it has been rare to have permanent ice sheets at both poles: this may only have happened during the <a href="Cenozoic">Cenozoic</a> Era which started about 66 million years ago. However, there are general physical, chemical and biological principles that can be applied throughout geological time.

Climate can be considered as the 'average' weather conditions in a given place over a given time (Fig. 3). Statistical definitions of weather and climate are useful when thinking about the present day, but are less useful in a geological context because we rarely have enough data before the last few

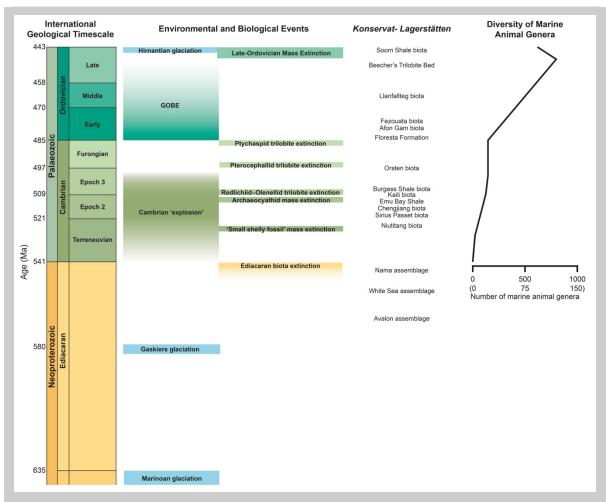


Figure 2 — The Cambrian explosion in context: timeline of major environmental and biological events during from the Ediacaran to Ordovician periods, with details of key fossil sites (*Konservat-Lagerstätten*) and a plot showing the diversity of marine animals through time (after Alroy *et al.*, 2008). Credit: T. Hearing.

thousand years. Instead, a more valuable definition is based on all avenues of palaeoclimatic evidence of the geological record for a given region and time. This gives a sense of the general climatic conditions, rather than probabilities of temperature and precipitation – such as rain or snow – on any given day.

The geological record is made up of a combination of palaeoclimate and other local and regional factors, including amount of available oxygen, altitude or water depth, and the plants and animals that lived in the area. So it is perhaps more sensible when thinking about changes over long timescales to look at palaeoenvironments, which take into account all of these factors, rather than just palaeoclimates.

Climates are divided into categories using a system called the <u>Köppen–Geiger climate classification</u>. If we could draw maps of palaeoclimate zones (Fig. 3) for several intervals of geological time using this scheme, we could compare regional and global palaeoenvironments between different time periods. However, to do this, we have to know with reasonable accuracy how and where the continents have moved over time.

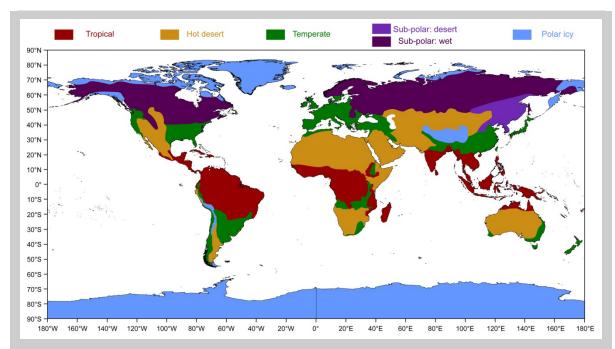


Figure 3 — Simplified Köppen–Geiger-type map indicating the distribution of modern climate zones. Today's climate zones are mainly determined by latitude, from an equatorial tropical belt, through an arid (dry) belt around 30° latitude and mid-latitude temperate belt, to sub-polar and polar regions. Data available from: <a href="http://koeppen-geiger.vu-wien.ac.at/present.htm">http://koeppen-geiger.vu-wien.ac.at/present.htm</a>

#### The Cambrian world map:

Reconstructing <u>palaeogeography</u> in this way is essential for interpreting palaeoclimate data and models. To properly interpret data that tell us something about ancient temperatures, for instance, we need to know the ancient location of that temperature information: e.g. is it from polar or equatorial latitudes. To reconstruct palaeogeography, a researcher must use multiple lines of evidence, including data on magnetic fields, sedimentology, geochemistry and palaeobiology, to build up a reconstruction that accounts for as many of these as possible. Some of these data sets can also be used for interpreting palaeoenvironmental conditions, so researchers need to be careful to avoid circular reasoning and placing too much emphasis on any one particular line of evidence.

Although challenging, palaeogeographic reconstructions are not impossible, and the current consensus for Cambrian palaeogeography is that Earth surface had four major continents (Gondwana, Laurentia, Baltica and Siberia) along with a host of smaller ones (Fig. 4). These had been spread across the Southern Hemisphere during the break-up of the previous <u>supercontinent</u> called Rodinia, which split apart between around 800 million to 550 million years ago.

Gondwana was by far the largest connected landmass, and would have acted as a major north—south barrier to ocean and atmospheric currents extending from a little north of the equator to the South Pole. Laurentia (modern North America and Greenland) was the other long-lived and very large continental mass, probably quite flat and straddling the equator throughout the whole of the Cambrian Period. Very little is known about the presumably expansive Northern Hemisphere Panthalassic Ocean, which has interesting implications for ocean circulation at the time. The precise positions of the smaller continental blocks are more hotly contested, but Fig. 4 presents a reasonably well accepted palaeogeographic reconstruction (although many others are available).

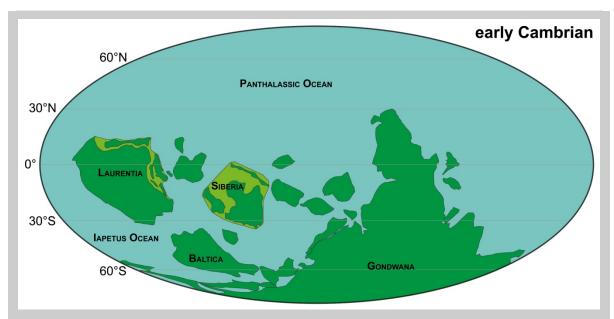


Figure 4 — Palaeogeographic reconstruction across the later part of the early Cambrian Period, around 520 million years ago. The major landmasses are all in the Southern Hemisphere, although Laurentia straddles the equator and northernmost Gondwana is located in the Northern Hemisphere. Many smaller continents were also distributed across the Southern Hemisphere after the supercontinent Rodinia broke up. Map after Torsvik and Cocks (2013).

#### Environmental 'past-casting':

The opportunity to measure palaeoenvironmental parameters directly is rare, and generally restricted to the last 800,000 years or so, for which atmospheric gas bubbles can be recovered from Antarctic <u>ice-core samples</u>. Gases and liquids can also become trapped when minerals crystallize, creating fluid inclusions. When these grow at an interface between sediments and the atmosphere or ocean, the trapped fluid can record information about the environment the crystals are growing in. To be useful to researchers, these inclusions must remain sealed and unaltered in a closed system after they form. One recent study suggests that crystals of halite (table salt or NaCl) that grew at the surface of an evaporating sea preserve inclusions of 810-million-year-old atmospheric gas, although over this age <u>diagenetic alteration</u> – changes that occur after the rocks were deposited – can affect the data. Nonetheless, these records are few and far between, both in geography and in time.

The principle of <u>uniformitarianism</u> can help get around the issue of sparse data. Uniformitarianism is the idea that "the present is the key to the past", and that fundamental processes of biology, chemistry and physics have operated throughout Earth's history in much the same way as they do today. Fossils and sedimentary rocks can preserve biological, physical and chemical signals of the environment in which they lived or formed, leading to a <u>proxy</u> record of palaeoenvironment. A series of proxy data records that generally agree with each other can lead to convincing palaeoenvironmental hypotheses.

# **Cambrian palaeoenvironmental proxies:**

#### Palaeobiological proxies:

Some animals require very particular environments to survive and thrive. Knowing this, researchers can use the fossil record to say where certain climate zones would have been. For instance, in the middle Cambrian Period, <a href="mailto:bradoriid">bradoriid</a> (bivalved) <a href="mailto:arthropods">arthropods</a> are generally concentrated around areas that would at the time have been at tropical or subtropical latitudes. However, in some 500 million year old rocks, they are known to range further towards the South Pole (at latitudes of about 70° S). This could mean several things: that the species was <a href="mailto:eurythermal">eurythermal</a>, or able to live in a range of temperatures; that at the time the subtropical belt stretched to high latitudes; or that the ocean currents took warm water currents into high southern latitudes.

It is not only creatures that could move around that are useful in understand palaeoenvironment. Reef ecosystems have been common throughout the Phanerozoic Eon from the early Cambrian Period onwards. However, the early reefs were not constructed by corals as in modern reefs; instead they were built by the Archaeocyatha. Now considered a group of sponges with a skeleton made of calcium carbonate, these have in the past been classified as <u>cnidarians</u> (jellyfish and their relatives) or as their own separate animal <u>phylum</u>. They have been thought to live like corals, in the shallow waters of warm clear seas with normal salinity conditions, and studies of these reefs and nearby sediments suggest that this is largely correct. However, some of the reefs have been found at high latitudes, which has left room for doubt here (Fig. 5).

Temperature is not the only environmental parameter that influences where creatures live; salinity, pH and ambient oxygen concentrations are also often significant. It is relatively straightforward to look at living species and their close relations and to work out what environments they would have lived in even a few million years ago, but extending this back over half a billion years to the evolution of some of the earliest animals is much harder. The number of potentially important palaeoenvironmental controls and the difficulties involved in finding out how those relate to the distribution of any extinct species make this the most difficult class of proxy to use reliably or with precision in deep time.

#### **Geological proxies:**

As some organisms require particular environments to survive in, so too do particular rock types, or lithologies (Fig. 6). Sedimentary rocks are the products of physical, chemical and biological interactions with environmental parameters such as temperature, humidity, prevailing currents and water depth. These provide characteristic boundary conditions required for some rock types to be deposited. Geological proxy data can be interpreted more reliably using uniformitarian principles in deep time than can palaeobiological proxies.

Evaporitic rocks – formed by minerals precipitating from evaporating sea water – have been particularly useful for unravelling environments in the Cambrian Period. Evaporites, including halite (NaCl) and gypsum (CaSO<sub>4</sub>·2H<sub>2</sub>O), form from water bodies in areas where climate conditions cause a lot of evaporation, which are usually hot and arid (Fig. 6). One example is the salt flats, or sabkhas, of the modern Arabian Peninsula. Today evaporite rocks form in the desert belts around 30° north and south, either side of the warm, wet tropical belt, where we find lithologies such as bauxite and laterite (aluminium oxide), and kaolinite. Evaporitic deposits from the early and middle Cambrian Period are found across a wide range of ancient latitudes (Fig. 7), supporting the idea that the Earth at the time had a low <u>climatic gradient</u> and globally warm climate.

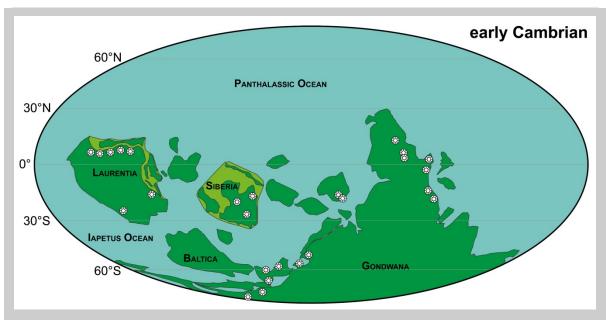


Figure 5 — Distribution of archaeocyathan reefs in the later part of the early Cambrian Period, around 520 to 515 million years ago. Base map after Torsvik and Cocks (2013).

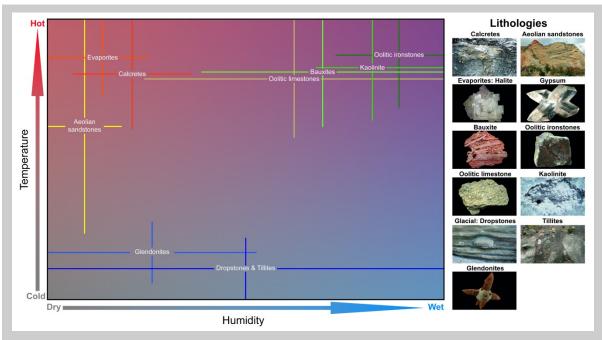


Figure 6 — Representation of the temperature and humidity conditions required to deposit some characteristic rock types. There are three main climates that can be characterised by rock types known from the Cambrian System: hot and arid climates (aeolian sandstones, calcretes and evaporites); hot and wet climates (oolitic limestones, bauxites, kaolinite and oolitic ironstones); and cold climates (glendonites, dropstones and tillites). Credits: figure by T. Hearing; lithology images from BGS and WikiCommons.

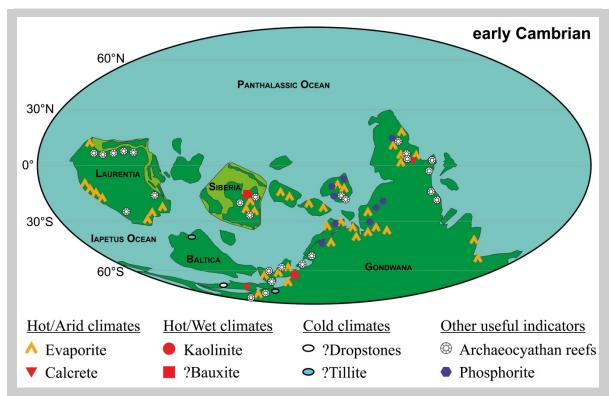


Figure 7 — Palaeogeographic reconstruction of the later part of the early Cambrian Period, around 520 million years ago, showing the distribution of some environmentally sensitive rock types. Rock types typical of warm and arid climates are found across a wide range of latitudes. There are very few deposits characteristic of cold climates, and those that exist are either ambiguous or poorly dated. Phosphorites usually indicate regions of high primary productivity (for example, regions where phytoplankton blooms may be common). Archaeocyathans may be restricted to warm shallow-water environments, although this is far from certain. Base map from Torsvik and Cocks (2013).

The tropical (aluminium oxide and clay) lithologies are quite easily changed after they have been laid down, and can also be formed by processes in modern weathering. This makes them hard to verify as true indicators of palaeoclimate. However, there are some accepted lateritic and bauxitic Cambrian deposits that suggest that the tropical belt was wider than it is now, and the period was characterised by a low climatic gradient and warm global climate (Fig. 7).

Calcretes, or 'caliches', are another useful lithology for determining dry climate regimes. These carbonate precipitates form in soils under semi-arid conditions with a fluctuating groundwater level. Only a few are known from the time of the Cambrian explosion, but again they are found across a wide range of latitudes, from northern tropical Gondwana to subpolar Avalonia (part of the larger Gondwanan palaeocontinent at this time). Indeed, most lithologies that are sensitive to humidity provide evidence for widespread dry climatic regimes during this interval.

Lithological indicators have been used to demonstrate cold (freezing) palaeoenvironments for nearly 200 years, ever since the Swiss-American geologist Louis Agassiz demonstrated evidence for a wideranging ice age with ice sheets extending into southern Europe. Despite the general picture of warm climates, there are a few reports of possible Cambrian glacial deposits. It has been reported that some rocks found in two areas of Avalonia, tentatively dated to about 535 million years ago, were deposited

by glaciers. Possible Cambrian tillites – rocks made from the debris of moving glaciers – have been reported from Baltica (northwest Europe, including European Russia, much of Central Europe and Scandinavia) and southernmost Gondwana. Unfortunately, these deposits have not been accurately dated, so it is difficult to integrate them with other Cambrian palaeoenvironmental data. It is possible that they are connected to the ice ages either side of the Cambrian explosion and the GOBE. The Cambrian Period seems to have been a warm interval between these two cold spells.

#### **Geochemical Proxies:**

Although geological proxies can be relatively straightforward to interpret, they lack the precision to resolve nuanced arguments in palaeoenvironmental and palaeoclimatic studies. This is where the relatively recent innovation of geochemical palaeoenvironmental proxies can be useful.

Everything made of carbon atoms comprises some mix of the more common carbon-12 ( $^{12}$ C) isotope and the less common carbon-13 ( $^{13}$ C). The proportion of the  $^{13}$ C isotope to the  $^{12}$ C isotope is called the stable carbon isotope ratio ( $\delta^{13}$ C, Box 1) and it is probably the most widely used geochemical proxy for palaeoenvironment. We now have a near-continuous record of  $\delta^{13}$ C going back through the whole Phanerozoic Eon and into rocks from the Neoproterozoic Era, between 1000 million and 541 million years ago (Fig. 8). Unlike the proxy records discussed above,  $\delta^{13}$ C is not directly linked to an individual environmental parameter, such as temperature: it records changes in the local and global carbon cycle. This can reflect increased burial of organic matter (for instance during an extinction) or the input of more carbon from Earth's mantle in the form of carbon dioxide gas from volcanic activity. The Cambrian  $\delta^{13}$ C record has been used to reinforce the timing and magnitude of extinctions of small shelly fossils, the Archaeocyatha, and certain types of trilobite (Fig. 8).

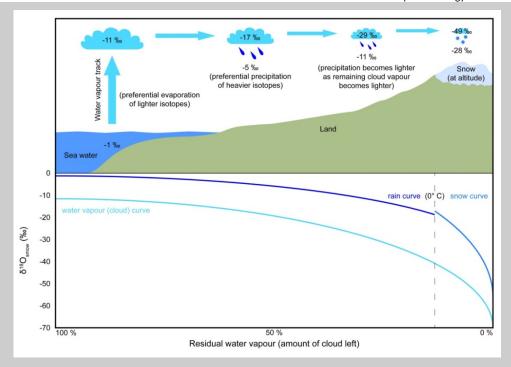
The most widely used palaeothermometer for the Phanerozoic Eon is the stable oxygen isotope proxy,  $\delta^{18}O$  (the proportion of rarer oxygen-18 to the more common oxygen-16). Developed by American chemist Harold Urey in the 1940s, it has been continuously refined since and is now widely used to determine changes in temperature and the volume of ice on land over time. Unfortunately, the Palaeozoic  $\delta^{18}O$  record at present is only reliably developed as far back as the earliest Ordovician Period (Fig. 2), so this tool is not currently used by Cambrian palaeoenvironmental scientists.

# **Box 1: Stable isotope ratios**

#### **Isotope fractionation:**

Probably the most widely used geochemical proxies for palaeoenvironmental conditions are the stable carbon and stable oxygen isotope ratios. These are ratios of the heavier <sup>13</sup>C and <sup>18</sup>O isotopes to the lighter <sup>12</sup>C and <sup>16</sup>O, respectively.

Isotope fractionation is a physical process controlled by mass differences of isotope nuclei. Box Fig. 1 gives a classic example from the oxygen isotope system. Similar process occur in the carbon isotope system, with most living organisms preferentially accepting the lighter stable carbon isotope, <sup>12</sup>C, and some biochemical reactions have characteristic isotope fractionation ranges. For instance, most methane creation by microbes involves a fractionation on the order of -50 ‰, compared to volcanic carbon dioxide which is roughly -6 ‰ to -7 ‰ – an order of magnitude difference.



Box Figure 1 — An example of isotope mass-dependent fractionation in the oxygen system – Rayleigh fractionation. Evaporation from sea water preferentially picks up the lighter isotope <sup>16</sup>O making the initial cloud water vapour lighter than the residual sea water (assuming that the volume of the sea is much greater than the volume of the evaporated portion). The process of precipitation and raining preferentially selects the heavier isotope <sup>18</sup>O. In this way, an already isotopically lighter cloud water vapour become lighter still as the heavier isotope is preferentially rained out. The first drop of moisture to precipitate is the isotopically heaviest and the last drop of moisture to precipitate is the isotopically lightest. Credit: T. Hearing.

The stable carbon isotope ratio ( $\delta^{13}$ C), usually extracted from carbonate rocks or organic matter in sediments, provides insights into the global and local carbon cycles and the nature of the material that is being analysed. The stable oxygen isotope ratio ( $\delta^{18}$ O), usually\* extracted from carbonate rocks or from the shells of aquatic animals, provides some insight into the global and local hydrological cycles and on the temperature of the water the minerals formed in.

\*The stable oxygen isotope ratio is also used to determine ancient animals' body temperatures to investigate if they are, for instance, warm- or cold-blooded.

#### Delta (δ) notation:

Delta notation is used to compare the relative amounts of two isotopes (e.g. <sup>18</sup>O and <sup>16</sup>O, or <sup>13</sup>C and <sup>12</sup>C) when their absolute magnitudes are several orders of magnitude different. Isotope abundances are measured using a mass spectrometer that counts the number of times atoms of a particular mass (an isotope) interact with a detector. The number of counts for each isotope are related to its abundance in the sample analysed, and we can calculate a ratio for these two isotopes, R.

The operating conditions of each instrument, and even of each measurement, are subtly different. Due to the sensitivity required of these instruments to produce useable data it is necessary to measure a 'standard' material with known isotopic composition to make measurements comparable. Delta notation accounts for this.

For measured isotope ratios R<sub>sample</sub> and R<sub>standard</sub>, the delta notation would be:

$$\delta R \ (\%_0) = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000 = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000$$

For example, in the oxygen isotope system counts of <sup>18</sup>O and <sup>16</sup>O are measured:

$$\delta^{18}O\left(\%_{0}\right) = \left(\frac{\binom{18}{0}/^{16}O}{\binom{18}{0}/^{16}O}\right)_{standard} - 1\right) \times 1000$$

Values given in delta notation are reported in per mille (‰), where 1 ‰ is a difference from the standard of one part per thousand.

The absolute values (counts and ratios) should also be reported, but delta notation is more readily understood. Simply, it is easier for us to comprehend the delta numbers (e.g.  $\delta^{18}O_{SMOW} = 11.57 \%$  versus  $\delta^{18}O_{SMOW} = 14.19 \%$ ) than the raw ratios (e.g.  $^{18}O/^{16}O = 0.002036892$  versus  $^{18}O/^{16}O = 0.002042173$  – these are comparing the data).

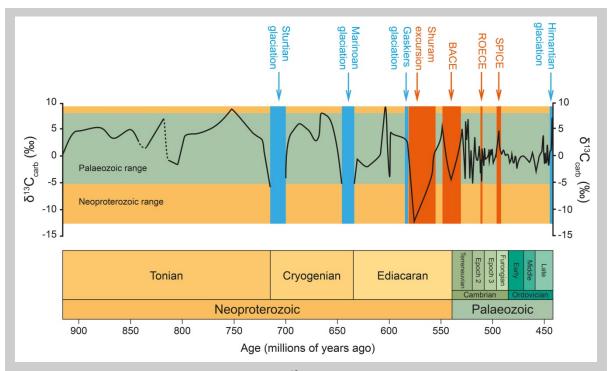


Figure 8 — The global stable carbon isotope ( $\delta^{13}$ C) curve through the Ediacaran–Cambrian transition indicates a change in state in the global carbon cycle, from large amplitude-low frequency oscillations to small amplitude-high frequency oscillations. Blue bars are major glaciation events. Orange bars are significant changes in  $\delta^{13}$ C: the Shuram excursion is the largest known in the geological record; BACE is the basal Cambrian carbon isotope excursion; ROECE is correlated with a big trilobite extinction event; and SPICE is one of the best known globally-correlated isotope excursions. Credit: T. Hearing, data after Saltzman & Thomas (2012).

A more nuanced but no less useful approach to palaeoenvironmental studies uses radiogenic isotopes – those produced by radioactive decay. The ratio of radiogenic strontium-87 (produced by the decay of mantle-derived rubidium-87 in granites) to stable strontium-86 indicates the degree of weathering of continental crust (essentially granite and its weathering products) into the global ocean. The extent of chemical weathering is both a cause and consequence of environmental conditions. Chemical weathering of minerals made with silicate (SiO<sub>4</sub>) is most efficient in warm, wet environments. However, it pulls carbon dioxide out of the atmosphere; this reduces the global greenhouse effect (Equation 1). This is a negative feedback process that operates on timescales of millions of years.

Chemical weathering of silicate rocks, using carbon dioxide  $\rightarrow$  CaSiO<sub>3(s)</sub> + 2CO<sub>2(g)</sub> + H<sub>2</sub>O<sub>(l)</sub>  $\leftrightarrow$  Ca<sup>2+</sup><sub>(aq)</sub> + 2HCO<sup>-</sup><sub>3(aq)</sub> + SiO<sub>2(aq)</sub>

← Metamorphic alteration of carbonate rocks during burial

Equation 1 — Chemical weathering of silicate rocks (from left to right) has the net effect of drawing down carbon dioxide from the atmosphere and emptying ions ( $Ca^{2+}$  and  $HCO_3^{-}$ ) into sea water. In reverse (from right to left; once these ions have been precipitated from sea water as rocks or biominerals), is the process of generating silicate rocks from carbonate rocks by metamorphic and magmatic activity.

It is interesting to note that the peak of the Phanerozoic <sup>87</sup>Sr/<sup>86</sup>Sr record, indeed the record for the past 900 million years, falls in the Cambrian Period, approximately 500 million years ago (Fig. 9). The early Cambrian marine transgression, in which relative sea levels rose and the shoreline moved towards the interior of the continents, has long been recognised in the geological record, for instance in the Great Unconformity across North America. It is observed throughout early Cambrian deposits around the world, such as the Avalonian Wrekin Quartzite of Nuneaton, UK, and the Laurentian Sauk Sequence in North America, providing further support to the hypothesis of a globally warm Cambrian climate.

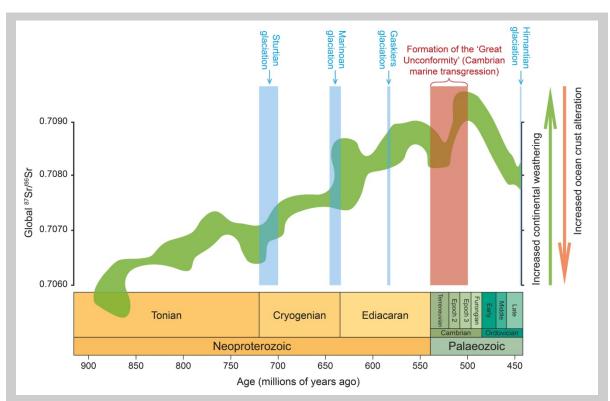


Figure 9 — Global strontium isotope curve shows that <sup>87</sup>Sr/<sup>86</sup>Sr levels reached their peak during the early to middle Cambrian Period. High <sup>87</sup>Sr/<sup>86</sup>Sr values indicate high rates of continental weather. After Peters and Gaines (2012).

# Combined palaeoenvironmental context of the Cambrian explosion:

Geochemical, geological and palaeobiological proxy data all have their foibles, and the palaeoenvironmental interpretations based on these data are complicated by the interplay of local and global signals and confusing environmental factors. However, using elements of all three and accepting their relative strengths and weaknesses, it is possible to develop an understanding of the global environment during the Cambrian explosion. Geological data are particularly useful in generating maps of palaeoclimatic belts (Fig. 7).

Importantly, the transition between the Ediacaran and Cambrian periods is more than just a geological boundary. It marks a step-change in global environmental and ecological conditions. Alongside the appearance of complex mobile animal body fossils and, particularly, trace fossils is a change in the nature of the  $\delta^{13}$ C record (Fig. 10). The large and slow oscillations of the late Neoproterozoic are replaced by smaller but more frequent oscillations around the beginning of the Cambrian Period. This has been connected to the Cambrian 'agronomic revolution', or the increased depth of sediment mixing by burrowing animals. The increase in burrowing changed the global carbon cycle by recycling into the biosphere organic matter that would previously have been buried and left for slow geological processes to recover. It also pushed nutrients and oxygen into the sediments, expanding the available habitat for oxygen-hungry animals. The presence of mobile animals had a moderating influence on environmental parameters and prevented a return to the major, potentially global, ice ages of the Neoproterozoic, and this change seems to be recorded in body fossils, trace fossils and geochemical signals. The consequences of the Cambrian radiation of animals were environmental, not just biological. Palaeoenvironmental signals are therefore another area to explore when considering whether the Cambrian explosion was a real biological event or an artefact of the fossil record.

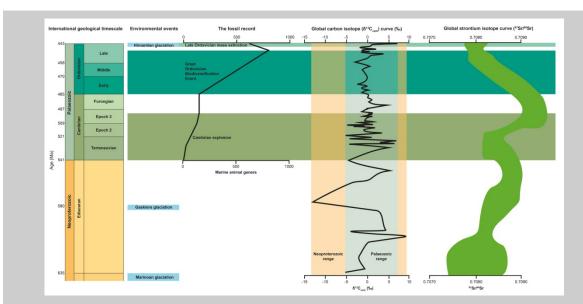


Figure 10 — Summary figure of the biological and geochemical changes associated with the Proterozoic – Phanerozoic transition. As marine animal genera increase in the Cambrian explosion, there is a step-change in the nature of the carbon cycle. The peak of the strontium isotope curve, reflecting high continental weathering rates, also occurs at this time. Although the Great Ordovician Biodiversification Event sees a greater rise in animal genera, there is no commensurate step-change in the carbon cycle. Credit: T. Hearing.

## **Summary:**

The current state of understanding of Cambrian environments is drawn largely from informative but qualitative data. These point towards a world that was substantially different from that of the preceding Precambrian, but had not yet quite settled into the 'norms' of the past 500 million years. Globally warm temperatures probably meant that the climate did not change much between the equator and the poles, as is characteristic of other warm intervals in Earth's history, and this in turn encouraged rapid weathering of the continents. This is seen in both geochemical and geological data throughout the Cambrian marine transgression and the development of the Great Unconformity. There remains plenty of active debate on both the causes and consequences of the Cambrian explosion, although it is clear that the establishment of animal-dominated ecosystems coincided with a fundamental change in the organization of global environments, particularly the carbon cycle. It is now important to gather more data to add detail to the emerging global picture of the environments of the Cambrian explosion.

# Suggestions for further reading:

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Erwin, D. H., Valentine, J. W. *The Cambrian Explosion: The Reconstruction of Animal Biodiversity* (Roberts & Co., 2013).

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