Chapter 1

Process, form and pattern

. . . an autopoietic system is a homeostat . . . a device for holding a critical systemic variable within physiological limits . . .: in the case of autopoietic homeostasis, the critical variable is the system's own organization. It does not matter, it seems, whether every measurable property of that organizational structure changes utterly in the system's process of continuing adaptation. It survives.

S. Beer, 1980

1.1 Living at the edge of chaos

This chapter provides a short history of the pre-biotic Earth and of organisms in the early stages of the evolution of life. It covers the origins of photosynthetic organisms, the setting of the stage for the evolution of plants and terrestrial ecosystems, and for the subsequent diversification of plants from the Silurian Period onwards. Key early events are the evolution of metabolism, including photosynthesis, of mechanisms of heredity and of cells. Later symbiotic associations between cells provide a much broader canvas for life-forms to diverge. Other important stages in the evolution of plants were the origin of multicellularity and subsequently the functional specialisation of cell types in the multicellular organism.

Process, form and pattern are three primary features of living systems. In this section we focus individually on each of these primary criteria of life. Process first, concentrating on the origin of the processes fundamental to life, and particularly to plants – photosynthesis. Then we focus on form, by describing some key aspects of the evolution of complex cells. Finally we look at pattern – cells together in multicellular organisms.

Using musical metaphors we trace in this section the origins of life from the white noise of chaos to the full symphony of life. The first notes of life are the complex molecules and beating out with the drum of metabolism. At first the noise is cacophonous as if the orchestra is tuning up, but with the origin of cellular life, coordinated metabolism arises, like snatches of melodies. Gradually at first, but then more and more speedily, as the rhythms of cellular life assert themselves, the first snatches of melody grow louder against the cacophonous background. Simple melodies are taken up and repeated in counterpoint as the seas and lakes become populated with living organisms, some complex and multicellular. Later symbiotic associations between cells, like the origin of musical harmony, provide a much broader potential for new life forms to diverge. The origin of multicellularity and subsequently the functional specialisation of cell types in the multicellular organism enrich the sound. At the margin of land and water some of these themes were to be taken up and elaborated by the first plants.

1.1.1 The pre-biotic Earth

The probability of life evolving is so small that is seems impossible, yet in the aeons that passed from the formation of the Earth the almost impossible became the probable. The key to understanding this distant past is in the present. All life is built on what has gone before and in order to understand how life evolved we must study the common metabolic processes that connect all living organisms, but we have to seek life's origins in processes of chemical evolution that occurred on the pre-biotic Earth.

Geological eras	Dates started (millions years ago)
Cenozoic	65
Mesozoic	250
Palaeozoic	570
Sinian	800
Riphean	1650
Animikean	2200
Huronian	2450
Randian	2800
Swazian	3500
Isuan	3800
Hadean	4650

The Earth is at least 5 billion years old and has been changing all the time. About 4.6 billion years ago, and for about 1 billion years thereafter, our planet was cooling and an atmosphere consisting of hydrogen and helium, and continental crust was forming. Then about 3.5 billion years ago the stage was set for the grandest chemical experiment, that was to create life.

At this stage the world was a huge laboratory test-tube and was constantly subjected to intense electrical storms, meteoric impacts and volcanic eruptions, and, because the Earth was not shielded by the oxygen-rich atmosphere that we have now, it was bombarded by ultra-violet (UV) and gamma radiation. There was a steady input of molecules from the out-gassing of volcanoes. There was also the input of complex molecules based on carbon (organic molecules) from meteorites. The steady intense energy of radiation and the cataclysms of storms and volcanic eruptions forced chemical elements to combine or compounds to break apart, setting off a myriad tiny fireworks, and sparked life into being. These chemical reactions were orderly, determined by the atomic structure of the elements and they happened again and again so that the products of particular reactions became more and more abundant.

It was hot because of high levels in the atmosphere of carbon dioxide (CO_2) and methane (CH_4) produced by volcanic activity. Hydrogen, hydrogen sulphide, hydrogen cyanide and formaldehyde were also present. These conditions have been replicated in the laboratory in

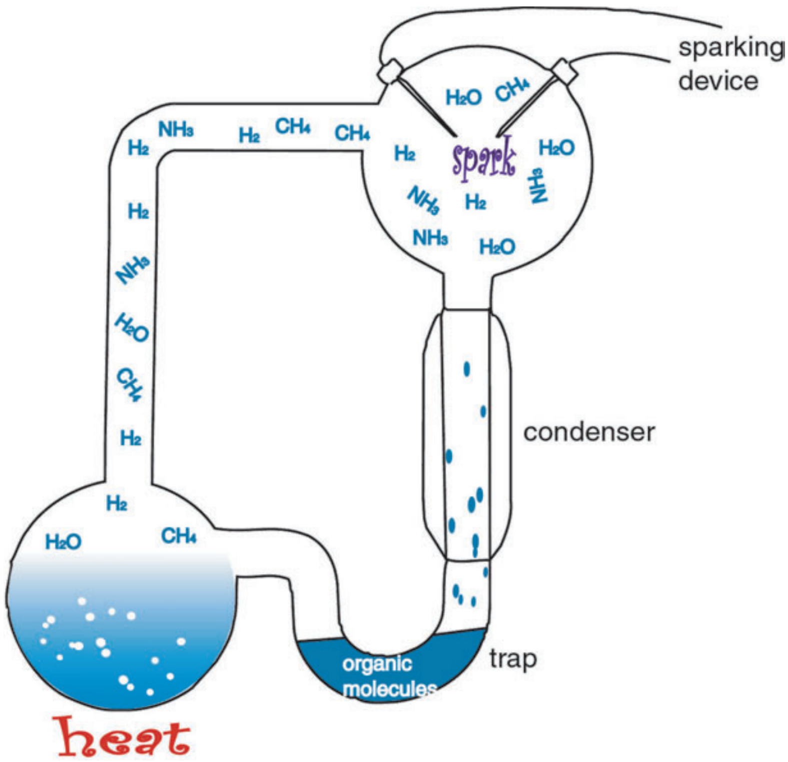

Figure 1.1. The Miller/Urey experiment. A continuous electric current was passed through an 'atmosphere' of methane (CH_4), ammonia (NH_3), hydrogen (H_2), and water (H_2O) to simulate lightning storms. After a week 10%–15% of the carbon was now in the form of organic compounds including 2% in amino acids.

the classic Miller/Urey experiment (Figure 1.1). Gradually more stable and more complex compounds were produced and accumulated but this was not yet life. For that a level of complexity had to be achieved that was self-sustaining and growing.

A vital component of the living mixture was the most important compound to accumulate at this early stage, water. It was almost the most simple molecule, made from a single oxygen atom and two hydrogen atoms. Together with other gases such as ammonia and methane, water formed in the atmosphere, and began to fill the pre-biotic ocean basins. The oceans were very warm, slightly acidic and rich in dissolved ferrous ions (Fe^{2+}), carbon dioxide (CO_2) and bicarbonate ions (HCO^-). A continuous process of chemical evolution led to a great diversity of molecular species that formed compounds possessing emergent properties not possessed by their constituent elements. For example, water has the properties of a liquid not possessed by either of the gases oxygen or hydrogen. Indeed water is a pretty unique liquid and life without water is only conceivable in science fiction.

Water has remarkable properties because although it is a very small molecule it has a very strong polarity from an uneven distribution of positive and negative charge, giving it a kind of stickiness. Consequently water molecules tend to join loosely together and stick to other charged atoms or molecules. Since the hydrogen atoms in the water molecule are involved this is called hydrogen bonding. Strong

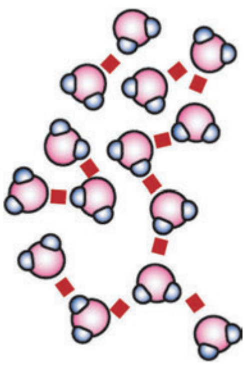

Figure 1.2. The asymmetric arrangement of hydrogen atoms leads to an unequal distribution of charge across the water molecule and attraction between the hydrogen atom of one molecule and the oxygen of another.

hydrogen bonding makes water an excellent solvent. In aqueous solution ionic compounds break down into their constituent ions each surrounded by a halo of water molecules.

Other polar molecules also dissolve readily in water. Water also takes part in many chemical reactions. By condensation large organic molecules, made up of a skeleton of carbon and hydrogen, are built up through the formation of a covalent bond and the elimination of water. Large organic molecules can also be broken down by the addition of water as covalent bonds are split by hydrolysis. As more complex compounds accumulated and became more concentrated, their formation and destruction established the first elements of living metabolism, the constant cycle of building and breaking, anabolism and catabolism, the work of life.

The stickiness of water also gives it remarkable physical properties. It has a high heat capacity so that it buffers aqueous systems from large temperature changes. In addition, as liquid water evaporates it cools the remaining liquid; and when it freezes the water molecules form an ice lattice taking up more space so that ice floats providing an insulating blanket. Water had a profound influence on the origin of life not only at the smallest scale, that of metabolism, by influencing chemical interactions between atoms and molecules, but also at the largest scale, that of the whole Earth, by buffering it from temperature extremes.

1.1.2 Complex molecules and self-organisation

The conditions on Earth before life began favoured the progressive evolution of complex molecules that had the ability to self-organise and replicate. These precursors of living chemical systems must have been stable, with the ability to correct replication errors. They must also have been capable of inheriting favourable replication errors. The ability to change over time became established, and, in this respect, these molecules are quite unlike non-living matter. Self-replication is a catalysed reaction, and catalytic cycles play an essential role in the metabolism of living organisms. In its simplest form, a living system may be modelled as an autocatalytic chemical cycle, but these self-organising molecules can hardly be called *living* because they are limited by factors that are independent of the catalytic process.

Living systems can maintain their existence in an energetic state that is relatively stable and far from thermodynamic equilibrium. They have been called dissipative structures by Ilya Prigogine. In contrast, thermodynamic equilibrium exists when all metabolic processes cease. These hypothesised dissipative systems must have possessed multiple feedback loops in the manner of catalytic cycles, what have been termed ‘hypercycles’ by Manfred Eigen. Hypercycles are those loops where each link is itself a catalytic cycle. Almost every pathway is linked to every other pathway in some way. As chemical instabilities originate the system is pushed farther and farther away from equilibrium until it reaches a threshold of stability. This hypothetical point is called the bifurcation point and it is at this stage that increased complexity and higher levels of organisation may emerge spontaneously.

If we apply the above ideas to living systems we can also say that living systems exist in a poised state far from equilibrium in that boundary region near 'the edge of chaos'. Evolution may favour living systems at the edge of chaos because these may be best able to coordinate complex interactions with the environment and evolve. In such 'poised' systems most perturbations have small consequences because of the system's homoeostatic nature but occasionally some cause larger cascades of change.

Living systems can be conceptualised as maintaining such hypercycles, thus allowing for evolutionary change without loss of the cyclic processes themselves. Living organisation is manifested therefore, not in the properties of its components, but in processes and relations between processes, as realised through its components, and in the context of the environment. Matter and energy continually flow through it but it maintains a stable form through self-organisation. This self-making characteristic of living systems has been termed 'autopoietic' by Humberto Maturana and Francisco Varela. Paraphrasing the cyberneticist Stafford Beer quoted at the beginning of the chapter, every measurable property of the system may change while it maintains itself. It is its continuation that is 'it'. Autopoiesis is a network of production processes in which the function of each component is to participate in the production or transformation of other components in the network. In this way the entire network continually 'makes itself'; the product of the operation is its own organisation. It becomes distinct from its environment through its own dynamics. It is in this context that we can recognise the three criteria of life: pattern, form and process.

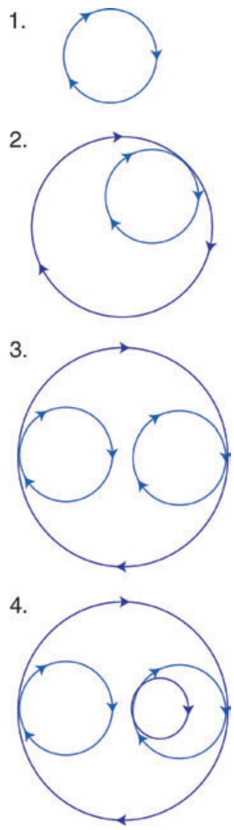

Figure 1.3. Four stages in the evolution of a hypothetical hypercycle: each loop represents a catalytic cycle like the citric acid cycle, or the production of a series of autocatalytic enzymes.

Autopoiesis = the process by which an organisation produces itself.

One of the best examples of an autopoietic system is the complete set of genes in an organism, the genome, which forms a vast interconnected network, rich in feedback loops, where genes directly and indirectly regulate each other's activities. At its simplest in transcription and translation the DNA sequence of genes provides the template for an RNA sequence (transcription) that codes for a polypeptide (translation) that may be required for either the processes of transcription or translation, or even DNA replication. But it is much more complex than that. The genes are only a part of a highly interwoven network of multiple relationships mediated through repressors, depressors, exons, introns, jumping genes, enzymes and structural proteins, constantly changing, evolving.

The autopoietic gene system does not exist in isolation but as part of the autopoietic living cell. The bacterial cell is the simplest autopoietic system found in nature, though it is hugely complex. Simpler autopoietic structures with semi-permeable membranes (but lacking a protein component) may have been the first autopoietic systems before the evolution of the cell. The evolution of autopoiesis was undoubtedly a landmark in the history of the Solar System, but almost 1 billion years were to elapse before the evolution of the first cells and the beginning of life at about 2.5 billion years ago.

1.1.3 The RNA world

A protobiological system (called a ‘chemoton’ by Tibor Ganti) should consist of a minimum of three sub-systems: a membrane, a metabolic cycle, and some genetic material. In the development of primordial living systems some sort of compartmentalisation such as a vesicle was necessary.

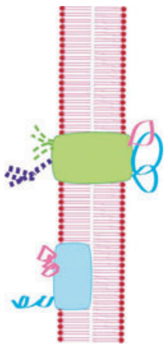

Figure 1.4. A bi-lipid membrane showing the hydrophilic heads situated on the surface of the membrane and the hydrophobic tails in the middle of the membrane. Various proteins float in or on the membrane.

Lipids and nucleic acids are complex organic molecules in which carbon-based chains form the main structural components. Carbon atoms have an outstanding capacity to combine with each other and with other kinds of atoms to produce an unlimited morphological diversity of molecules. A key feature must have been vesicles formed from fatty acids. Fatty acids are organic molecules with a long water-repellant (hydrophobic) hydrocarbon tail and a hydrophilic polar head. They orientate with their tails together and the heads towards water, and consequently form globules or two layered sheets called membranes. Membranes provide the outer layer of vesicles. At the earliest stages of life membrane-bound vesicles probably formed in shallow tidal pools as a consequence of repeated cycles of desiccation and rehydration. Only certain molecular species possessed the necessary characteristics for living systems; of forming membranes sufficiently stable and plastic to be effective barriers and to have changing properties for the diffusion of ions and molecules. Such membranes were necessary for the formation of organic molecules such as nucleotides that had the potential to act as catalysts and to replicate.

Because of some extra properties of the membrane, imparted by other molecular components floating in it, vesicles can contain a solution with a different chemical constitution to the surrounding aqueous solution. They are semi-permeable, completely permeable to water and some other small molecules, but less permeable to other molecules, so that they can encapsulate and keep large molecules concentrated.

Reactive molecules are called radicals. The appearance of autocatalytic networks of carbon-based radicals, containing one carbon atom (plus hydrogen, oxygen and nitrogen) and organic compounds such as sugars and acids could lead to the evolution of simple enzyme-free metabolic pathways. However, the synthesis of more complex potentially replicating chemical compounds is problematical. It is now thought that the early evolution of life was dominated by the nucleic acid RNA, and that the original genetic material was an RNA analogue. Like DNA, RNA is a series of four different nucleotide bases strung together; differences in the sequence of bases, the four-letter alphabet, gives limitless variation in the molecule, providing a language. RNA also has catalytic properties. For the evolution of RNA to occur, some sort of intermediary mechanism must have occurred within the vesicle, for example, a polynucleotide analogue of RNA could have been replicating within chemoton-like systems.

One key feature of the nucleic acids like RNA and DNA is their ability to splice together; parts of the molecule can be looped out or into the sequence of bases. The parts of the sequence excised are called introns and those spliced together exons. Thus, in the evolution of life before the emergence of bacteria, we envisage an 'RNA world' where some molecules are active enzymes, others contain introns and exons and convert themselves, either to RNA by self-splicing, or recombine to yield novel combinations by trans-splicing. Subsequently DNA took the replication and information-storing role, and proteins the catalytic role, and RNA was left as an intermediary. In our 'DNA world' proteins have taken over almost every catalytic activity.

In a chemical system change is likely to extinguish a chemical reaction, but a living system has the potential to change without destroying the circular processes that makes its components. There is change because self-replication is not perfect and slightly different but stable daughter molecules are sometimes produced, but the living system continues to replicate instead of spluttering to a halt. The system could evolve because some of these altered daughter molecules had an improved ability for autocatalysis as if they 'remembered' the changes that brought them about. This was the birth of inheritance. With the combination of self-regulating hypercycles and inheritance, the brake was taken off chemical evolution and new kinds of metabolism evolved.

Creativity, the generation of novelty, is a key property of all living systems. A special form of creativity is the generation of diversity through reproduction, from simple cell division to the highly complex dance of sexual reproduction. Driven by the creativity inherent in all living systems the life of the planet diversified in forms of ever-increasing complexity.

> Life emerged, I suggest, not simple, but complex and whole, and has remained complex and whole ever since – not because of a mysterious élan vital, but thanks to the simple profound transformation of dead molecules into an organization by which each molecule's formation is catalyzed by some other molecule in the organization. The secret of life, the wellspring of reproduction, is not to be found in the beauty of Watson–Crick pairing, but in the achievement of collective catalytic closure. So, in another sense, life – complex, whole, emergent – is simple after all, a natural outgrowth of the world in which we live.
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> Stuart Kauffman, *At Home in the Universe*, Oxford University Press 1995 pp. 47–48.

1.1.4 How to recognise a living system

The age of the microcosm lasted (from about 3.5 billion years ago) for about 2 billion years, during which time many of the metabolic processes essential to life evolved. These processes include fermentation, nitrogen fixation, and oxygenic photosynthesis, the most important single metabolic innovation in the history of life on the planet. About 1.5 billion years ago self-regulation of the biosphere and an oxidising atmosphere were established, setting the stage for the evolution of macrocosmic life.

It is the traces of patterned cellular structure in rocks (and chemical processes in sediments and atmosphere) that provide the first hard evidence for the presence of life. The earliest traces date back to the early Archaean age 3500 million years ago from several parts of the world. The fossils are recognisable because they are composed of alternating dark and light layers of sediment. The fossil structures can be understood by reference to living stromatolites, 'living' rocks found in shallow water that grow in layers consisting of alternating

Figure 1.5. Stromatolites in Laguna, NE Mexico. Changes in lake level here exposed them above the surface of the water.

mats of photosynthetic microbes, cyanobacteria, and precipitated calcium carbonate. The cyanobacterial mats trap sediment and the photosynthetic activity of these microbes precipitates a layer of calcium carbonate on top. Eventually the microbes establish a new living layer on top of the calcium carbonate layer. The alternating light and dark bands of fossil stromatolites are the earliest evidence of a living process. The living examples, discovered only in the last century in Shark Bay in Australia, are often mentioned, but stromatolites are found in a few other places in the world such as Laguna in NE Mexico (Figure 1.5). The earliest kinds are cone-shaped fossil stromatolites (*Conophyton*) similar to living stromatolites from the hot springs of Yellowstone National Park in the USA.

It has been suggested that some fossil stromatolites may have a purely physical origin, but nevertheless microbial filaments of presumed cyanobacterial origin, from the Apex Basalt of Western Australia about 2700 million years old, have also been described. The presence of characteristic hydrocarbons such as 2 alpha-methylhopanes indicates the presence of cyanobacteria long before the atmosphere became oxidising. It is probably not coincidental that the first evidence for oxygen production is found around 2.8 billion years ago at about the time cyanobacteria were colonising shallower waters.

The evolution of oxygen producing photosynthesis was a pivotal event in the history of life on Earth because it permitted dramatically increased rates of carbon production, and a much wider range of metabolism associated with novel ecosystems. By changing the atmosphere to one that was rich in oxygen it set the stage for the evolution of aerobic organisms. However, it is likely that other organisms pre-date the cyanobacteria. Numerous bacterial species capable of metabolising sulphur are found near the root of the 'Tree of Life'. Many are active at very high temperatures and are commonly found in modern sulphide-rich hydrothermal systems, such as geysers and fuming deep-ocean vents. Here they utilise chemical energy trapped in the rocks from the time of the formation of the Earth. It is in these organisms that we must look for evidence about the first stages in the evolution of metabolism including photosynthesis, because they also include species that carry out photosynthesis but do not produce oxygen.

1.2 Process: the evolution of photosynthesis

Chemical energy trapped in the rocks is a kind of leftover from the very origins of the Earth. This energy is still utilised by some microorganisms, but life would have been very limited if it had been restricted to geysers or hydrothermal vents and sediments. Photosynthesis, by harnessing an inexhaustible supply of energy, vastly expanded the possibilities of life. Today plants and some kinds of plankton are the major photosynthetic organisms but the origins of photosynthesis must be sought in bacteria.

The fundamental chemical equation of plant photosynthesis is

$$6\ CO_2 + 12\ H_2O + \text{energy from sunlight} \rightarrow C_6H_{12}O_6 + 6O_2 + 6H_2O.$$

This kind of photosynthesis is oxygenic (releases oxygen). Carbon dioxide and water are combined in the presence of energy to make energy-storing sugars. Oxygen is released as a by-product. In fact photosynthesis occurs in two main stages. In the first light-dependent stage, light energy is used to form the energy-containing compound, ATP, and to produce chemical power, mainly in the form of a compound called NADPH. Fundamentally it does this by providing electrons to compounds thereby making them chemically reactive.

There are a number of distinct events in the first stage. Light is caught by an array of pigments, acting as an antenna, and the energy of the light photons raises electrons in the pigments to an excited state. The energy of excitation is transferred via intermediates to the reaction centre (RC). At the reaction centre energy is transduced into chemical energy by the donation of an electron to an electron acceptor, which is thereby chemically 'reduced'. Then, by a series of reactions associated with electron transport, molecules storing energy (ATP) and reducing power (NADPH) are formed. In the second stage of photosynthesis, the light-independent stage, ATP and NADPH are used to chemically link carbon dioxide covalently to an organic molecule, thereby creating a sugar. Sugars are suitable molecules for the transport and storage of energy and can be broken down later in respiration to release that energy.

Any hypothesis about the evolution of photosynthesis must explain how such a complex series of events might have arisen step by step. One possible starting point is in the origin of pigments that protected the earliest living organisms from the damaging effects of ultra-violet (UV) light.

1.2.1 Pigments

The portion of a pigment molecule that absorbs light and hence imparts colour is called a chromophore. At the earliest stages it is likely that pigments evolved in a purely protective role, providing protection from UV. The amount of UV radiation was considerably higher then because of the lack of UV-absorbing oxygen in the atmosphere. The radiation reaching the surface of the Earth included the potentially highly damaging short wavelengths (UV-C, wavelength 190–280 nm) that are now completely shielded out, as well as slightly less-damaging longer wavelengths (UV-B, 280–320 nm). Even today cyanobacteria produce a pigment in their sheath called scytonemin, which strongly absorbs UV-C radiation. The presence of this pigment may explain their ability to have colonised shallow marine environments prior to 2.5 billion years ago.

Absorption of a photon of light energy in a chromophore elevates electrons to an excited state. The energy must then be dissipated in a way that does not produce toxic photoproducts. It can occur in one of four different ways:

- by emission of infra-red radiation, i.e. heat;
- by fluorescence;
- by transferring the excited electron state to a neighbouring molecule;
- by the receptor molecule becoming an electron donor.

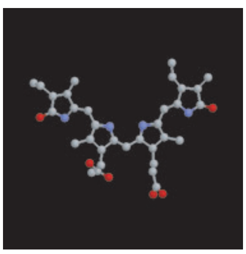

Figure 1.6. The pigment phycocyanobilin (ball and stick model: grey represents the hydrocarbon backbone, blue – nitrogen, red – oxygen).

For example the phycobilin pigments found in cyanobacteria and red algae (Rhodophyta) absorb strong light at different wavelengths and release it by fluorescing at a very narrow range of wavelengths.

Phycobiliproteins (= phycobilins) have a tetrapyrrole-based structure like haemoglobin. One kind is the bluish pigment phycocyanin that gives the cyanobacteria or blue-green algae their name. Another phycobilin called phycoerythrin makes the red algae, Rhodophyta, red. The absorbance spectra of phycocyanin and phycoerythrin pigments are shown in Figure 1.8.

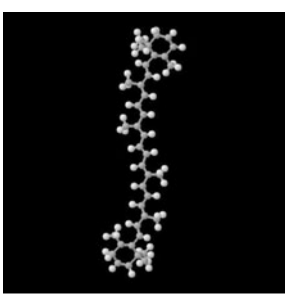

Figure 1.7. The pigment β-carotene.

Another class of pigments is the carotenoids of which β-carotene, the carrot pigment, is one. It absorbs blue light strongly and so looks orange. Others are red. Different carotenoid pigments absorb wavelengths between 400 and 550 nm. The carotenoids also have a protective role in plants though not only by shielding the cell. They seem to have gained another way of protecting the cell from damage because they scavenge toxic products such as superoxide (O_2^-) and singlet oxygen ($^1O_2^*$) that are created by absorbing light. Like many pigments, carotenoids have a ring-based structure but here with two six-carbon rings attached to either end of a long carbon chain. The carotene found in some green photosynthetic bacteria has a carbon ring at only one end. Carotenoids are soluble in lipids and are normally attached to the cell membrane or found in specialised vesicles (plastids) called chromoplasts.

Another interesting class of compounds that absorb light are the phytochromes. They are used by green plants as photoreceptors, signal-receiving molecules, directing their development depending on the quality of light. Phytochrome-like proteins may have