Chapter 1

The evolution of photosynthetic organisms in the oceans

The Big Bang started our universe some 14.7 billion years ago, but our planet, Earth (or Oceanus as we like to call it), was formed only 4.5 billion years ago … making it possible that life started elsewhere in the universe[1] (see the below box by John Raven). In any case, fossil evidence[2] suggests that the first life forms appeared on Earth about 1 billion years after its formation, i.e. ~3.5 billion years ago. If we favour the theory that life started on Earth (rather than on another planet), then it is commonly thought, or at least taught, that the organic compounds that eventually led to the living cells formed at the time when water vapour condensed as our planet cooled. The atmosphere was then anoxic (no molecular oxygen, O_2, was present) but contained high concentrations of carbon dioxide (CO_2) and methane (CH_3), as well as nitrogen gas (N_2), and those same conditions were also present

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[1] The fact that no one was around to witness the evolution of living organisms on Earth renders deductions only of the evolution of life as based on fossil findings[2], and are influenced also by a dust of logics and/or imagination. Also, given the enormous amount of planets orbiting the enormous numbers of stars in the (possibly) infinite number of galaxies (and perhaps also universes, i.e. our universe may be part of a multiverse), lends thought to the, we think very realistic, likelihood that life formed also elsewhere in parallel with, or before or after, life on Earth, lending thought to the possibility that primitive life forms were brought to Earth from other planets by meteorites that impacted the early Earth. These primitive organisms then evolved on our planet during the last 3.5 billion years. (See also the following box by John Raven.)

[2] We note that ~3.5-billion-year old fossils of 'bacteria-like' life forms were recently found in sandstones at the base of the Strelley Pool rock formation in Western Australia. However, such fossils often appear as rather fuzzy and must be hard to interpret as representing this or that organism.

Photosynthesis in the Marine Environment, First Edition. Sven Beer, Mats Björk and John Beardall.

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in the ponds that were in equilibrium with the atmosphere (see Box 1.1 for a glimpse into air-water equilibria), or the haze (see below), in which the first organic molecules were formed. Under those conditions, it is thought that simple organic compounds (sugars, amino acids and organic acids) were formed by chemically combining water (H_2O) with the dissolved gases CO_2, N_2 and possibly hydrogen (H_2), methane (CH_4), ammonia (NH_3) and hydrogen sulphide (H_2S). (We note with interest that C, H, O and N make up >95% of the elemental content in living organisms.) In the absence of photosynthesis (which probably developed later), the energy for forming these organic compounds came not from sunlight but from lightning, high levels of UV radiation and possibly also radioactivity, or a combination of those energy sources. That lightning could cause such gases to combine into simple organic compounds in an aquatic medium was shown experimentally in the 1950s: Stanley Miller and Harold Urey (and co-workers) showed then that organic compounds could be formed from simpler compounds believed to be present in Earth's atmosphere some 3.5 billion years ago. This was done by introducing the gases CH_4, NH_3 and H_2 into a loop of water vapour generated by boiling water; when the gas mixture passed through an electrical discharge, organic molecules were formed, and these accumulated in a cooled water trap at the bottom of the apparatus (representing the droplet, pond or ocean where life originated, see Figure 1.1). Subsequent complementary experiments have confirmed that up to 20 different amino acids, and small proteins, can be formed in a similar fashion. Amino acids were, however, also found in a meteorite that fell to Earth in 1969 (see Box 1.2 by John Raven for a discussion on alternative sites to our planet for the origins of life).

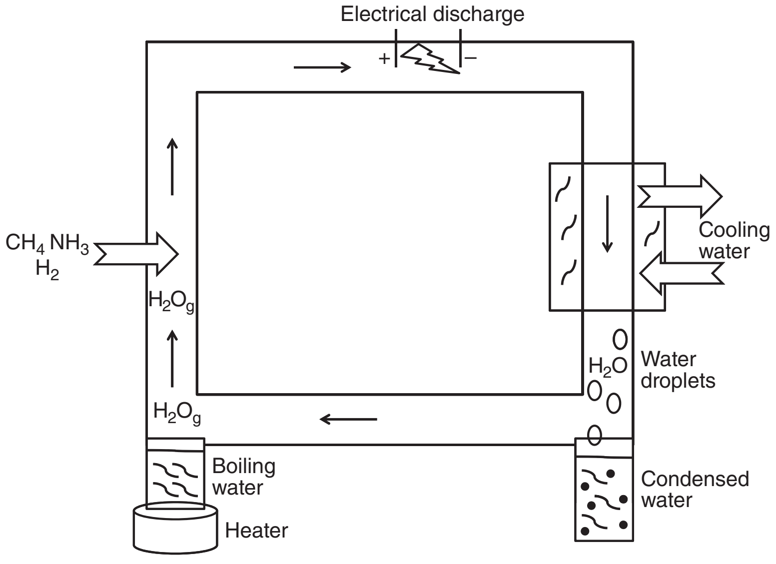

Figure 1.1 **The Miller and Urey experiment.** Gases assumed to be present in the primordial atmosphere 3.5 billion years ago were introduced into a closed glass apparatus in which they were carried in a loop of water vapour (H_2O_g) generated from boiling water (lower left). After passing through electrical discharges, the gases were cooled, and the droplets formed by condensation filled up a cup (lower right). Organic compounds (black dots) were then identified in the collected condensate. Drawing by Sven Beer.

Box 1.1 Air–water equilibria

It is unfortunate that **atmospheric** gas compositions are usually reported when discussing chemical and biochemical reactions; at least the latter always take place in **liquid media**! While the relative concentrations of dissolved gases correlate directly with those of the atmosphere (that they are in equilibrium with) according to Henry's law (e.g. a doubling of O_2 in the gas phase will cause a doubling of dissolved O_2 at air–water equilibrium at a set temperature), the absolute concentrations of gases in those two media may differ greatly. For example, while the concentration of CO_2 in seawater water is about 75% of that in air at 20 °C (on a mol per volume, or molar, basis[3]), that of O_2 is only 2.6% of that in air. Thus, the O_2 concentration in air is rather irrelevant when discussing, e.g. rates of respiration in marine organisms. Also for respiration in terrestrial organisms it is rather irrelevant to discuss biochemical processes with respect to aerial O_2 concentrations since there, too, they take place in the liquid medium of the cells (or, rather, liquid-filled cellular compartments where they occur). Thus, there may be little difference in concentrations of dissolved gases in a huge-volume oceanic water body and a small-volume cell; the latter may be seen as being a tiny ocean. (Unlike **concentrations** in air-equilibrated water bodies, there **is** a difference in **diffusivity** of, e.g. gases in small and large water bodies, but more about that in Chapter 3).

[3] Molarity will mostly be used in this book when referring to dissolved compounds (including gases). In the gas phase, percentages (or parts per million, ppm) can easily be converted to molarity with the knowledge that 1 mol of any gas equals 22.4 litres (L) (at normal conditions): micromol L^{-1} (or micromolar, μM) thus equals ppm/22.4.

Box 1.2 Life in Far Away Places

by **John Raven**, University of Dundee, UK (j.a.raven@dundee.ac.uk)

Astrobiology has developed over the last few decades as the science that considers the possibility of life elsewhere in the Universe. The subject originated in earlier speculations about life elsewhere, with such concepts as panspermia. The subject has become more firmly grounded since the discovery of planets orbiting stars other than our sun: in mid-July 2013 there are about 900 (depending on the source consulted) well-authenticated reports of exoplanets.

Consideration of life elsewhere in the universe is inevitably based on our understanding of life on Earth, i.e. LAWKI (Life As We Know It), and the limits of its occurrence. LAWKI depends on water, hence NASA's mantra "Follow the Water". The occurrence of liquid water on a planet depends on the radiant energy emitted by the parent star and the orbital distance of the planet, as modulated by factors such as the greenhouse effect of the planetary atmosphere. The solar energy output determines the habitable zone, i.e. the range of orbital distances at which liquid water can occur. Since the energy output of stars increases with time, the habitable zone moves out from the star and this gave rise to the concept of the continuously habitable zone, a narrower range of distances from the star at which liquid water could occur over times (hundreds of millions to billions of years) consistent with the origin and, particularly, the evolution of life.

Another aspect of astrobiology is the concept of the Earth-like planet, i.e. a rocky planet large enough to retain an atmosphere rather than a gas giant. The available methods for detecting exoplanets are all biased toward larger planets with small orbital distances, i.e. well inside the continuously habitable zone, so that most of the known exoplanets are not Earth-like planets in the continuously habitable zone. However, with improved means of detecting exoplanets it is likely that many more exoplanets capable of supporting life will be detected over the coming decades.

The possibility of supporting life does not necessarily mean the same as life originating and persisting on an exoplanet. While the 'seeding' of a planet with life on meteorites originating from a planet on which life has already evolved is plausible, this life must have had an origin on some Earth-like planet. Assuming that life on Earth originated here, there are two main contrasting hypotheses. One involves the production of organic monomers of nucleic acids and proteins in the anoxic atmosphere, energized by solar UV radiation or lightning, also ultimately energized by solar radiation. The other hypothesis, which I prefer, is that life originated at hydrothermal vents; here the energy comes from tectonic processes, yielding chemolithotrophic life. The retention of either of these mechanisms of supplying energy to life would not, however, provide an Earth-like planet orbiting a distant star that would produce a signature of life detectable remotely by reflectance spectroscopy from Earth.

There are two reasons for this lack of detectability. One is the low yield (biomass produced per unit time per unit area of planet) of either of the proposed mechanisms for the origin of life. The other is that there are no obvious spectral signatures necessarily produced by these modes of powering biota. The first problem is overcome by the evolution of the catalysed use of solar energy in photosynthesis, permitting primary production rates four or more orders of magnitude greater than those of either of the trophic modes suggested for the origin of life. The second problem is overcome by the basis of oxygenic photosynthesis with water as the source of reductant. Oxygen build-up occurs if, as happens on Earth, some of the organic matter generated in oxygenic photosynthesis escapes oxidation by heterotrophs and can be stored for millions to hundreds of millions of years by subduction through tectonic activity. Oxygen can be remotely detected, either directly or as ozone generated by UV radiation from the star. Since oxygen can be produced by abiological photodissociation of water, consideration of other characteristics of an exoplanet must be used to judge the biological component of oxygen build-up. As Lovelock pointed out almost 40 year ago, the evidence of life on an exoplanet based on the occurrence of oxygen is strengthened by finding thermodynamic disequilibrium in the atmosphere by the simultaneous occurrence of oxygen and (biogenic) methane.

The above arguments suggest not only that photosynthesis by organisms at the bacterial and algal level of organisation is the major means of producing a productive biosphere, but also that oxygen accumulation relying on the activities of these organisms provides the best means of the remote detection of life on exoplanets. While oxygenic photosynthesis on an exoplanet could fit most closely in the template of oxygenic photosynthesis on Earth if the planet was orbiting a G spectral type star like our G2V sun, oxygenic photosynthesis could occur on Earth-like planets in the continuously habitable zone of M stars (Red Dwarfs) with a much longer wavelength of peak photon absorption, beyond the approximately 1000-nm long-wavelength limit of photochemistry.

Substantial productivity by oxygenic photosynthesis under these conditions could take place using three photosystems rather than the two used on Earth.

Could such photosynthetic life be transferred between Earth-like planets? This could occur by an incoming meteorite chipping off a piece of rock bearing life from a planetary surface that, if it had escape velocity, could transfer life to another planet, at least in the same solar system. Cockell has argued that the transfer of life between planets in a solar system is relatively likely for heterotrophs that could occur quite deep (tens of mm or more) in the continental biosphere, and so would not be killed by heating of the surface of the meteorite during entry to the receiving planet's atmosphere. This means of escape from thermal sterilization would be much less likely for the necessarily surface-located photosynthetic organisms. Transfer of even heterotrophic life between solar systems is much less likely.

It is often stated that the simple organic compounds synthesised before the evolution of photosynthesis were formed in rainwater ponds rather than in the seas, possibly because the former were shallow enough for their whole water bodies to be affected by lightning energy. A more recent theory, however, has it that these organic compounds were formed in a mist, or 'organic haze', generated as gases such as N_2 mixed with the condensing water vapour, that then precipitated into the primordial (or Archaean) ocean. In parallel with organic compounds being formed in ponds or hazes some 3.5 billion years ago, Earth cooled and atmospheric water vapour condensed into rains that started to fill up the oceanic basins. (On the way to the oceans, the water also carried with it minerals, the salts of which made the seas salty.) Thus, it is thought that the organic compounds were washed from the ponds, or precipitated from the hazes by the rains, to the sea. There, in what is sometimes termed the 'primordial soup' or 'pre-biotic broth', they aggregated to form primitive cells containing more complex organic compounds surrounded by a lipid-based membrane, and developed metabolic processes and the ability to reproduce (through division) and pass down their properties to the daughter cells, all of which are characteristics of what we call life. These simple cells were thus the first life forms on our planet, and with time they developed and evolved into more complex organisms in the seas, and much, much later on land (see Figure 1.2).

It is thought that during the first 0.1 billion (100 million) years of life on Earth, the primitive cells drifting around in the early seas supplied their metabolic needs by feeding on the organic compounds washed (or precipitated) into the sea. Since, again, photosynthesis probably was absent at that time (and the organic 'foods' present in the seawater were the products of combining the primordial gases through lightning energy), these cells were, by definition, **heterotrophs**[4] (see Box 1.3). As they multiplied, a new factor came into play: competition; and as their multitude diluted their

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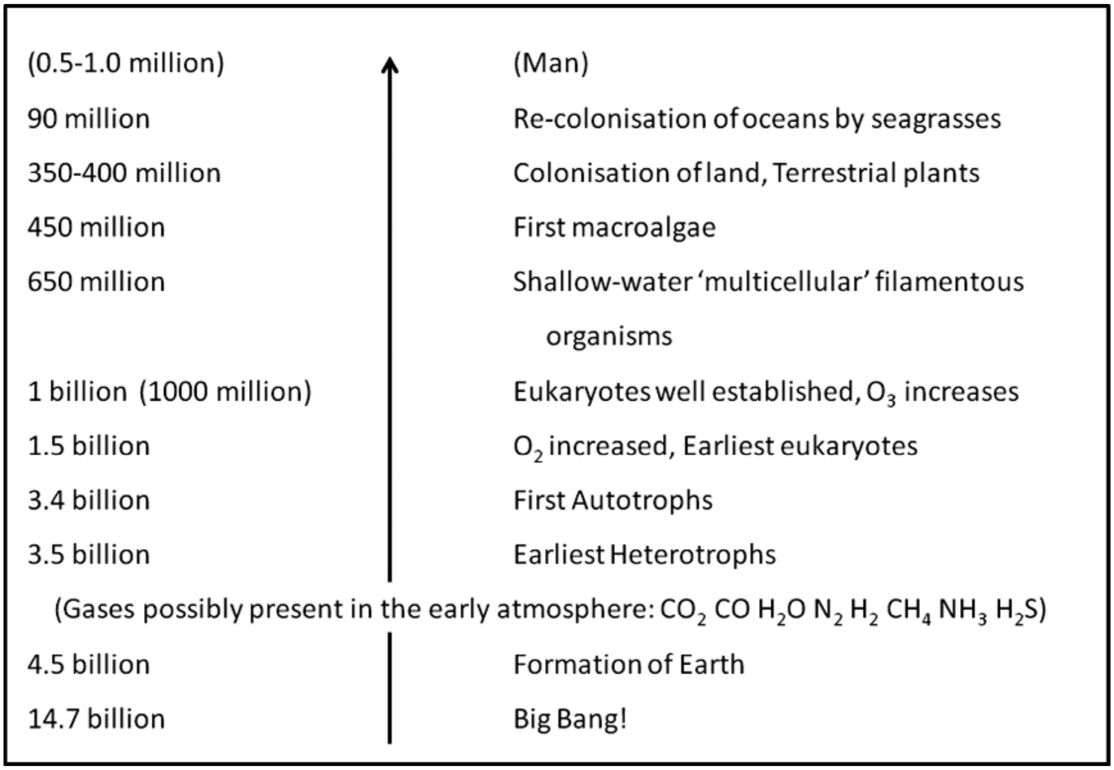
[4] **Heterotrophs** (hetero = other; troph = feed/feeder) are those organisms that need to feed on high energy containing organic compounds for their metabolic energy needs; these are today typically represented by most of the bacteria, fungi and animals. On the other hand, **autotrophs** (auto = self; troph = feed/feeder) are those organisms that can synthesise their own food from low energy containing inorganic compounds, mainly through photosynthesis (the **photoautotrophs**, though some, the **chemoautotrophs**, use oxidation of reduced forms of elements as an energy source instead). The photoautotrophs are today typically represented by some of the bacteria (the cyanobacteria) and the plants (including algae) (see however exceptions in Box 1.3).



(0.5-1.0 million)	(Man)
90 million	Re-colonisation of oceans by seagrasses
350-400 million	Colonisation of land, Terrestrial plants
450 million	First macroalgae
650 million	Shallow-water 'multicellular' filamentous organisms
1 billion (1000 million)	Eukaryotes well established, O_3 increases
1.5 billion	O_2 increased, Earliest eukaryotes
3.4 billion	First Autotrophs
3.5 billion	Earliest Heterotrophs
(Gases possibly present in the early atmosphere: CO_2 CO H_2O N_2 H_2 CH_4 NH_3 H_2S)	
4.5 billion	Formation of Earth
14.7 billion	Big Bang!

Figure 1.2 **A plausible time-line of life's evolution on our planet** shows that, e.g. heterotrophs may have formed before autotrophs, prokaryotes (bacteria) were present for most of the time that life has existed on our planet (2–2.5 billion years), the increase in O_3 (formed from photosynthesis-derived O_2) allowed for eukaryotic filamentous algae to grow in shallow water, seagrasses re-invaded the shallow seas after their forefathers had been on land for several hundred million years and, if evolution is visualised on a 24-h clock (and after some calculations), man appeared ½ min before midnight. Comprised by Sven Beer.

source of organic 'foods', there developed an advantage to those that could generate their own food out of inorganic chemicals. This ability evolved into what we know today as **photosynthesis**, i.e. the capability to utilise sunlight as an energy source in order to form high-energy-containing organic compounds (primarily sugars) out of low-energy inorganic compounds (largely CO_2 and water). Those later organisms were thus **autotrophs**[4], and they appeared on Earth ~100 million years after the first heterotrophic cells (i.e. ~3.4 billion years ago).

Relative to the time it took for autotrophic cells to evolve from heterotrophic ones (0.1 billion years), it took much longer (~2 billion years) for cells to evolve from being **prokaryotic**[5] to becoming **eukaryotic**[5], and this happened through the process of **endosymbiosis** (see Box 1.4). During this time the process of photosynthesis became well

[5] Karyos = nucleus and, accordingly, the **prokaroytes** lack nucleus (pro- = before) while the **eukaroytes** feature a well-defined nucleus in their cells (eu- = good/well). Today, the bacteria are prokaryotic, while all other organisms are eukaryotic. Incidentally, as we all know, the nucleus contains the hereditary basis of the eukaryotic cells and organisms in the form of linear DNA. In contrast, the prokaryotes have their DNA arranged in circular molecules.

Box 1.3 Autotrophs and heterotrophs

The term **autotroph** is usually associated with the photosynthesising plants (including algae and cyanobacteria) and **heterotroph** with animals and some other groups of organisms that need to be provided high-energy containing organic foods (e.g. the fungi and many bacteria). However, many exceptions exist: Some plants are parasitic and may be devoid of chlorophyll and, thus, lack photosynthesis altogether[6], and some animals contain chloroplasts or photosynthesising algae or cyanobacteria and may function, in part, autotrophically; some corals rely on the photosynthetic algae within their bodies to the extent that they don't have to eat at all (see Section 7.2). If some plants are heterotrophic and some animals autotrophic, what then differentiates plants from animals? It is usually said that what differs the two groups is the absence (animals) or presence (plants) of a cell wall. The cell wall is deposited outside the cell membrane in plants, and forms a type of exo-skeleton made of polysaccharides (e.g. cellulose or agar in some red algae, or silica in the case of diatoms) that renders rigidity to plant cells and to the whole plant.

[6] Most plants also contain organs that are heterotrophic (e.g. roots, which exist largely in darkness, as well as flowers and fruits, and holdfasts and sporangia in the algae, etc. However, the organism they belong to (i.e. a plant or alga) is as a whole, of course, most often autotrophic.

Box 1.4 Endosymbiosis

The theory of serial endosymbiosis is a major evolutionary step-ladder that is deeply woven into the fabric of our understanding of the origins of eukaryotic organisms. Central to this is the concept, propounded especially by Lynn Margulis, that the chloroplast and mitochondrion originated from prokaryotes that were engulfed by an ancestral phagocytotic heterotroph. The sequence of events involved is illustrated in Figure 1.3 and can be described thus (the different stages are also numbered in the figure):

1. An ancestral cell-wall-less prokaryotic cell (pale grey circle) started to develop a complex set of internal membranes around the DNA, giving rise to a primordial nucleus, and forming other organelles of the endomembrane system such as the endoplasmic reticulum, Golgi and lysosomes. At the same time, evolution of a cytoskeleton allowed this primitive cell to control flexing and in-folding of the plasma membrane.
2. This primitive phagocytotic cell (which now, with a membrane-bound nucleus, could be thought of as an ancestral eukaryote) was able to engulf bacteria (white oval with dashed border), some of which became established as endosymbionts, eventually passing on some of their DNA to the host's nucleus and becoming what we now see as mitochondria.
3. The ancestral heterotrophic eukaryote could then engulf photosynthetic bacteria (i.e. cyanobacteria; black oval in 3). Some of the latter became established in the host and, as with mitochondria, lost a large part of their DNA to the host nucleus. These endosymbionts became chloroplasts.

Although the engulfed prokaryotes gave up much of their DNA to the host nucleus, the fact that many genes are retained in a circular DNA genome within the mitochondria and chloroplasts is a strong testament to the evolutionary origins of these organelles.

4. The serial endosymbiotic theory does not stop here: What is described above is the process of primary endosymbiosis; chloroplasts initially arose when a host cell engulfed a cyanobacterium. Consequently, the chloroplasts that evolved from this process are bound by an envelope based on two membranes. Such 'primary plastids' are found in the green algae (and their descendants, the higher plants), in the red algae and in a group of algae called the glaucophytes, though whether these represent different primary endosymbiotic events or originated from a common ancestor is vigorously debated. However, many algal lines developed from further secondary endosymbiotic events where the ancestral eukaryote engulfed another alga. Plastids such as these are found in the haptophytes, cryptomonads, and in many dinoflagellates, euglenoids and stramenopiles giving rise to chloroplasts with three (e.g. euglenoids and dinoflagellates) or four (e.g. diatoms) envelope membranes (5 in Figure 1.3).

   Estimates for the timing of the primary endosymbiosis suggest that this must have occurred prior to 1.6 billion years ago. The earliest likely date for the secondary endosymbiosis, in which a non-photosynthetic 'protist' captured a red algal plastid (step 4 in Figure 1.3), is ~1.3 billion years ago (see the reference of Yoon, Hackett, Ciniglia, Pinto and Battacharya, 2004), though algal groups such as the diatoms evolved much more recently (<250 million years ago).

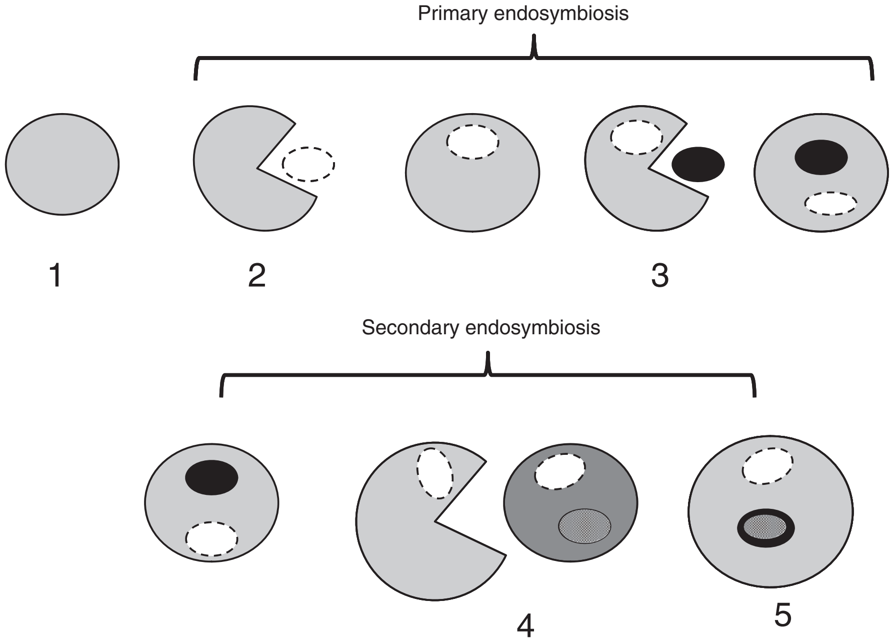


Figure 1.3 **The endosymbiotic evolutionary origin of mitochondria** (white oval, dashed border) **and chloroplasts** (black or hatched ovals) in algae and 'plants'. See text for details. Drawing by John Beardall.

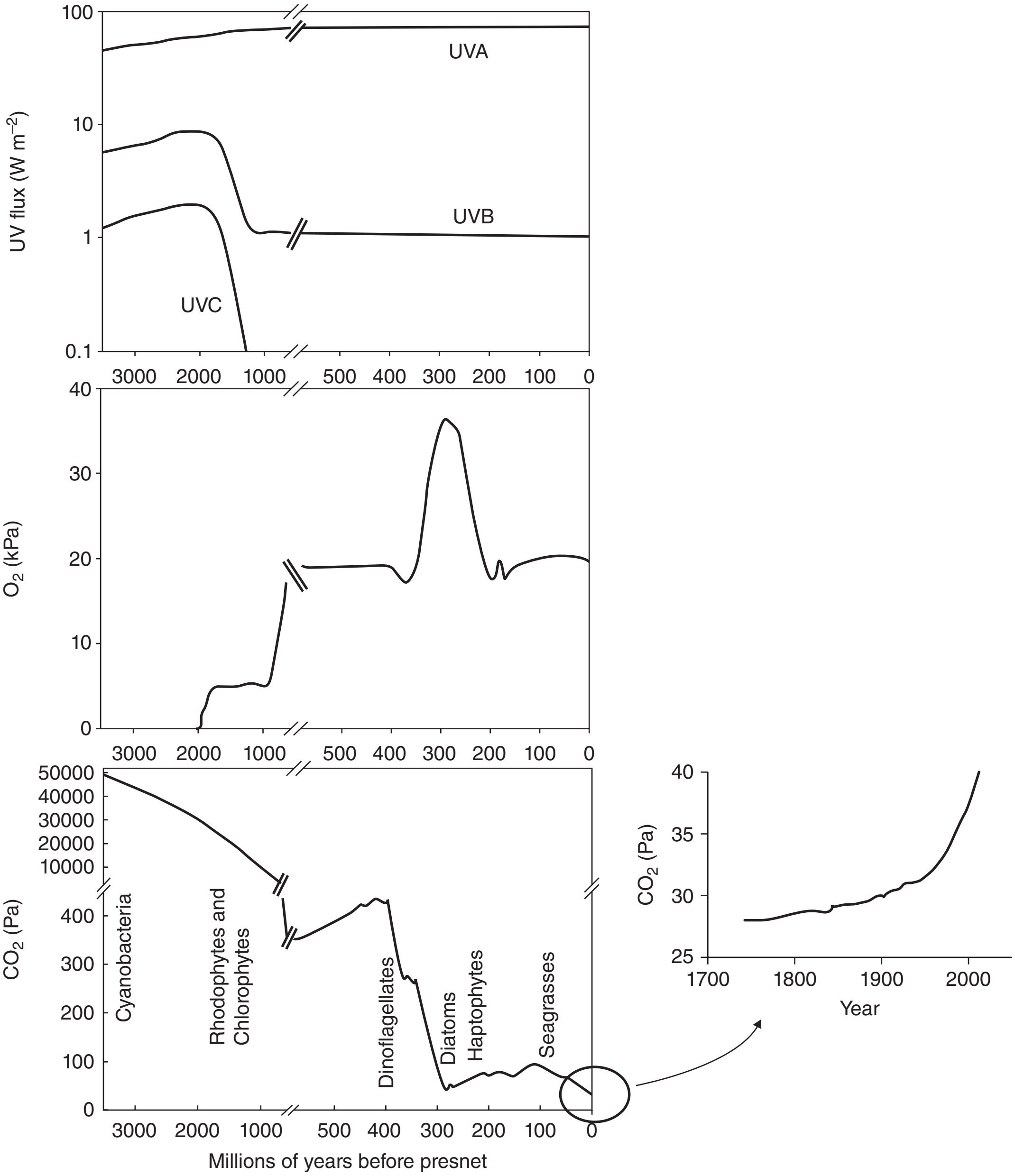


Figure 1.4 **Changes, in geological time, in UV radiation** (upper panel; UVA, 320–400 nm; UVB, 280–320 nm; UVC, 200–280 nm)**, atmospheric oxygen** (O_2, middle panel) **and atmospheric carbon dioxide** (CO_2, lower panel); the unit Pascal (Pa) equals close to 10 ppm at standard temperature and pressure. Also indicated in the lower panel are the approximate evolutionary origins of major marine 'plant' groups. The inset shows trends in atmospheric CO_2 over the last 250 years. Adapted from: Beardall J, Raven JA, 2004. The potential effects of global climate change on microalgal photosynthesis, growth and ecology. *Phycologia* 43: 26–40. Copyright (2013), with permission from Allen Press Publishing Services.

established as the ultimate way of forming high-energy organic compounds, as did that of respiration, the most efficient form of which relied on a by-product of photosynthesis: molecular oxygen (O_2); this type of respiration is also called oxidative respiration. As photosynthesising organisms multiplied and evolved, O_2 levels slowly rose in the atmosphere, transforming it from a reducing to an oxidising one. While such an atmosphere indeed is favourable for oxidative respiration, it inhibits photosynthesis of most terrestrial plants (but more about that in Chapter 6).

This is not a book on evolution, so that subject is dealt with only briefly as it pertains to the evolution of marine photosynthetic organisms. During the first 2 billion years of organisms' evolution on the planet, levels of O_2 derived from photosynthesis rose in the oceans as well as in the ocean-equilibrated atmosphere (again, see Box 1.1). This led to the formation and successive accumulation of ozone (O_3) in the upper atmosphere, which protected both the prokaryotic (which ruled the seas during 2 billion years) and eukaryotic (which became well established ~1 billion years ago) cells from part of the harmful UV radiation present in the upper water layers. Consequently, the unicellular organisms could move up in the water column towards surface waters, the higher irradiances of which further favoured photosynthesis (especially of eukaryotic phytoplankton, which generally utilise higher irradiances than cyanobacteria, see Section 9.3). At the same time, competition to obtain both organic (for the heterotrophs) and inorganic (for the autotrophs) nutrients increased as the cells multiplied and resources, accordingly, became scarcer. For the autotrophs, this meant that there was an advantage if they could live close to the shores where inorganic nutrient concentrations were higher (because of mineral-rich runoffs from land) than in the upper water layer of off-shore locations. However, living closer to shore also meant greater effects of wave action, which would alter, e.g. the light availability on shorter than diel-term frequencies. Under such conditions, there would be an advantage to be able to stay put in the seawater, and under those conditions it is thought that filamentous photosynthetic organisms were formed from autotrophic cells (*ca.* 650 million years ago), which eventually resulted in macroalgae (some 450 million years ago) featuring holdfast tissues that could adhere them to rocky substrates. (While most of today's 'macroalgae' are eukaryotic, there are also cyanobacterial filaments that stick to bottom substrates, see Section 2.1.)

Very briefly now, the green macroalgae were the ancestors of terrestrial plants, which started to invade land *ca.* 400 million years ago (followed by the animals). It is interesting (and logical) to note that the successful plant invasion of land caused an increased rate at which O_2 levels rose in Earth's atmosphere (see Figure 1.4). Long after terrestrial plants were established, there was an interesting (especially to SB and MB) secondary re-invasion of some grasses back to the marine environment which (luckily for us that study them), some 90–100 million years ago, gave rise to the seagrasses (see Section 2.5).