Lecture 6: Astrobiological Implications of the History of Life on Earth and the Terrestrial Environment

Aims of Lecture

(1) To discuss the major evolutionary innovations of life on Earth, and to discuss their astrobiological implications; and

(2) To discuss whether there is anything special about the terrestrial environment which has made it uniquely able to support a diverse biosphere over geological time.

Contents of Lecture

Fig. 1. Earth – the only known inhabited planet in the Universe (NASA).

1. Introduction

There is good evidence that life existed on the Earth (Fig. 1) almost as soon as the planet was habitable for microorganisms (Lecture 3). In itself, this is good news for astrobiology, as it implies that life, at least microbial life, may be common in the Universe. However, the subsequent history of life on Earth over the last 3.5 billion years also has important astrobiological implications, and these are not as optimistic for the prevalence of more advanced forms of life as the early appearance of life on Earth might suggest.

2. Evolutionary relationships

While the earliest physical evidence for life on Earth comes from the palaeontological and isotopic analyses, evidence for the evolutionary relationships of early life comes from family trees based genetic similarities and differences between living species. Such studies (phylogenetic analyses), attempt to determine how closely one species is related to another, and how far back in evolutionary history they last shared a common ancestor. The results of one such analysis are shown in Fig. 2, from which several important conclusions can be drawn:

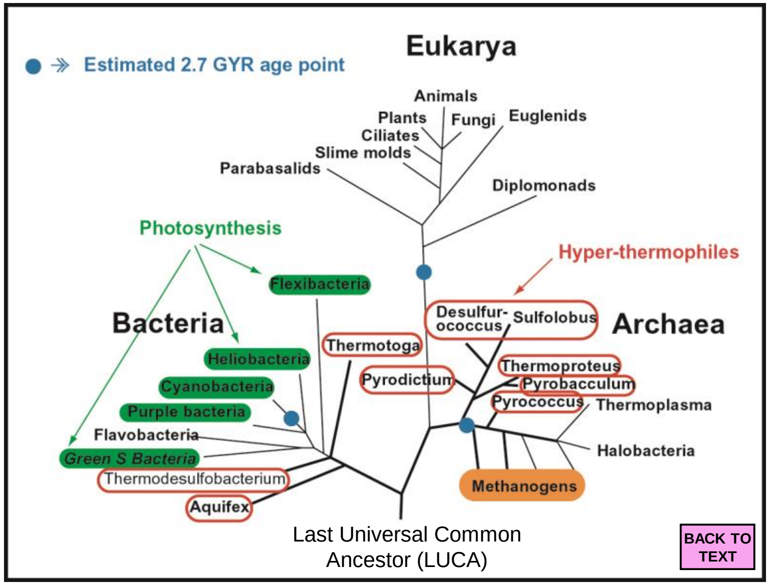

Fig. 2. The ‘tree of life’, showing the evolutionary relationships between the three ‘domains’: archaea, bacteria, and eukarya. Hyperthermophiles are indicated in red, photosynthesizers in green, and methanogens in orange. An estimated time marker is included at 2.7 Gyr ago, but this is very uncertain. (After Andrew H. Knoll, *Life on a Young Planet*).

- All life on Earth is descended from a single common ancestor (the ‘Last Universal Common Ancestor’: LUCA);
- The split into archaea and bacteria occurred early (probably by 3.5 Gyr ago), but the timing of the origin of the eukarya is debated (and probably protracted);
- The eukarya (which include plants, animals and fungi) contain a mixture of characteristics, but appear to be more closely related to the archaea than to bacteria;
- Photosynthesis was strictly a bacterial invention;
- The deepest branches of the tree (both for bacteria and archaea) are represented by hyperthermophiles – organisms which thrive best at high temperatures (typically 80 to 100°C).

3. Implications of a high temperature ancestry

If the high-temperature ancestry of terrestrial life is confirmed, there are two possible explanations, both of which have interesting astrobiological implications:

- Life may have originated in a high-temperature environment, for example at a hydrothermal vent. While this would be consistent with the hydrothermal production of pre-biotic organic molecules (discussed in Lecture 5), it would greatly complicate the synthesis of larger biomolecules (e.g. proteins and nucleic acids) which are easily destroyed at high temperatures. Thus, while thermophilic organisms have managed to evolve special adaptations to survive at high temperatures, such environments may have been too challenging to permit the initial origin of life itself.

- Alternatively, life may have formed at lower temperatures, but at some point retreated to a high-temperature refuge, from which the planet was subsequently re-colonised. As we saw in Lecture 2, the period of heavy bombardment is likely to have resulted in repeated and severe heating events. Such an environment would favour organisms able to survive high temperatures, and any which managed to colonise hydrothermal vents at the bottom of the oceans, or deep in the crust, would probably have been the most protected of all.

In an interesting paper, Madeline Weiss et al. (*Nature Microbiology*, Vol. 1., Article No. 16116, 2016) attempted to determine the physiology and habitat of LUCA by identifying genes common to archaea and bacteria. They found that LUCA was most probably an anaerobic, CO_2 and N_2-fixing thermophile, dependent on H_2 as an electron donor. These characteristics are consistent with what we believe conditions on the early Earth may have been like (Lectures 2, 5 and 7). Note, however, that we don't necessarily expect LUCA to have been the first lifeform on Earth – earlier species may well have existed and become extinct.

4. Key evolutionary events

Several key evolutionary events can be identified in the history of life on Earth. These have astrobiological relevance insofar as they inform consideration of how evolution might proceed on other planets, and the extent to which we might expect Earth-like planets to develop Earth-like life.

4.1 Oxygenic photosynthesis

Lecture 7 will discuss the many different ways life has found to extract energy from its environment, but the ability to utilise freely available sunlight for this purpose was a key innovation that transformed not only the biosphere, but the planet itself. The process involves using chlorophyll and associated protein/enzyme complexes (which had first to be evolved through natural selection) to absorb the energy of sunlight. This is used to extract hydrogen from water and react it with carbon dioxide to synthesise organic compounds for use by the organism. Schematically, it may be represented as:

$$\mathbf{2H_2O + CO_2 + sunlight \rightarrow ``CH_2O" + H_2O + O_2}$$

Here, "CH_2O" represents newly synthesised organic material, and O_2 is released as a waste product. Note, however, that this reaction is mediated by numerous complicated enzymes and cannot occur spontaneously.

The first appearance of oxygenic photosynthesis on Earth is controversial, ranging between 3.5 Gyr ago (if the interpretation of the oldest stromatolites discussed in Lecture 3 is correct) to 2.3 Gyr ago (i.e. the so-called 'Great Oxidation Event'). Eventually, photosynthesis transformed the chemical composition of Earth's atmosphere, but it did so slowly: the atmospheric concentration of O_2 remained low (≤ 1% the present level) until about 2.3 Gyr ago, and may have been < 10% of its present level until about 600 million years ago (Fig. 3 on the next page)

The presence of oxygen makes possible aerobic respiration as an energy source for organisms which can obtain carbohydrates from their environment:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6H_2O + 6CO_2 + \text{Energy}$$

Early in the history of life on Earth, some bacteria evolved to exploit this new source of energy (Fig. 2) and it was essential for the later evolution of multi-celled organisms.

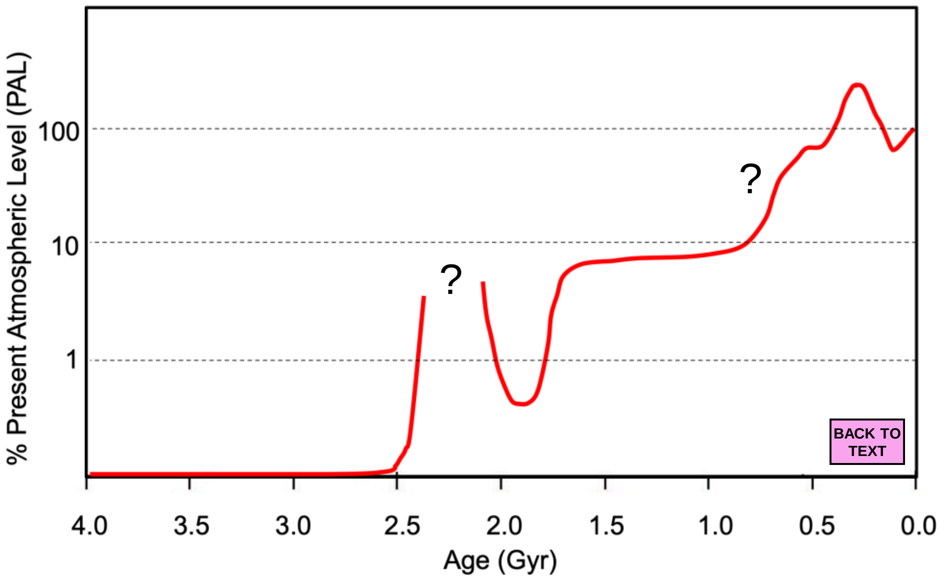

Fig. 3. Estimated O_2 levels in Earth's atmosphere over geological time, relative to the present atmospheric level (PAL). Adapted from L.M. Och and G. Shields-Zhou, *Earth Science Reviews,* 110, 26-57 (2012).

4.2 Origin of the eukaryotic cell

The complex structure of Eukaryotic cells (see Lecture 4) is unlikely to have evolved all at once, and very likely had a protracted history. Chemical signatures ('bio-markers') which are apparently unique to eukaryotic cells have been found in 2.7 Gyr old shales, which implies an origin of eukaryotes by at least that time, although this interpretation has been questioned. The earliest eukaryotes were probably much simpler than those around us today, and may have been distinguished from the other two 'domains' of life by possession of a cytoskeleton, intra-cellular membranes, and, less certainly, a discrete nucleus. The major organelles (e.g. mitochondria and chloroplasts) were added later by a process known as 'endosymbiosis'.

Both mitochondria and chloroplasts are derived from once free-living bacteria, which we know because, amongst other things, they retain some of their original DNA.

Mitochondria are derived from oxygen-respiring bacteria (most likely related to contemporary purple bacteria), while chloroplasts are derived from photosynthetic bacteria (probably cyanobacteria). At some date, these free-living bacteria became incorporated within a(proto-) eukaryotic host cell, forming symbiotic relationships – providing energy to the host, in return for a safe environment and a regular supply of nutrients. The estimated times of these endosymbiotic events range between ~2.1 and 1.1 Gyr ago, with the incorporation of mitochondria preceding that of chloroplasts by an unknown interval but possibly several hundred million years (Fig. 4; see also Betts et al., *Nature Ecology & Evolution*, Vol. 2, pp. 1556-1562, 2018).

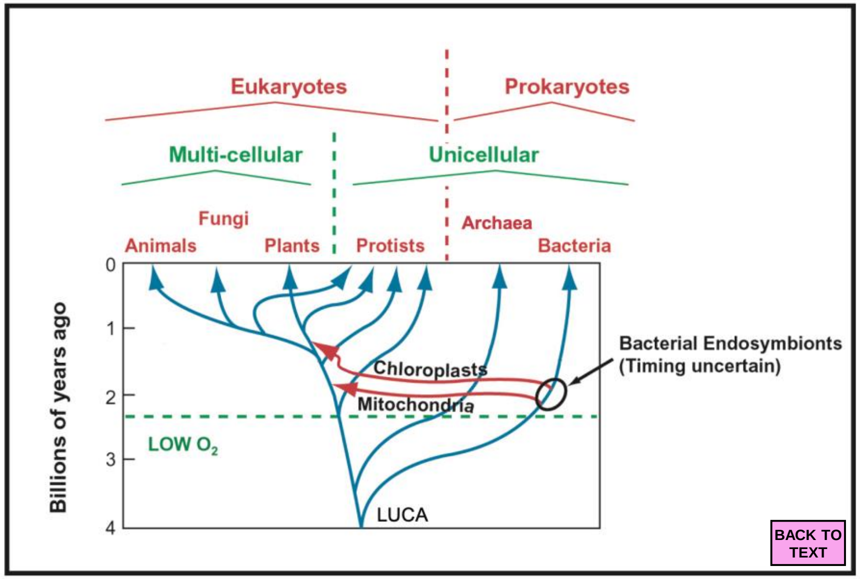

Fig. 4. Evolutionary relationships between the various kingdoms and domains of life, illustrating the approximate timing of the incorporation of bacterial endosymbionts into eukaryotic cells.

Study of mitochondrial DNA implies that they are ultimately derived from a single common ancestor, and thus that they became incorporated in eukaryotic cells in a single endosymbiotic event. The same appears also to be true of chloroplasts (although there is a known exception, see below, and secondary endosymbiotic transfer of chloroplasts is common). If these were literally chance events, then the astrobiological implications are profound – cells of eukaryotic complexity may be very rare in the Universe, even if prokaryotic life is common. On the other hand, the fact that endosymbiotic creation of organelles has happened at least twice indicates that the process is not strictly unique. Moreover, there is evidence that the unicellular alga *Paulinella chromatophora* has independently acquired photosynthesising organelles within the last 60-200 Myrs, which implies that, while rare, endosymbiosis may be an on-going process.

4.3 Multicellular life

Multicellular life is mostly based on eukaryotic cells, apart from microbial multi-cellular filaments (e.g. some cyanobacteria; Fig. 4 of Lecture 3) and rare bacterial species where many individuals cooperate for feeding and/or reproduction (e.g. myxobacteria). There are clearly many advantages to multicellularity, not only in size but in the division of labour that can be achieved by having different cells specialise for different functions. In fact, multicellularity appears to have arisen independently multiple times in both prokaryotes and eukaryotes. Excluding multicellular prokaryotic colonies, the earliest palaeontological evidence for multicellular life on Earth can be summarised as follows:

- The 2.1 Gyr cm-sized Francevillian Biota fossils from Gabon are the earliest known fossil structures generally accepted as being multicellular, but may represent colonies of independently living cells.
- The 1.2 Gyr multicellular red alga Bangiomorpha is the earliest known organism that has differentiated, specialized cells, and could therefore count as the oldest known multicellular plant (although a claimed discovery of 1.6 Gyr-old multicellular red algae has recently been made; S. Bengston et al., *PLOS Biology*, March, 2017).
- The ~0.6 Gyr Ediacaran fauna represents the earliest known multicellular animals (Fig. 5). Although the precise relationship between the Ediacaran fauna and later Cambrian animals is uncertain, recent work by Bobrovskiy et al. (*Science*, 361, 1246, 2018) has demonstrated that the Ediacaran fauna were related to modern animals and represent a prelude to the later development of animal life.

A review on the origins of multicellularity has been given by A.H. Knoll, "The multiple origins of complex multicellularity," *Ann. Rev. Earth Planet. Science*, 39, 217 (2011), and comprehensive information on the Ediacaran fauna can be found at www.ediacaran.org.

The Ediacaran fauna was shortly followed (~540 Myr ago) by the so-called 'Cambrian Explosion' of animal diversity and the origin of the major animal phyla (body plans). Thus, on the face of it, it took three thousand million years from the initial appearance of life on Earth to the origin of multicellular animal life. That said, the oldest fossil evidence for animals may not represent the time of their actual evolution – the first animals were probably very small and soft-bodied and difficult to preserve (or to find!).

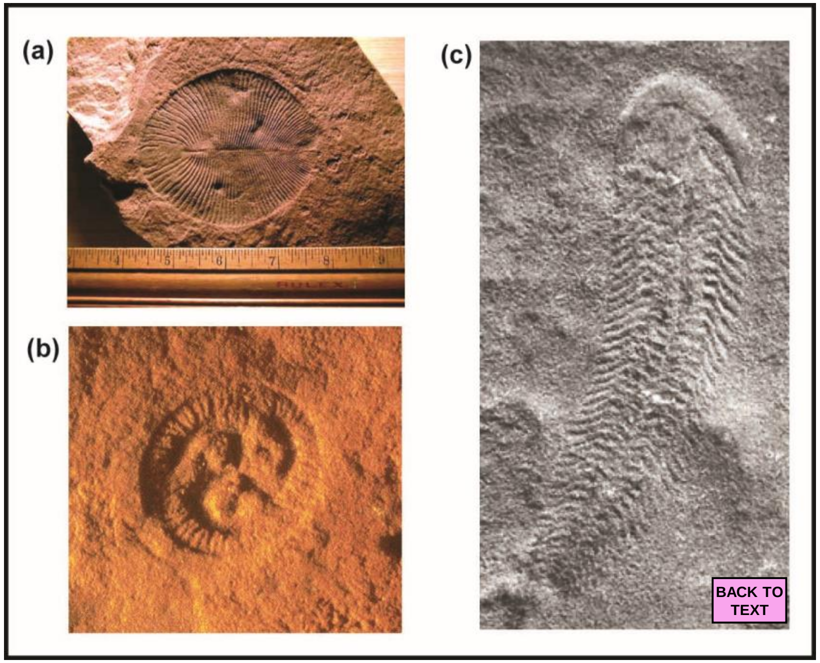

Fig. 5. Examples of the pre-Cambrian Ediacaran fauna. (a) Dickinsonia (affinity uncertain); (b) Tribrachidium (affinity uncertain); (c) Spriggina, originally interpreted as an annelid worm, but now thought more likely to be an early arthropod (specimen is 3 cm long). Current thinking on affinities with extant animals can be found at http://www.ediacaran.org. Images are from: http://www.ucmp.berkeley.edu/vendian/vendian.html.

Molecular clocks may help to resolve this issue: at a molecular level, genes accumulate random changes that are passed on to later generations. If the rate of the accumulation of genetic variations can be estimated, they provide a way to estimate the time since two taxonomic groups (species, phyla, even kingdoms) shared a common ancestor, although there is controversy over the calibration of these clocks and a correspondingly wide range of results.

Most recent molecular clocks suggest that animals first appeared about 700 million years ago, i.e. only about 100 Myr before the Ediacaran fauna (Fig. 6). If true, this implies a span of about a billion years (albeit with wide uncertainty, say 950±450 Myr) between the incorporation of mitochondria into eukaryotic cells and the appearance of multi-celled animals. This might imply that this is another difficult evolutionary step.

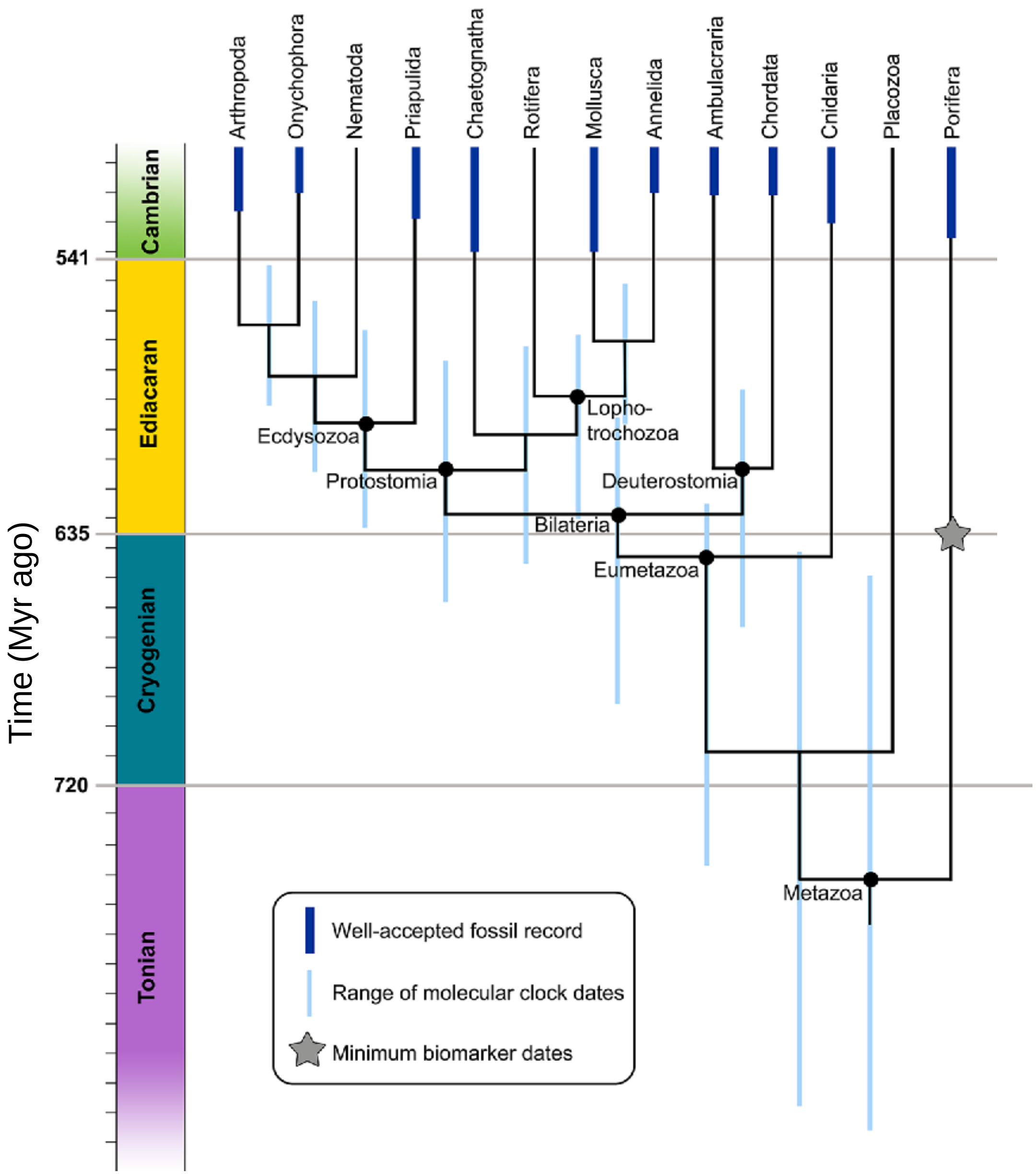

Fig. 6. Comparison between fossil (dark blue) and molecular clock (light blue) estimates for the appearance of existing animal phyla on Earth; note the large uncertainties in the latter. The star at 635 Myr shows the earliest generally accepted biomarker evidence for metazoans. Note that, as expected, the molecular clock data imply earlier origins for most phyla than their fossil record, but only by a few tens to ~100 Myr. The Eumetazoa comprise all major existing animal groups except sponges and placozoa (arguably the simplest of all living animals), and several other obscure or extinct life forms such as the Ediacaran fauna. Diagram reproduced from John Cunningham et al., “The origin of animals: Can molecular clocks and the fossil record be reconciled”, *Bioessays*, 39, 1, 1600120 (2016; open access), to which interested students are referred for further details.

This time delay is a little surprising because we might expect multi-cellular organisms to appear rapidly once sufficient cellular complexity had evolved. This was articulated by the American biologist John Tyler Bonner in his book on the evolution of complex life ("The Evolution of Complexity", Princeton University Press, 1988):

> *"If cells come together by any means, either by chance aggregation or failure to separate after division, they are in a position …. to do something which capitalises on the increased size, and which in turn may end up as selectively advantageous."*

Possibly the evolution of multi-celled animals was restrained by some external factor, such as the low level of atmospheric oxygen, or possibly animals actually arose earlier than either the fossil record or the majority of molecular clocks suggest (recall that small fossils are difficult to find, and that uncertainty remains in the calibration of molecular clocks).

The reason for the subsequent explosion of size and diversity in the Cambrian period is unknown, but could have had several (non-mutually exclusive) causes (for a review, see Douglas Fox "What Sparked the Cambrian Explosion?" *Nature*, vol. 530, pp. 268-270, 2016):

- Further rise in atmospheric oxygen, which is a prerequisite for large animals.
- Radiation into a "permissive ecology" lacking predators.
- The crossing of some critical threshold in genetic diversity permitting rapid evolutionary innovation.

4.4 Key astrobiological questions

The major events in the history of life on Earth are summarised in Fig. 7.

The major astrobiological questions resulting from this history are:

- Will life arise spontaneously on a planet such as Earth was 3.5 to 4.0 billion years ago?
- Is the evolution of cells of a eukaryotic level of complexity inevitable, or did it depend on chance events (such as the endosymbiotic incorporation of organelles)?
- Given cells of a eukaryotic level of complexity, will natural selection inevitably lead to complex, multicellular organisms?

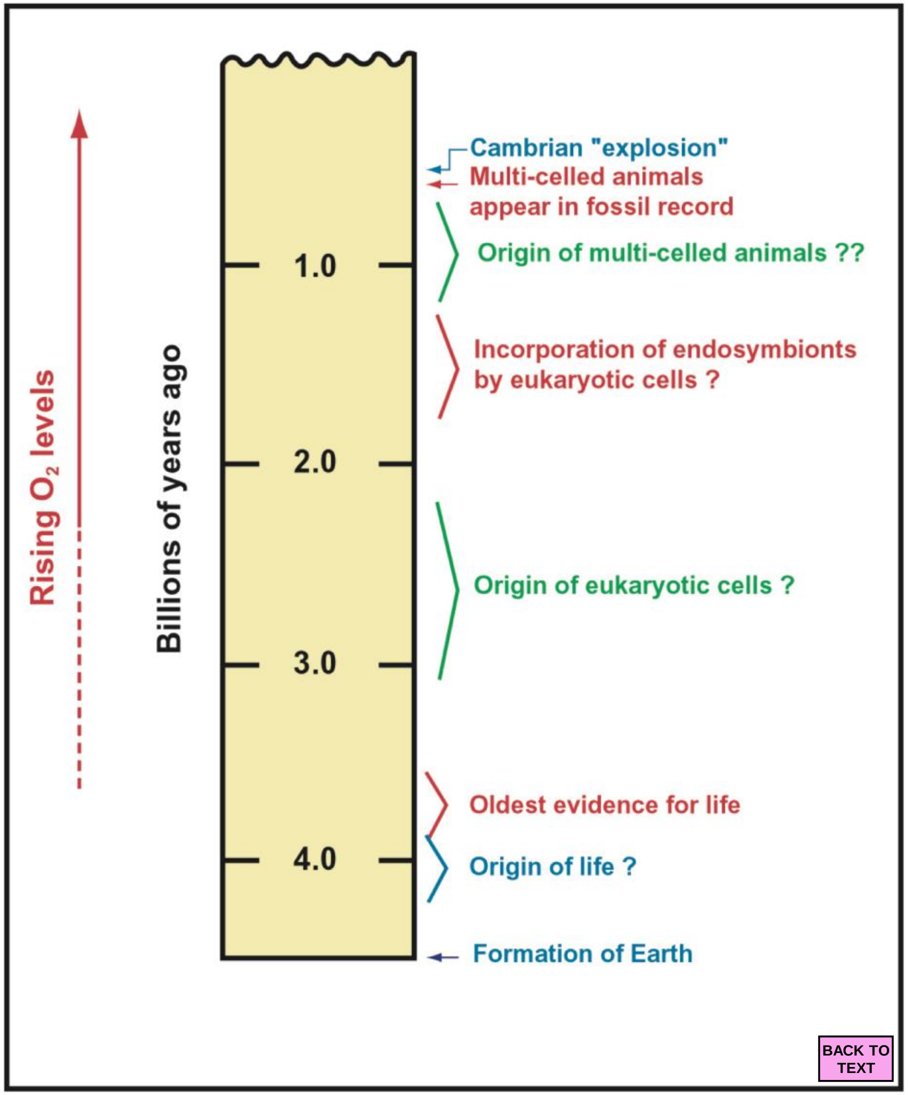

Fig. 7. Summary of the major events in the history of life on Earth.

5. Rare Earth?

Is there anything unique about the Earth as a planet which has made it especially conducive to the origin and evolution of life? There are two broad possibilities, one geological and the other astronomical:

5.1 Geological arguments for 'Rare Earth': plate tectonics

The Earth appears to be unique in the Solar System in having a system of plate tectonics, which could have influenced biological evolution in several ways:

(a) A planetary thermostat: the carbonate-silicate cycle

Plate tectonics recycles CO_2 which has become locked in carbonate rocks, as these are eventually subducted and the CO_2 returned to the atmosphere through volcanism (Fig. 8). Chemical weathering of silicate rocks by CO_2 and H_2O releases positively charged ions (cations) such as Ca^{2+} and Mg^{2+}, e.g.:

$$CaSiO_3 + 2CO_2 + H_2O \rightarrow Ca^{2+} + 2HCO_3^- + SiO_2$$

In the oceans, the cations react with carbonate ions to produce insoluble carbonates which precipitate onto the ocean floor:

$$Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + CO_2 + H_2O$$

Such reactions remove CO_2 from the atmosphere. They can be greatly aided by biology, as organisms form carbonate shells, but will also occur abiotically.

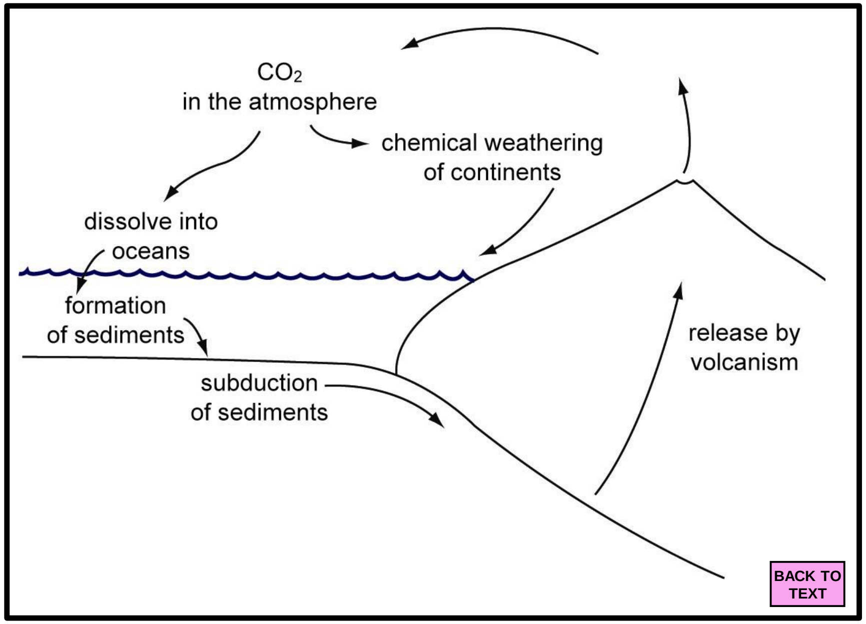

Fig.8. Schematic illustration of the terrestrial carbonate-silicate cycle. Note that it relies on the presence of both liquid water and plate tectonics.

On Earth, because of plate tectonics, these carbonates are eventually subducted, and CO_2 released back into the atmosphere, as shown in Fig. 8. Note that the rate of chemical weathering is dependent on temperature for two reasons:

- A higher temperature results in greater evaporation from the oceans, and thus more rainfall; and
- A higher water temperature increases the concentration of dissolved cations.

As a consequence, the carbonate-silicate cycle acts as a planetary thermostat: if the Earth's temperature rises, weathering rates increase, more CO_2 is locked in carbonates, the greenhouse effect is reduced, and the temperature will start to fall. Conversely, if the Earth cools down, weathering will be reduced, CO_2 will build up in the atmosphere due to volcanic outgassing, the greenhouse effect will be strengthened, and temperatures will start to rise. By this means, the Earth appears to have maintained relatively stable surface temperatures over the last four billion years, despite the gradually increasing luminosity of the Sun.

However, although plate tectonics is important for this process on Earth, it is not clear how essential it is. For example, we could envisage a situation like that shown in Fig. 9, where CO_2 is out-gassed from the deep mantle by mantle plumes (such as are responsible for intra-plate volcanism on Earth, and the large shield volcanoes on Mars and Venus).

A thermostat is still possible in this case, but without recycling it will only persist for as long as mantle reserves of CO_2 hold out.

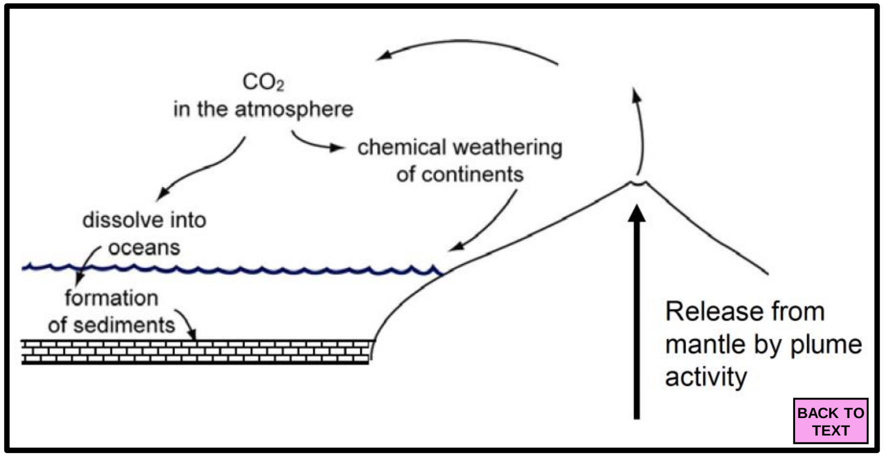

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Fig.9. An alternative view where CO_2 is supplied from mantle out-gassing and deposited on the ocean floor in thick carbonate deposits. A thermostat is still possible, but without recycling will only persist for as long as mantle reserves of CO_2 hold out.

Given that on Earth today, subduction-related and plume-related volcanism appear to contribute about equally to atmospheric CO_2 (e.g. Marty & Tolstikhin, *Chemical Geology*, 145, 233-248, 1998), it appears that a carbonate-silicate thermostat might persist oh Earth-like planets for billions of years in the absence of plate tectonics, and might last even longer 'super-Earth' type planets which appear to be common (Lecture 10).

For these reasons, it may be premature to draw the conclusion that plate tectonics is essential for the long-term maintenance of a planetary thermostat. Rather, the key requirements appear to be CO_2 out-gassing (whether due to subduction-related volcanism or not), large bodies of liquid water, an active hydrological cycle to permit chemical weathering, and possibly the presence of life to help sequester carbonates.

The latter point is often overlooked, but could be especially important in an astrobiology context. For example, it led Chopra and Lineweaver (*Astrobiology*, 16, 7-22, 2016) to propose a 'Gaian Bottleneck' to planetary habitability. Named after James Lovelock's 'Gaia hypothesis' that life on Earth may help maintain Earth's habitability, it proposes that only planets on which life arises early, and plays a major role in sequestering CO_2, will be able to establish a planetary thermostat to maintain habitability for billions of years as stars continually brighten during their main-sequence evolution.

(b) Cooling of Earth's interior

It has been suggested that plate tectonics may play an important role in transporting heat from the Earth's interior, aiding the crystallization of the inner core. This in turn plays a central role in the generation of the Earth's magnetic field, which protects the surface from cosmic radiation, and protects the atmosphere from being stripped away through collisions with the solar wind (as appears to have happened for Mars). It is true that the Earth currently has the strongest magnetic field of any terrestrial planet in our Solar System, and that this is important for habitability, but whether it really depends on plate tectonics is unknown.

(c) Other possible consequences of plate tectonics for habitability

Some other beneficial consequences of plate tectonics have been proposed, but none are as important as the possible role of plate tectonics in maintaining the carbonate-silicate cycle, and would at most only influence habitability for complex multi-cellular life rather than life *per se*:

- Build up of continental crust: Subduction-related volcanism is central to the generation of the Earth's low-density, silicic continental crust, without which there would be few, in any, exposed land surfaces for life to colonise.
- Continental drift: Plate tectonics may have helped increase biodiversity due to continental drift resulting in a wide range of changing habitats.
- Hydrothermal vents: Plate tectonics results in hydrothermal vents at the mid-ocean ridges, which, as we have seen, are potential sites of pre-biotic synthesis, and which may have been important for the origin of life. Moreover, they provide habits for some species, and may have been important as refuges at the time of heavy bombardment. However, we don't know for sure that plate tectonics was active then, and in any case plate tectonics is not a prerequisite for submarine volcanism or hydrothermal vents.

In summary, although plate tectonics is unique to the Earth in our Solar System, we don't know how common the phenomenon is likely to be on terrestrial planets elsewhere in the Universe. Nor do we know the role it may play in planetary habitability, but there are reasons for thinking that its importance may have been overestimated in the context of the 'Rare Earth' hypothesis.

5.2 Astronomical arguments for 'Rare Earth': a large Moon

Earth is also unique as a terrestrial planet in having a large natural satellite. The biological consequences of the Moon's existence can be divided into those resulting from its mode of formation, and those resulting from its continued presence.

5.2.1 Consequences of the formation of the Moon

The Moon is thought to have been formed as a result of a collision between the early Earth and a Mars-sized planetesimal during the final stages of Solar System formation. This impact is thought to have removed part of Earth' upper mantle (some of which ended up in the Moon) and likely also removed a large quantity of volatiles (e.g. H_2O and CO_2) from the early Earth. This in turn may have reduced its later susceptibility to an early runaway greenhouse effect. However, the extent of volatile loss from the Earth following the Moon-forming impact remains uncertain, with widely different estimates in the literature.

5.2.2 Consequences of the continued presence of the Moon

Once the Moon formed, its continued presence has at least two beneficial consequences for life on Earth:

(a) Stabilization of Earth's obliquity

The Moon stabilizes the Earth's obliquity, the angle between the rotation axis and a perpendicular to the plane of its orbit (Fig. 10). This angle is responsible for the seasons and currently has a value of 23.3°, about which it may oscillate by ±1.3°. It is this nearly constant obliquity which gives the Earth its stable seasons.

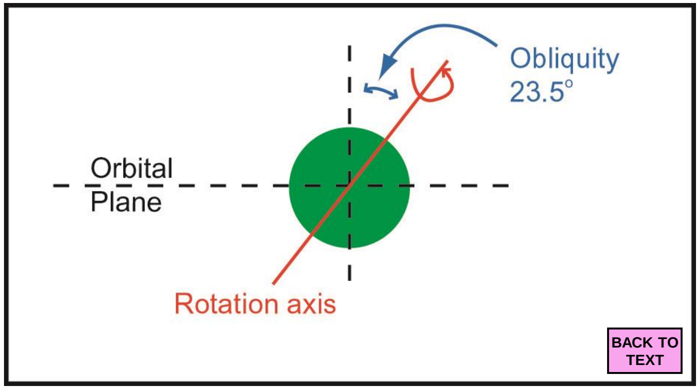

Fig. 10. Diagram to define the term 'obliquity'. The Earth's obliquity remains fairly constant due to the gravitational influence of the Moon.

Without the stabilising influence of the Moon, the Earth's obliquity would vary chaotically between about zero and 50° over timescales of a few million years, and perhaps up to 85° on longer timescales. Without the stabilizing effect of a large moon, Mars' obliquity varies chaotically in this way. While simple, unicellular, ecosystems could doubtless survive the resulting severe climatic variations, the evolution of 'higher' forms of life may have been impeded.

Note, however, that the situation isn't quite as simple as this implies. If the Earth were spinning more rapidly the its obliquity might be stable even without a larger Moon. Moreover, it is the gravitational influence of the giant planets in the outer Solar System which lead to the instability of the obliquities of the terrestrial planets in the first place – in a planetary system with different numbers and spacings of giant planets obliquity instability might be less (or more) of a problem than it is here. For an interesting discussion of this topic see the article by D. Waltham in *Astronomy and Geophysics*, vol. 48, pp. 3.22-3.24, 2007.

(b) Tides

The large tidal range of Earth's oceans is mostly due to the Moon. Moreover, the tides would have been larger in the past when the Moon was closer. By providing inter-tidal habitats the tides, and hence the Moon, may have facilitated the colonisation of the land (but this wouldn't affect the habitability of the oceans).

5.3 Astrobiological implications

Insofar as the Moon appears to have formed as a result of a chance collision, we might expect only a small fraction of terrestrial-mass planets to have a comparably large satellite. If it should turn out that such planets require both a large moon and a system of plate tectonics to support the evolution of complex, multicellular lifeforms over billions of years then these may be rare in the Universe, even if simpler, microbial, ecosystems are common. Arguably, this pessimistic conclusion is consistent with the non-detection of advanced extraterrestrial civilisations discussed in Lecture 11.