AUTOTROPHIC, HETEROTROPHIC AND OTHER NUTRITIONAL PATTERNS

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Summary

The first life forms were probably autotrophic and used inorganic materials as their source of energy, i.e. they were chemotrophic in the darkness of sea bottoms. When photosynthesis evolved, the usage of light energy became possible and oxygen became available. The autotrophic organisms provided the possibility to use oxidative energy in energy supply, and a new heterotrophic category of life forms could develop. The eukaryotes developed from cells by engulfing other bacterial cells which provided the components of the nucleus and mitochondria as well as algae with chloroplasts in the lineage to end up in plants. The animals are heterotrophs. They benefit from photosynthesis either directly by eating plants as herbivores or indirectly by eating other animals (carnivores) or both animals and plants (omnivores), but also by using oxygen. Pluricellular organisms have specialized cells and tissues with different tasks. The development of present day plants and animals are outcomes of ca 4000 million years of development. Very primitive forms of life still exist, but new simple forms are still developing, as indicated by recent dangerous infections. Thus diversification of life forms continues with unfortunate extinction of others, often as a result of human activities.

1. Introduction: Different Life Forms

The basic requirement for the life of cells and organisms is the need for energy. Life is impossible without energy, although life can be stored as spores or seeds for a long time and in very harsh environments without any or with extremely small energy utilization. Energy is needed for the synthesis of organic substances and for the dynamics of life functions. Functions need energy sources that can be changed to suitable chemical forms. The life forms we know are based on carbon metabolism. Energy flow can thus be described by carbon transformations. Energy metabolism in all life forms is very similar, as if they had originated from the same beginning. Even rather similar enzymes can be found in all organisms.

Energy comes from either chemical compounds or light. The word "autotrophism" (Greek "auto" = self, "trophein" = feed) means that the organism is able to obtain energy either from inorganic chemicals (chemotrophism) or from sunlight (phototrophism). All other life forms are "heterotrophic" (Greek "hetero" = different), and they have to use the energy originally from autotrophics. Autotrophic organisms are called "primary producers" (green plants, algae, photo- or chemotrophic bacteriae or archae).

Some bacteria metabolize iron, arsenic, nitrogen, sulfur, and other inorganic materials. Typical chemotrophic microbes use chemical energy to make organic compounds from inorganic substrates such as carbon dioxide ($CO_{2)}$, hydrogen (H_2), and sulfide (H_2S). Theoretically, there may have existed organotrophic chemotrophs, which had been using "organic" substances like methane (CH_4) accumulated before life existed on the young Earth.

Heterotrophs use organic energy sources, normally produced by other living organisms as secondary or tertiary producers. Herbivores (vegans) use plants and vegetarians mostly plants. Predators or carnivores hunt other animals. Ecto- (outside) or endo- (inside) parasites use their host animal or plant as their source of energy. Commensals share food produced by others and utilize the skills of other animals to get their food. Saprophytes feed on dead or decaying organisms and recycle the nutrients. Some organisms get their nutrients from simple organic substances as a final end of a heterotrophic food chain. They can therefore be called organotrophic and be classified among chemotrophs, although the origin of the organics is now from some other organism. Organotrophs use reduced carbon compounds such as glucose and fatty acids. They could also be classified as heterotrophs. So they can be included among chemotrophs, autotrophs and heterotrophs.

Chemotrophic metabolism also includes glycolysis and fermentation. Biological oxidations usually involve the removal of both electrons and protons, and are highly exergonic. Most chemotrophs meet their energy needs by oxidizing organic food molecules. The oxidation of glucose is highly exergonic. Glucose catabolism yields much more energy in the presence of oxygen (Krebs cycle) than in its absence (fermentation). Based on their need for oxygen, organisms are either aerobic, anaerobic, or facultative.

Glycolysis and fermentation generate ATP without oxygen. In glycolysis this takes place by catabolizing glucose to pyruvate. The fate of pyruvate depends on the availability of oxygen. In its absence, pyruvate undergoes fermentation to lactate, etc., to regenerate NAD+ needed in glycolysis. Fermentation provides only a small fraction of the substrate energy, but it efficiently conserves energy as ATP. Polysaccharides like glycogen in animals are cleaved to form sugar phosphates that also enter the glycolytic pathway.

The citric acid cycle is also known as the Krebs cycle, which derives its name from the work of Hans Krebs in 1937 (Nobel prize in 1953) or the TCA (tricarboxylic acid) cycle (see Figure 1). It is amphibolic (both catabolic and anabolic) in character. Without the presence of free oxygen as well as the tools for efficient burning of energy by oxygen (mitochondria with Krebs cycle) hardly any macroscopic animals or plants could exist.

Heterotrophs are secondary and tertiary producers. They produce structures and support their functions using the energy obtained from the primary or secondary producers. They are therefore either vegetarians, predators, saprobionts or parasites. Some life forms between auto- and heterotrophic organisms can sometimes be either autotrophic or heterotrophic (facultative auto- and heterotrophs, for example some Cyanobacteriae). Also some species obtain their energy sometimes as parasites and sometimes as saprophytes.

There are very complex relationships among symbionts. For example lichens on rocks, soil and trees are dual organisms having a fungus and a cyanobacteria or chlorophyte as partners. The green organism is autotrophic, providing food for itself and the fungus. The fungus attaches the lichen onto the surface and provides protection and moisture.

Some parasitic life forms such as viruses use the energy metabolism and enzymes of their host organisms. Viruses have a DNA (retroviruses RNA) core and a protein coat. In their lytic cycle they take command over the cell to make new viruses and finally may kill the cell. In a lysogenic cycle, viruses incorporate their DNA into the host DNA of other cells.

2. Origin of Life and Energy Sources

The four most common elements in the universe are hydrogen, helium, carbon, and oxygen. Helium is inert. The three most abundant, chemically active elements in the cosmos are also the top three ones of life on Earth. Hydrogen is the basic fuel for nuclear energy and with great importance in biology. Hydrogen, oxygen, and carbon account for over 95% of the atoms in the human body and in all known life.

Aristotle based his idea on the beginning of life on abiogenesis, birth of life from putrid matter, etc. Only very much later could Louis Pasteur show that sterilized organic matter stayed without microbes. The question of abiogenesis of the simplest forms of life from primordial chemicals has remained essentially unsolved. Although a lot of amino acids, sugars and other organic chemicals had been produced from the "original environment" or "primordial soup", the crucial adenine was rare and the result was racemic (a mixture of L- and D-forms).

The hypothesis of panspermia, the seeds of life diffused throughout the universe, has been favored by some thinkers since Anaxagoras (c500 to 428 BC). Some 1000 to 10 000 tons of dust and rock land on Earth each day. In the 1970s, Hoyle and

Wickramasinghe began to suspect that life on Earth could have come from space. The spectra of some interstellar dust particles fits with dried bacteria.

All atoms except H and He, (Li) have been liberated from the interior parts of stars by their supernova explosions. Supernova remnants condense while they are travelling through space. Metals and silicates condense first followed by mantles of more volatile substances including complex organic compounds like those found in the debris of comets and meteorites. When added to water, some of these materials form tiny (10 micron diameter) capsule-like droplets similar to cell membranes. Extracts of organics from some meteorites also form these capsule-like droplets when added to water. It is possible that comets and meteorites could have provided the Earth with organic materials that were a springboard for life. Comets are big dirty, loosely formed balls, composed of water, carbon dioxide, ammonia and dust.

Around 1446 BC	Moses	“Then God said: ' Let the land produce 'sprouts'…” (3rd day; 'sprouts' as something primitive vegetation, 'land'=just as ecological niches should produce species fitting into their circumstances (Gen 1:11, 24).
c500-428 BC	Anaxagoras	Panspermia: life coming from space.
384-322 BC	Aristoteles	Abiogenesis: many animals are born from putrid matters ('observed facts').
1668	F. Ferni	Against abiogenesis: no maggots bred in meat without flies.
1745	J. Needham	Claimed victory for spontaneous generation by testing microbes in meat after boiling.
1859-	L. Pasteur	Abiogenesis wrong: Not even microbes can be born from putrid matter, only life from life *(omne vivum ex vivo*). Life also without oxygen.
1859-	C.Darwin	All life forms originally from a single, simple progenitor. The Creator originally breathed life 'into a new forms or into one'. Then evolution took over. In a private discussion: Life may have started in a natural way in a pond with ammonia, phosphoric salts, light, heat and electricity.
1870s	T.H. Huxley	'Primordial archebiosis': abiogenesis of protolife in original conditions, complex polymers spontaneously from abiotic monomers.
1938-	A.I. Oparin, J.B.S Haldane	Proposal: Life started in a 'primordial soup'.
1953-	H.C. Urey, S.L. Miller	Primaeval soup with original air and lightning produced basic small molecules for life as most of the essential amino acids, many sugars and other organics (but result in racemic mixtures, not suitable for life). Phospholipids spontaneously form lipid bilayers resembling cell membranes.
1961	J. Oró	Hydrogen cyanide and ammonia in 'original reducing atmosphere' yielded mostly adenine. Adenine necessary for ATP and RNA etc.
Late 1960s	C.R.Woese, F. Crick,	RNA world scenario, if replication without proteins and catalyzing every step of protein synthesis.

	L.E. Orgel	
1968	B. Donn	Polycyclic aromatic compounds in interstellar dust.
1974-	F. Hoyle, N.C. Wickramasinghe	Support for panspermia: Complex organic polymers in space. Later: Comets include black tar-like surface layer with similar substances as in the 'primordial soup'.
1982	C. Ponnampera, M. Hobish	Neoabiogenesis. Origin of life maybe around hydrothermal vents; Later: some genetic studies show that archae could be older than bacteria.
1983	T.R Cech	Ribozymes, ribonucleic acids (RNA) function as enzymes.
1986	W. Gilbert	RNA world hypotheses supported: ribozymes can act as enzymes and copy themselves. Later: ribosomes are essentially RNA, proteins are only giving support.
1987	J.P. Ferris	Origin from clay: montmorillonite catalyzes the synthesis of RNA oligonucleotides. Clay crystalls resemble somehow cellular conditions. Mg and other bivalent metals could touch clay and RNA. It might solve the problem of left-handed polypetides instead of racemic mixtures.
1992	T. Gold	Life could be originated in deep layers of rock with original archae.
1994-	E.O. Kajander et al.	Nanobacteria, primitive life forms; later suspected their existence in chondrite meteors of Mars.
1996	D. Lee *et al*	Autocatalytic set: 32-amino acid peptide can autocatalyse its own synthesis from 15- and 17 amino acid fragments (exergonic reaction).
1998	J.V. Smith	Porous zeolites (esp. mutinaite) as the origin of life by helping catalysis and even solving left-handedness of peptides.
1999	A. Eschenmoser	By polymerization of formaldehyde yielding phosphorylated derivative of ribose.
2000	P.B. Weiss, J.L. Kirschvink	Panspermia supported: magnetofossils in meteorites from Mars.
2001	M.J. Russell et al.	FeS (machinawite) as a "smart" electrochemical reactor (protometabolism). Original cells could be formed by FeS. It is also a source of energy for chemotrophic archae.

Table 1. Findings and hypotheses on origin of life.

It has been estimated that the first bacteria colonized the Earth almost 4000 million years ago (see Figure 1). The environment was then “hostile” for most life forms of our time. Nuclear radiation from decaying element U235 was about fifty times greater than now. The air was hot and full of “noxious” chemicals such as sulfurous gases released by volcanoes. There was no free oxygen and no ozone to block out the dangerous ultraviolet radiation of sun. Some bacteria and archae can withstand extreme heat and pressure by thriving in oil reservoirs a mile underground. Maybe the first life forms were created so deep in water or rock that UV radiation could not cause any damage. Some species of cyanobacteria are highly resistant to ultraviolet radiation, but they appeared much later.

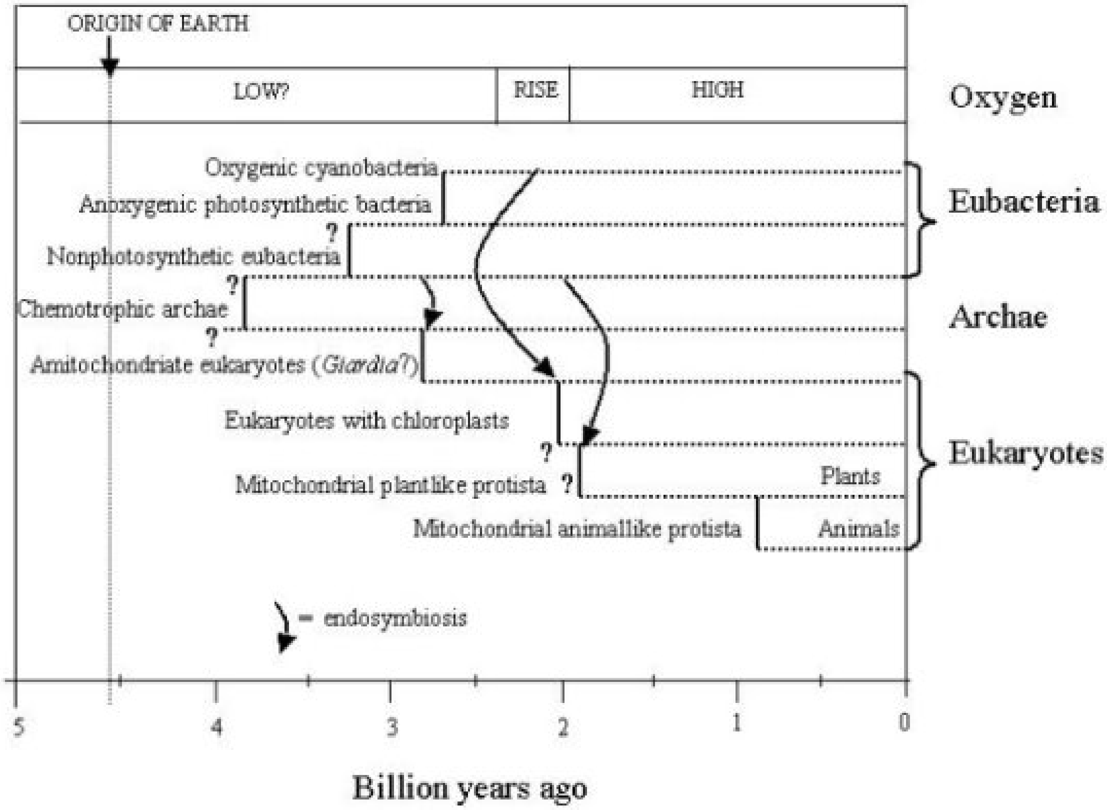

Figure 1. Evolution of different lifeforms.

Rasmussen says: "Life manages very well without oxygen, evolving into flourishing communities of anaerobes. Acidity... presents no problem, as sulfur bacteria and their co-habitants illustrate, nor does a considerable degree of alkalinity bother alkophiles.... Water purity is a trivial matter: saturated salt brines support abundant bacterial life. And pressure is quite irrelevant, with bacteria growing happily in a near vacuum or at the huge hydrostatic pressure of deep ocean trenches. Temperature, too, presents little problem: boiling hot springs support bacterial life, and bacteria have been found growing at 112 °C in superheated geothermal water under hydrostatic pressure; conversely, other types of bacteria thrive at well below zero °C, provided the water is salty enough not to freeze. And even if they do get frozen, many bacteria revive, when their habitat thaws. Even organic food is not a prerequisite..."

Only water is absolutely essential for bacteria to grow and multiply. In the early Earth water condensed to form the hydrosphere, most probably from about 4.4 gigayears ago (Ga). Hydrothermal processes have played and still play an important role in evolution. These processes link the lithosphere, hydrosphere and biosphere. The hydrothermal circulation in modern seafloor accounts still for approximately 33% of the heat transferred through the seafloor, and it has a significant role in global geochemical cycling.

3. Early Chemotrophic Life

Chemotrophic hyperthermophilic microbes at the seafloor in hydrothermal vents support the idea that life on Earth originated in hydrothermal environments. The early life forms some 4000 to 3000 million years ago did not use sunlight as the energy source. Chemotrophic archae or bacteriae used hydrogen sulfide or iron sulfide originally emitted from the vents as an energy source to fix carbon dioxide from the surrounding sea water into sugars. The role of heat-shock proteins as chaperons, which have a crucial part in assembling and reassembling complex proteins, may date from this hazardous environment. The sulfur cycle is very old. Recent high-resolution studies show a wide range of isotope ratios in 2700 million years old sediments. Geological evidence suggests that such organisms were present in the Archaean. Even so toxic elements such as arsenic has been an important source of energy. It has been estimated that >100 different chemical reactions are used by chemotrophics, The most common sources are H_2, Fe-, S-, N-compounds, CH_4 and many organics, but also such metals as As, Se, and U. Iron sulfide (machinawite) has been studied in submarine alkaline seepage as a "smart" electrochemical reactor mimicking chemiosmosis. Machinawite as well as clay (montmorillonite) particles may resemble electrochemical "cell walls" suitable for a primitive RNA world, but allowing quite a free lateral "gene" transfer.

Evidence of early microbial life has been found in 3000 million year old volcanic rocks. The thread-like filaments may be fossils. The filaments occur in massive volcanogenic sulfide formed on the sea floor, at depths far below the light-penetration zone, and at temperatures near or above the limits tolerated by life. Accumulation of banded iron-formations reached a peak during the Palaeoproterozoic era. Large quantities of ferrous Fe have been formed in hydrothermal systems at oceanic spreading centers. Are iron bacteria involved with it?

The oldest organisms are prokaryotes (without "karyo", cell nucleus) belonging to Monera, either Archae (Archaebacteria, ancient "bacteria") or Bacteriae (Eubacteria, true bacteria). They have no membrane bound organelles. Some of them still exist, and they are mostly autotrophs (photosynthetic or chemotrophic) but there are some heterotrophs.

Normal present day archae do not live in the presence of free oxygen. They can be important as decomposers in food production or antibiotic production. Some are thermoacidophiles or methanogens (producing methane). They may be extremophiles, i.e. living in extreme environments such as around sulfur hot springs, in the deep sea, in caves or deep in rocks or ice. Other chemotrophs such as iron bacteria can be found on the surface of small water pools. They can oxidize iron in many environments. They convert ferric to ferrous iron to obtain energy. Methane bacteria actually belong to archae. They use as their energy source H_2 and CO_2 and produce methane (methanogenic bacteria; methanotrophic bacteria are metabolising methane). Data on ancient carbon and sulfur isotopes support the deduction that methanogens recycled dead organic matter in sediment. A diverse, hydrothermal-associated, microbial community of chemotrophs existed in waters of shallow and medium depths.

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Biographical Sketch

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