12. Origin and evolution of life (part II)

The earliest form of life was probably a prokaryote. Unlike the eukaryotic cell, the prokaryotic cell has a more simple structure with no nucleus and no membrane-bound organelle (organelle = specialized subunit of the cell). This early prokaryote must have been able to survive without oxygen (anaerobic prokaryote). Anaerobic metabolism is carried out today by some species of bacteria and archaea.
In the text below, I review some of the main stages of the evolution of life and the evidence from the geological record.

12.1. The Great Oxygenation Event (GOE)

The free oxygen (O_2) present in the atmosphere today was probably produced initially by photosynthetic prokaryotes similar to modern cyanobacteria (the same microorganisms behind the formation of stromatolites, see chapter 7). The first unambiguous occurrence of cyanobacteria in the geological record is in 2.15 Ga old rocks from Canada. Fossilized stromatolites and microfossils with an age of 3.5 Ga suggests an earlier origin (but controversial, Fig. 1B). Geologic and molecular evidence suggests that cyanobacteria evolved after various other types of bacteria, including anoxygenic photoautotrophs (organisms performing photosynthesis but which do not produce oxygen).

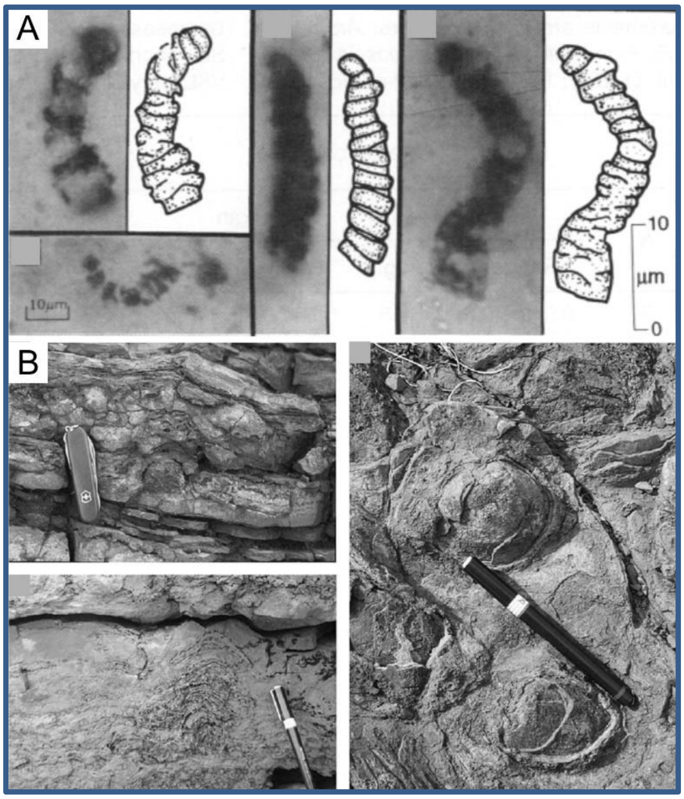


Figure 1: 3.5 Ga old microfossils (A) and stromatolites (B) from Western Australia (sources: A. Schopf, 1993; B. Van Krakendonk, 2006)

The oxygen produced by photosynthesis did not accumulate directly in the atmosphere. Oxygen, a powerful oxidizing agent, first reacted with various elements. Massive amounts of iron oxide (Fe_2O_3) precipitated in the oceans when Fe^{2+} (ferrous ions)-rich water mixed with O_2. These "mass-rusting" events are believed to be responsible for the formation of thick accumulations of red stratified sedimentary rocks rich in iron oxide that are now referred to as ***Banded Iron Formations*** (BIFs, Fig. 2A). Once the oxidation process was completed, oxygen started to accumulate in the atmosphere and gave rise to the ***Great Oxygenation Event*** (GOE), which is a sharp increase in atmospheric oxygen at around 2.4-2.3 Ga ago. The occurrence of fluvial deposits older than 2.4 Ga containing sediments composed of mineral grains that would not be stable under oxidizing conditions is one evidence of the lack of free oxygen in the atmosphere prior to the GOE (Fig. 2B). The GOE had a major impact on life. First, oxygen being toxic for anaerobic prokaryotes, the GOE probably caused the first major mass extinction event. Second, the GOE led to a major innovation: the ***aerobic metabolism***. Cellular respiration using O_2 as an electron acceptor produces much more energy than anaerobic respiration and was an essential step to sustain the energetic needs of more complex forms of life. Third, the adaptation of large prokaryotic cells to the toxicity of oxygen may be the mechanism behind the emergence of eukaryotes (see next section).

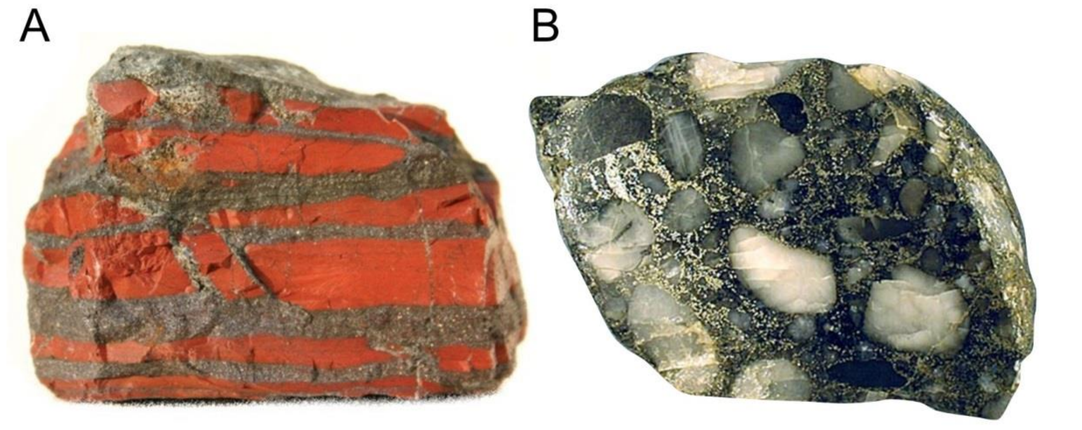


Figure 2: Banded Iron Formation (A) and 2.7 Ga old Witwatersrand conglomerate (South Africa) containing Pyrite flakes and uraninite (B) (sources: A. Encyclopedia Britannica, B. Natural Museum of Humbolt State Univiversity)

12.2. The eukaryotic cell

Another important step in the evolution of life is the development of a new way to obtain carbon by feeding directly on biological matter: ***predation***. This innovation requires the cell to have a flexible, non-rigid membrane to engulf its prey. This mechanism may have led to the evolution of eukaryotic cells. Indeed, one hypothesis suggests that the eukaryotic cell may have evolved from the ingestion by large anaerobic bacteria of small aerobic bacteria which later became a structural part of the larger cells. The small aerobic prokaryotes may have survived inside the larger cells by using organic molecules produced by their host. The larger anaerobic prokaryotes, on the other hand, may have benefited from the ability of aerobic prokaryotes to use O_2 and to produce energy through aerobic respiration. These aerobic prokaryotes may have evolved into the mitochondria of eukaryotic cells, organelles used for cellular respiration. In a similar manner, photosynthetic prokaryotes may have been ingested by larger cells and evolved into chloroplasts, organelles of plant and algal eukaryotic cells which carry out photosynthesis. This scenario, which implies the evolution from a predator-prey to a host-symbiont relationship, is called the ***endosymbiont hypothesis*** (proposed by Lynn Margulis in 1966, Fig. 3).

The oldest fossils of eukaryotes are found in a 1.8 Ga old rock formation in China (Fig. 4). Biomarkers indicate the existence of eukaryotes as early as 2.7 Ga. A recent molecular study suggests that the oldest ancestors of extant eukaryotes may have emerged between 2.5 and 1.6 Ga ago, and then quickly diversified.

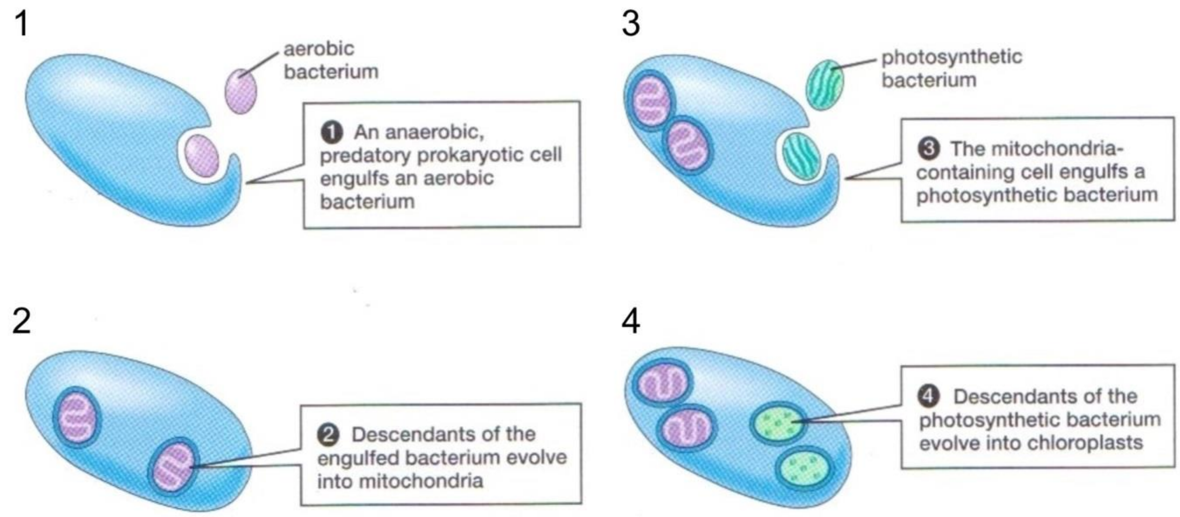


Figure 3: The Endosymbiont Hypothesis (source: Biology, Life on Earth, 9th edition)

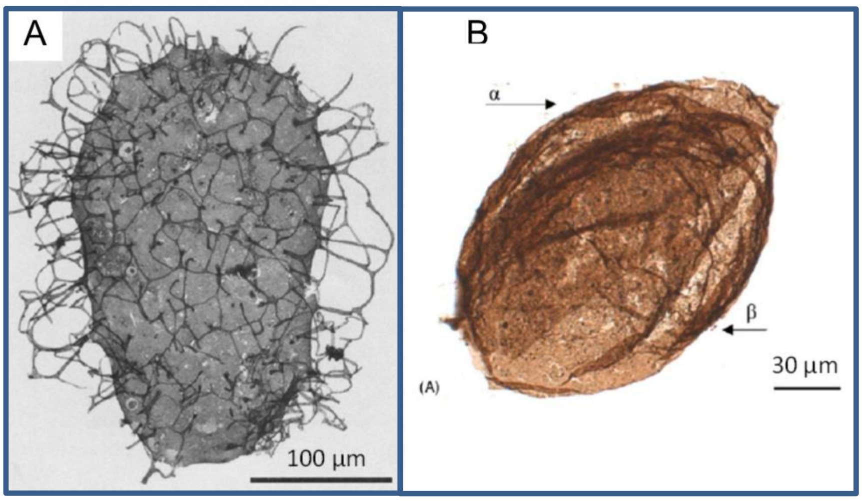
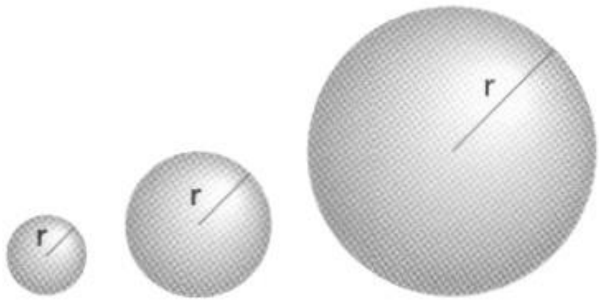


Figure 4: 1.4 Gyr eukaryote from Canada (A) and 1.8 Gyr eukaryote from China (B)
(sources: A. *Butterfield, 2005, B. Lamb et al., 2009)*

12.3. Multicellularity

Once predation became established as a new strategy to obtain carbon, larger single-celled organisms may have had an advantage over smaller ones. For a cell, it is easier to engulf a prey which is comparatively smaller. Larger cells have also less chance to be ingested by others. However, larger single-celled organisms require more exchange of matter through the cell membrane (intake of O_2 and nutrients, waste removal). Since the surface/volume ratio decreases as the cell becomes larger, there is a limit to the size of a single-celled organism (Fig. 5). Beyond such limit, the surface of the cell is not large enough to permit enough exchange to sustain cellular metabolism. The solution to grow larger without slowing down metabolic reactions is to adopt a ***multicellular*** body. Besides greater predation efficiency and better protection against predator cells, multicellularity enables the evolution of specialized cells and body parts. For example, a multicellular alga can have roots to anchor itself on the seafloor and leaves to harvest the Sun's energy for photosynthesis.



distance to center (r)	1.0	2.0	4.0
surface area ($4\pi r^2$)	12.6	50.3	201.1
volume ($4/3\,\pi r^3$)	4.2	33.5	268.1
area/volume	3.0	1.5	0.75

Figure 5: Surface area and volume relationships (source: Biology, Life on Earth, 9th edition)

In the fossil record, the oldest undisputed occurrence of a multicellular organism with a clear affinity with an extant group is the red algae *Bangiomorpha pubescens* found in a 1.2 Ga old rock formation in Canada (Fig. 6A). An older fossils of unknown affinity and possibly derived from a multicellular organism is *Grypania spiralis* (Fig. 6B). The oldest specimen of *G. spiralis* is from a 1.85 Ga old rock formation in the USA.

Multicellular organisms evolved shortly after the GOE once aerobic respiration provided the energy needed to sustain more complex forms of life.

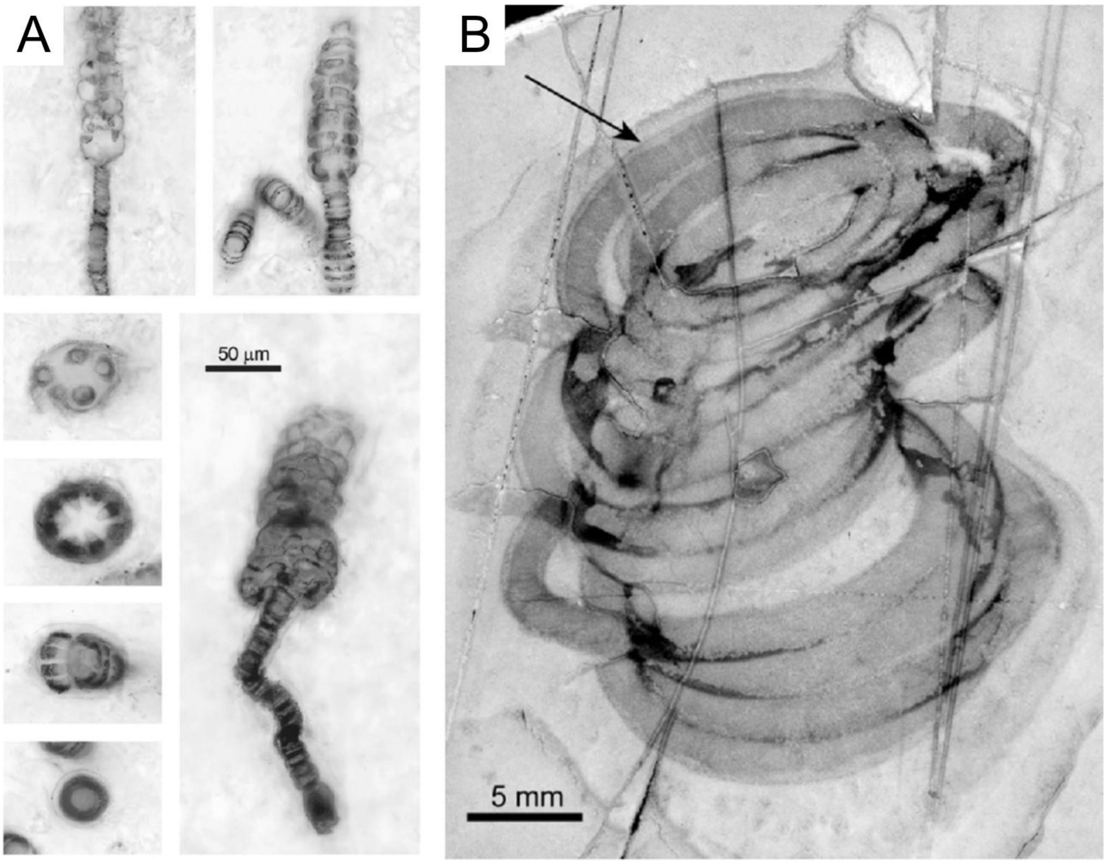


Figure 6: 1.2 Ga multicellular red algae *Bangiomorpha pubescens* from arctic Canada (A) and 1.6 Ga problematic *Grypania spiralis* from India (B) (sources: A. Butterfield, 2000, B. Butterfield, 2009)

12.4. The Cambrian radiation of life

A sharp increase in animal diversity is recorded in the fossil record at the end of the Precambrian 600-550 million years ago. This is the first phase of animal diversification and the resulting group of organisms is referred to as the ***Ediacara biota*** (Fig. 7). Ediacaran animals were the first large and complex forms of life. They had a bilateral or radial symmetry and were mostly soft-bodied. Their taxonomic relationship with extant groups is still debated. They disappeared at the onset of the Cambrian period. Ediacara marks the transition between two distinct biospheres: the Precambrian biosphere dominated by single-celled organisms ("the age of bacteria") and the Cambrian biosphere comprising all known animal phyla.

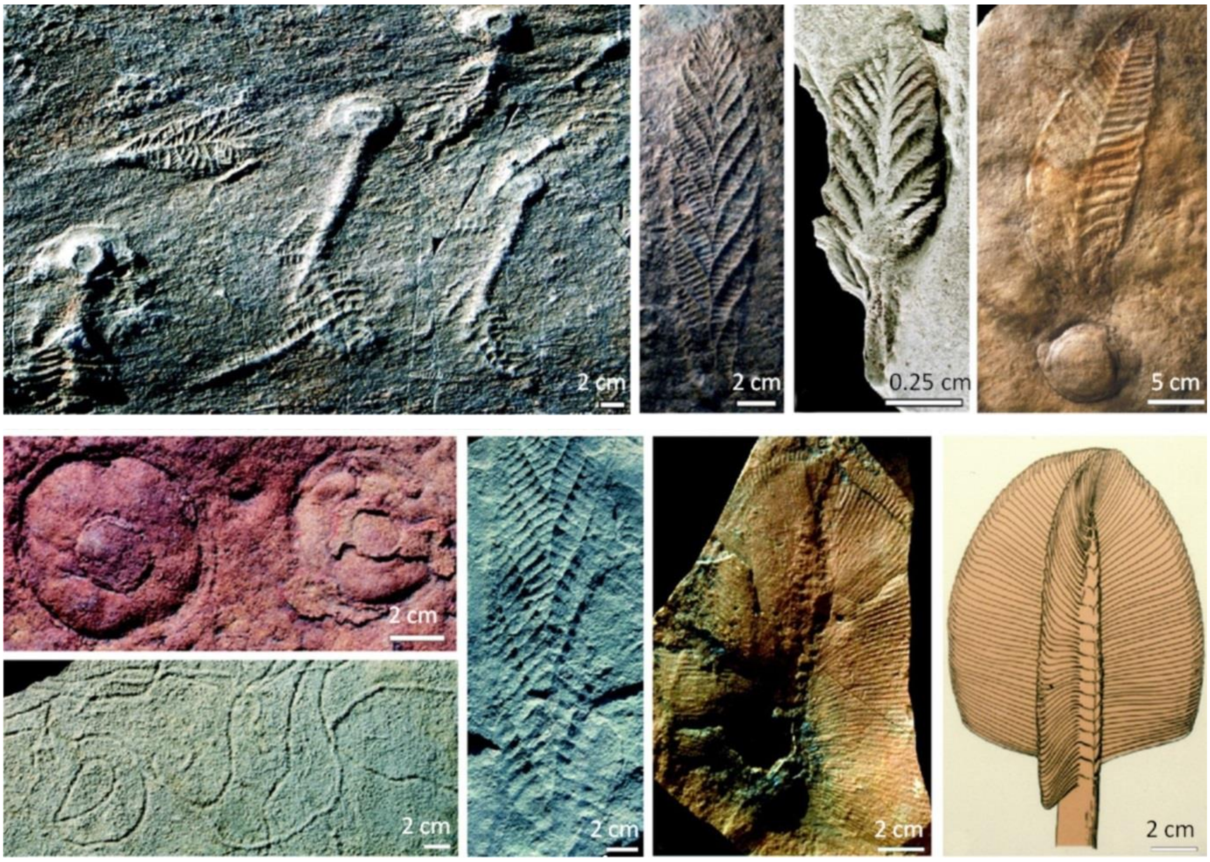


Figure 7: Examples of Ediacaran fossils — note the trackways on the bottom left corner (source: Narbonne, 2005)

Cambrian life is characterized by a major innovation: the ***shell*** or ***carapace***, and a rapid and prodigious diversification of complex life forms. This explosion of life forms is known as the ***Cambrian radiation of life***. All known animal phyla were already present during the early Cambrian. However, the diversification of life and the emergence of modern phyla had already begun in the Precambrian. For example, the first traces of Porifera (sponges) and Cnidaria (anemones, corals…) are found in Precambrian rocks. The explosion of diversity around the Precambrian-Cambrian boundary gave rise to an astonishing variety of body plans and architectures, some of which are difficult to link with today's life forms, and have even been interpreted by some researchers as potential evolutionary "dead-ends" (Fig. 8).

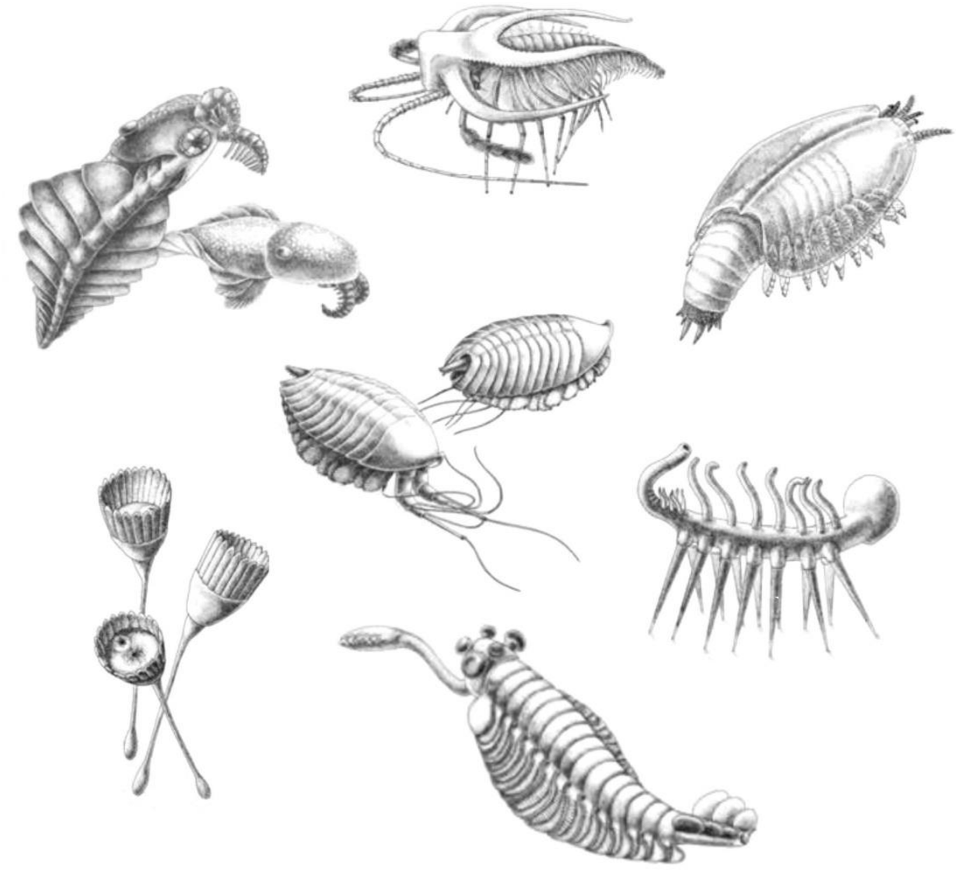


Figure 8: Examples of early Cambrian animals (source: Steven J. Gould, 1989)

A combination of factors is probably responsible for the Cambrian radiation of life. Here are several factors which may have played an important role:

① Environmental factors

• End of the Proterozoic glaciations

• Rise in atmospheric O_2* providing an energetic advantage

• Change in ocean chemistry facilitating biomineralization

② Genetic factors

• Emergence of key developmental genes resulting in new evolutionary possibilities

③ Ecological factors

• Adaptations related to a predator-prey relationship. For example, preys evolved traits to avoid being caught by predators, such as a shell or a carapace, a pelagic** mode of life, or body parts which improved their mobility. Predators on the other hand evolved traits to help them catch preys,

* Some scientists suggest that this second "oxygenation event" may have been triggered by the break-up of the supercontinent Rodinia. The break-up of Rodinia created more extensive continental margins on which large amounts of organic matter could be buried and escaped decomposition ($C_6H_{12}O_6 + 6\ O_2 \rightarrow 6CO_2 + 6H_2O$). Less O_2 consumed by the decomposition of organic matter meant more O_2 left in the atmosphere.

** Pelagic organisms live in the water column. Benthic organisms live on or near the seafloor.

such as improved sensory organs (e.g., the eye). The evolutionary interdependence between different groups of organisms is referred to as coevolution (distinct groups of organisms can influence each other's evolution). This may have led to rapid biological diversification.

12.5. The colonization of land

The earliest multicellular fossils of land plants are found in rocks of Ordovician age approximately 475 million years old (Fig. 9A). The advantage of a terrestrial mode of life for the earliest land plants was threefold: (1) abundant sunlight, (2) abundant nutrients, and (3) absence of predators. The arthropods (crabs, spiders, scorpions, centipedes…) were the first animals to colonize the land. The earliest fossil evidence is based on trackways preserved in Late Cambrian-Early Ordovician eolian sandstone in Canada (Fig. 9B). Optimal environmental conditions and the lack of predators enabled some arthropods to reach a gigantic size during the Carboniferous (e.g., 70 cm large dragonflies, 2 m long millipedes). The first terrestrial vertebrates (tetrapods) evolved from a group of Silurian fish. An example of an early tetrapod is *Ichtyostega* which lived during the Devonian period (Fig. 9C). Reptiles appeared during the Carboniferous. In this group, the dinosaurs became extremely diverse and some grew larger than any other land vertebrates during the Jurassic and Cretaceous. They flourished for a hundred million years before vanishing 65 million years ago (see section 12.6.2.). Their only living descendants are the birds. The last 65 million years is known as the Cenozoic and is marked by the diversification of mammals. This group includes the genus homo (us and our ancestors), the earliest representative of which appeared around 2.3 million years ago.

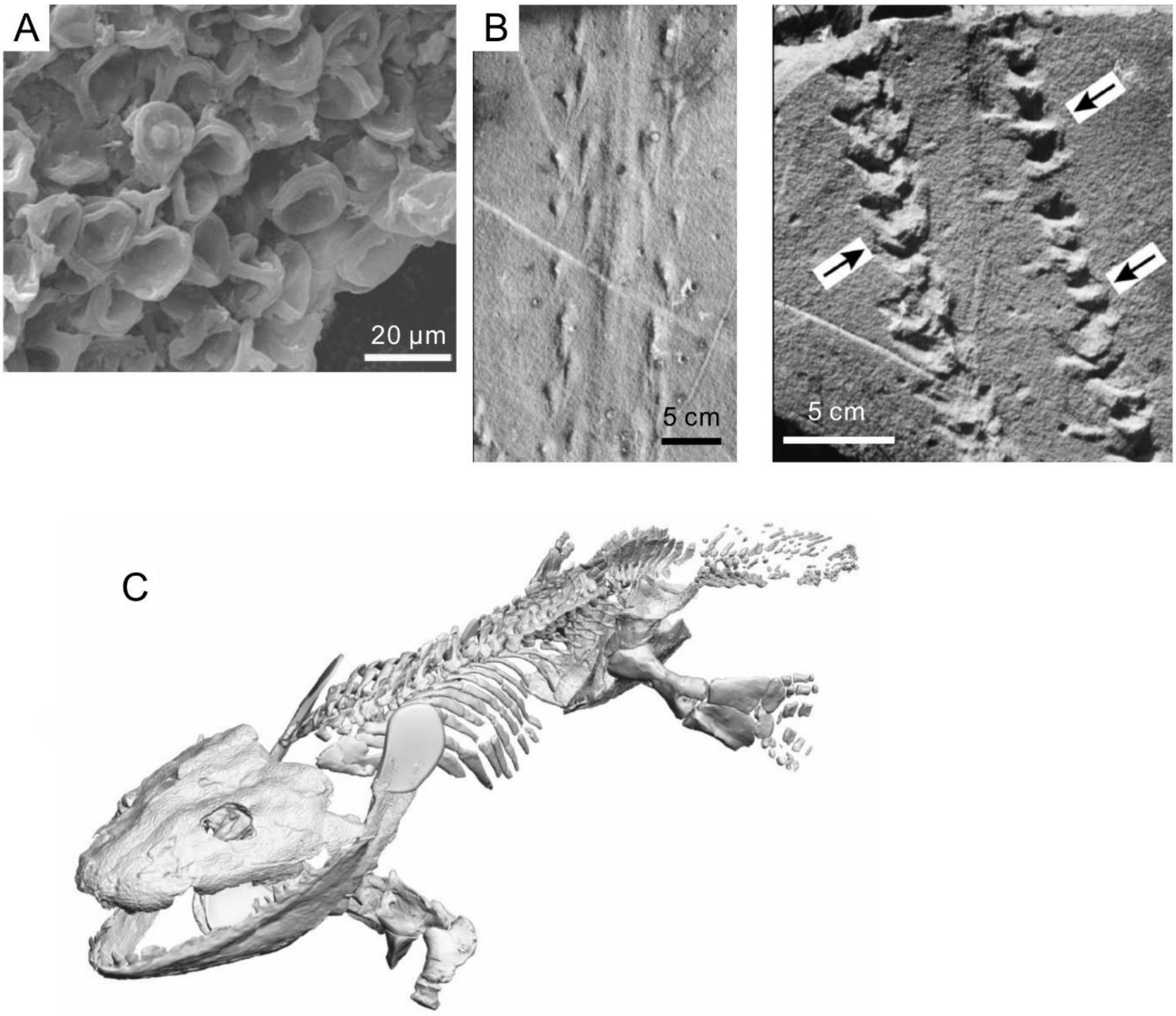


Figure 9: 475 million years old spores of an early land plant (A), Late Cambrian or Early Ordovician trackways of arthropods, and a 3D image of a skeleton of Ichtyostega (sources: A. Wellman et al., 2003, B. McNaughton et al., 2002, C. Pierce et al., 2012).

12.6. Mass extinctions

The history of life is characterized by five major extinction events (Fig. 10). Each mass extinction was followed by a period of diversification.

We will now focus on two of these mass extinction events: (1) the most severe of all: the end-Permian mass extinction; and (2) the most famous of all: the end-Cretaceous mass extinction.

12.6.1. End-Permian mass extinction

The end-Permian mass extinction occurred 250 million years ago. Roughly 90% of all species went extinct. The crisis affected both marine and terrestrial ecosystems.

The Permian is a geologic period which began 300 million years ago and ended 50 million years later. The geography of the Permian is characterized by the presence of a single supercontinent called Pangaea. The reduction of shallow marine environments enhanced the competition for resources and may have contributed to species extinction. However, other factors must have played a role to cause a mass extinction of such a magnitude. One of the most likely factors is a catastrophic volcanic eruption which disrupted global climate. Such an intense and long-lasting eruption has never been witnessed in human history. However, the geological record shows evidence that gigantic eruptions have occurred several times in the past. These eruptions have produced tremendous amounts of basalt called ***flood basalt***. Flood basalts cover extensive regions of the crust called ***flood basalt provinces***. One such province, the largest one on a continent, is found in Siberia and its age coincides with the end-Permian extinction: the Siberian flood basalts (or ***Siberian Traps***) which have accumulated during a million years and cover approximately 2 million km^2.

What was the impact of such catastrophic volcanic eruptions on global climate?

① On the short term: massive amounts of volcanic ashes released in the upper atmosphere would reflect some of the incoming sunlight and cause a short-lived global cooling.

② Acid rains would result from the reaction between volcanic gases and condensing water droplets (H_2SO_4, HCl, HF) present in the atmosphere.

③ On the long term: the release of massive amounts of CO_2 in the atmosphere would trigger a global warming. The consequences of global warming are complex.
For example, global warming may disrupt the ocean circulation and prevent the renewal of O_2 in the deep ocean*. The warming of seawater also decreases the solubility of O_2 in the oceans. Moreover, the stability of ***methane hydrate*** present in deep sea sediments and in high-latitude permafrost may be affected by global warming. Methane hydrate is composed of water ice with molecules of methane trapped in the crystal lattice of the ice. Methane is mainly produced by methanogen archaea through anaerobic respiration involving the byproducts of the decomposition of organic matter. During global warming, there is risk of destabilization of methane hydrate which may lead to a massive input of methane in the atmosphere. Methane is a very potent greenhouse gas which would further enhance global warming and amplify the destabilization of methane hydrate, creating a ***positive feedback loop***.

12.6.2. End-Cretaceous mass extinction

The end-Cretaceous mass extinction 65 million years ago is the most famous mass extinction event because it caused the extinction of dinosaurs. Unlike the other mass extinction events, the cause of the end-Cretaceous mass extinction is relatively well constrained. There are several convincing lines of evidence supporting the hypothesis of a large ***meteorite impact*** as the main cause.

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* One of the main source of deep ocean water is in the North Atlantic where cold and salty (dense) water sinks to the bottom of the ocean and begins its journey to the south hemisphere (= thermohaline circulation). If the ocean surface warms, the downwelling of O_2-rich surface water in the North Atlantic and elsewhere may be disrupted and prevent the oxygenation of the deep ocean.

The Cretaceous-Tertiary boundary (known as the K-T or K-Pg boundary; Pg stands for the Paleogene period) is characterized by a distinctive sedimentary layer that can be followed worldwide and which contains a high concentration of Iridium (rare in earth's crust but abundant in meteorites) and components indicative of a meteoritic impact (shocked quartz, tektite, nano-diamonds). The crater associated with the K-T boundary has been located near the Yucatan Peninsula in Mexico (Chicxulub Crater). The meteorite that produced the Chicxulub Crater must have been at least 10 km in diameter. The consequences of such a large meteorite impact on the environment are multiple and take place at various time and spatial scales (Table 1).

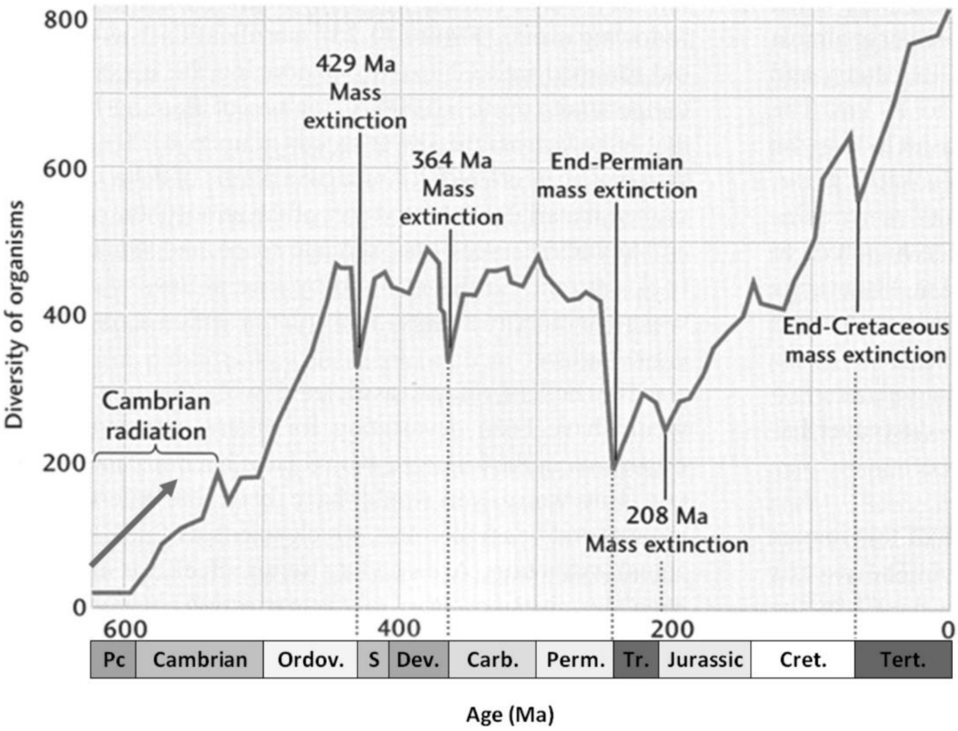

Figure 10: Evolution of biological diversity over the past 600 million years (source: Understanding Earth 6th edition)

TABLE 1. Suggested Mechanisms for K-T Extinctions

Agent	*Mechanism*	*Time-scale**	*Geographic Scale†*
Dust loading	cooling	Y	G
	cessation of photosynthesis	M	
	loss of vision	M	
Fires	burning	M	G
	soot cooling	M	
	pyrotoxins	M	
	acid rain	M	
NO_x generation	ozone loss	Y	G
	acid rain	M	R
	cooling	Y	G
Shock wave	high wind	I	R
Earthquakes	shaking	I	R
Tsunami	drowning	I	R
Heavy metals, etc.	poisoning	Y	G
Water/CO_2 injections	warming	D	G
SO_2 injections	cooling	Y	G
	acid rain	Y	G

*I, instantaneous; M, months; Y, years; D, decades.
†L, local; R, regional (10^6 km^2); G, global.

Table 1: Environmental effects of the meteorite impact at the K-T boundary (source: Toon et al., 1997)