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EVOLUTION AS THE MEANS OF EXISTENCE OF LIVING MATTER

1. INTRODUCTION

In 1980, British mathematician John Little published a short paper entitled "Evolution: myth, metaphysics or science?"[1]. Although it is more than fifteen years old by now, I believe it is still of interest to evolutionary biologists and philosophers of biology. In his article Little examines Karl Popper's well known claim that the Darwin's theory of evolution is metaphysical rather than scientific. Such a statement requires, however, clarification of the terms "metaphysical" as opposed to "scientific". While "metaphysical" is frequently used as a synonym of "pseudo-scientific", Popper uses this term to label any theory which is either not falsifiable, or does not provide means for generating precise and accurate predictions. However, in this sense, very few theories, indeed, can be described as being truly "scientific". There are, after all, many theories or notions which are neither falsifiable nor have the exact predictive power and yet constitute the very canon of contemporary "scientific thinking". A very good case in point is the concept of realism according to which the external world exists outside our sensory experience. A concept as fundamental to modern science as this would seem almost by definition "scientific". And yet, as not falsifiable, it should properly be called, in keeping with Popper's definition, "metaphysical". Apparently there are theories "metaphysical" in the Popper's sense, which are scientific, or at least "scientific enough". The question, therefore, is whether theory of biological evolution (Darwinian, neo-Darwinian, or any other) is after all scientific despite being "metaphysical" in the Popper's sense, or is it merely a myth, a mental construct which one may or may not believe, depending on one's intellectual predilection. In other words, are contemporary theories of biological evolution "scientific enough"? Little quotes Popper who have said that "neither Darwin nor any Darwinian,

[1] J. Little, Evolution: myth, metaphysics, or science?, "New Scientist" 1980, 4 September, p. 708-709.

has so far given an actual causal explanation of the adaptative evolution of any single organism or any single organ". This, indeed, poses a problem since according to the general formulation of Darwin's concept of natural selection the survival of the fittest can only be measured post factum by observing the actual success of survival. Such a formulation sounds tautological and it can hardly be taken as the ultimate explanation of the process of evolution.

At the conclusion of his article Little once more quotes Popper saying: "There is a reality behind this world as it appears to us, possibly a many-layered reality, of which the appearances are the outermost layers. What the great scientist does is boldly to guess, daringly to conjecture, what the inner realities are like. This is akin to mythmaking". And perhaps this thought should guide us when we venture to fathom and, in a sense, explain the process of biological evolution. What we see as the "survival of the fittest" is perhaps the outer-most layer of reality. Shouldn't we try to guess what the inner realities are like? Even if it will not make the theory of biological evolution "scientific" in the Popper's sense...

In the present paper I propose and discuss a general concept that the very nature of "living matter" creates the necessity for the continuous process of biological evolution. I suggest, in other words, that biological evolution is the means of existence of "living matter". The Darwinian natural selection is thus seen as a mechanism best suited to explain certain aspects of biological evolution, although it may not be the only mechanism by which "living matter" evolves and maintains its existence. There is some evidence indicating that in the course of evolution organisms acquired new means of evolving, that they "learned" how to evolve "more efficiently". The last and perhaps the ultimate step in this "evolution of Evolution" may be the ability to directly manipulate the genetic material (i.e., genetic engineering). Human beings, please note, are living organisms too. But are we, humans, still the subject of biological evolution? This is an important point which I will briefly refer to at the conclusion of the considerations which follow.

2. ON THE DEFINITION OF LIFE

In the development of biology the concept of evolution (i.e., of a multistep process of directional changes) emerged in opposition to the famous static concept of Charles Linne (which, indeed, was more "static" than the Aristotelian "Scala Naturae"). While in "Philosophia botanica"[2] Linne stated expressis verbis that the number of species had not change since creation (and conse-

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[2] C. Linne, Philosophia botanica, Stockholmiae 1751, p. 100.

quently a system of taxonomy should just try to reflect this fact), J.B. Lamarck[3] underlined first of all that living organisms (both alive and already extinct) are not a set of unchangeable species but a *continuum* of minutely different forms, more complex of which had emerged from less complex through the process of "evolutionary change". The very same concept of continuum was adopted by Darwin, and later by neo-Darwinists. What changed between Lamarck and Darwin was the location of the driving force of the evolutionary process, from Lamarckian "intrinsic desire for improvement" to Darwinian external "natural selection". Yet one question remains that has not been conclusively answered: is the existence of all living organisms predicated upon the evolutionary process? In other words, is it possible to conceive of living organisms that did not evolve by the Darwinian (or any other) mechanism?

Before attempting to answer this question we need to decide on a definition of living organisms and that, in turn, entails providing a definition of life. However, in spite of many attempts to arrive at such definition, none adequate or generally accepted seems to have been found yet. There is no consensus on how to answer such questions, as "How we can justify and explain taking organs for transplants – such as a heart or kidneys – from a 'dead' human body, these organs being ostentatiously 'alive'? Is 'being alive' the attribute of a cell, or an organism, or perhaps a population, or of a species?" On the other hand it seems perfectly clear that "living matter", i.e., the matter of which the living organisms are built, is clearly distinguishable from the non-living matter on the basis of its chemical composition, cellular structure, metabolism, self-reproductive ability, etc. We may reasonably agree to define "living matter" by a set of such attributes (some of them are listed in Table I). May we, therefore, define life simply by the set of the above-mentioned attributes? One may argue that in fact such a definition is trivial, because it has only a broadly descriptive character and by no means helps to understand or explain the phenomenon of life. Also, if we artificially create and organize matter in such a way that it possesses all "descriptive" attributes of life such as those listed in table I, would it really mean that we created "life"?

The last question seems to have no obvious answer but we can easily circumvent the problem by incorporating into the definition of "life" the fact that it has its own history. Most scientists concerned with origin of life agree that the process of biogenesis was driven by natural forces (there was no "creator") and that it was a one-time event, at least in the sense of one event (or one set of events) of biogenesis being sufficient to create life on Earth as a continuous phenomenon whose existence can be dated back to that single occurrence.

[3] J.B. Lamarck, Philosophie zoologique, Paris 1809.

Natural "living matter" proved its ability to exist in changing environments for several billions of years. Therefore long-term ability of continuous existence in changing environments may be added to the "descriptive" list as one more, though a very important one, attribute of "real" "living matter". Life, as we know it, had emerged once and from that time it has been able to perpetuate itself despite frequent (in the geological time scale) and profound changes in environmental conditions. Clearly, during these past times living organisms created a continuum of forms, i.e., evolved. But does it mean that biological evolution really was a necessity?

3. LIFE IS INTRINSICALY ERROR-PRONE PHENOMENON

The attributes of "living matter" listed in table I are essential constituents of its property called "self-organization". Thermodynamically self-organization can be defined as the capacity to preserve order, or, in other words, ability to accumulate negative entropy. In general evolutionary processes, defined as gradual, directional change, are common throughout the universe but all presently known, with one exception, that of life, are directed in the long term towards the increase of entropy. In isolated areas entropy may be preserved or may even decrease for short periods of time, but the general direction of change always ultimately leads, by virtue of the second law of thermodynamics, towards "less organized" forms of matter. In the sea of inanimate world's rising entropy life is an archipelago of isolated islands of "biological order" (cells and organisms).

Once the cellular theory of Schleiden and Schwann gained general acceptance, biologists agreed to regard cell as a basic unit of life. The next level in the hierarchy of organization of "living matter" is organism (although many organisms are unicellular), and the next one is population. Living cells and organisms are able to accumulate "negative entropy", that is are endowed with the ability to create and maintain an orderly and "seemingly purposeful" design. This is possible thanks to catalytic ("machine-like") properties of proteins, which are structured in networks and cycles of metabolism. Cells and organisms are sometimes described as "self-organizing dissipative structures" to indicate, somewhat counter-intuitively, that they are created and maintained by the dissipative, entropy-producing processes[4]. It has been demonstrated that the maintenance of "biological order" within cells is made possible by the release of heat energy from cells[5]. But still the question remains whether such

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[4] I. Prigogine, G. Nicolis, A. Babloyantz, Nonequilibrium problems in biological phenomena, "Annals of the New York Academy of Sciences" 1974, v. 231, p. 99-100.
[5] B. Hess, M. Markus, Order and chaos in biochemistry, "Trends in Biochemical Sciences" 1988, v. 12, p. 45-48.

structures must evolve, and if they do, must they evolve by the Darwinian natural selection?

Any kind of catalytic protein (enzyme) in a given cell has its own characteristic half-time, i.e., time by which one half of its molecules are dismounted and substituted by those newly synthesized. As time passes, every enzymatic molecule will progressively lose its catalytic activity in consequence of an array of chemical and physical interactions. Even if the primary structure of a protein would not change due to some chemical reactions (such as, e.g., oxidation of amino acid residues), protein molecule would still gradually loose its active conformation (will become "misfolded", or "physiologically senescent"). This necessitates recognition and elimination of damaged or "old" protein macromolecules and their substitution by those newly synthesized. Selective protein turnover in *Eucaryota* is determined by an universal mechanism, the so-called "ubiquitin-dependent proteolytic pathway"[6]. Some proteins are even specifically "marked" for relatively fast decomposition[7].

The limited duration of the catalytic activity is, therefore, the intrinsic property of catalytic proteins. The consequence of this, which is frequently overlooked, is the demand for their continuous breakdown and synthesis. In the absence of such a mechanism, the only conceivable alternative would be continuous biogenesis, repetitive synthesis of catalytic peptides de novo from the inanimate matter. However, the major breakthrough of biogenesis, i.e., linking protein synthesis to the much more stable "blueprint" preserved in DNA sequence, one that can replicate with high fidelity and undergo translation into protein structure, provided for stable "memory of the biological order". Once the primitive cells acquired the ability to memorize sequences of amino acids of their catalytic proteins in the form of DNA helix which could be accurately copied, repetitive generation of catalytic peptides from inanimate matter was no more a requirement. Life become a continuous phenomenon.

One of the basic processes which makes the maintenance of biological order possible is the phenomenon of molecular recognition. In the famous "Molecular biology of the cell" molecular recognition is characterized as follows: "The sequence of subunits in a macromolecule contains information that determines the three-dimensional contours of its surface. These contours in turn govern the recognition between one molecule and another, or between different parts of the same molecule, by means of a weak non-covalent

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[6] A. Hershko, A. Ciechanover, The ubiquitin system for protein degradation, "Annual Review of Biochemistry" 1992, v. 61, p. 761-807.

[7] A. Varshavsky, The N-end rule, "Cell" 1992, v. 69, p. 725-735.

bonds"[8]. Molecular recognition is essential for all kinds of processes which are involved in the generation and maintenance of biological order, including the transcription and translation of genetic information, as well as DNA replication. However, "molecular recognition can never be perfect. Because of random factor in molecular interactions, minor 'side reactions' are bound to occur occasionally. As a consequence, a cell continually makes errors (...) Mistakes could be avoided completely only if the cell could evolve mechanisms with infinite energy differences between alternatives. Since this is not possible, cells are forced to tolerate a certain level of failure and have instead evolved a variety of repair reactions to correct those errors that are the most damaging"[9]. It should be added that repair reactions also cannot be perfect, by virtue of the same chemical principle, so that cells must, indeed, make mistakes.

"On the other hand, errors [in molecular recognition] are essential to life as we know it. If it were not for occasional mistakes in the maintenance of DNA sequences, evolution could not occur"[10]. This is a somehow misleading statement, because it implicitly suggests that "biological order" without mistakes is thinkable – while it is not. The difference is quite fundamental, if we consider the following: If the only source of random variations were errors (mutations) inflicted by harmful environmental interactions (ionizing radiation, etc.) or avoidable flaws in the design of biological structures, cells and organisms which do not make mistakes and do not generate variability would be thinkable. But, because the "living matter" has its particular molecular design, the system of biological recognition is error-prone and molecular mistakes in the cells and organisms are not avoidable.

Maintenance of the biological order entails the existence, in the long run, of some kind of mistake-correcting mechanism. Obviously, when errors are unavoidable, there must be some means of verifying their functional meaning. Neo-Darwinian theory postulates that the verification is through the mechanism of natural selection, i.e., the survival of the fittest.

4. THE MYSTERY OF ADAPTATION

Charles Darwin was a naturalist. His ingenious contention that organisms marvellously fit to their environments and that the species gradually change was based on pure naturalistic observations. His theory of natural selection aimed to explain how this apparent perfect fit – commonly found throughout the world of *fauna* and *flora* – came about. However, he had no knowledge

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[8] B. Alberts, D. Bray, J. Lewis, M. Raff, K. Roberts, J.D. Watson, Molecular biology of the cell, 3 ed., New York 1994 Garland, p. 98.
[9] Ibidem, p. 97.
[10] Ibidem.

about how organisms, or "living matter" in general, manage to "keep alive" and how adaptative traits, or any other biological properties, are inherited. For this reason his explanation was in fact only descriptive. The concept of natural selection seemed, however, so adequate and general that in due time it seemed to embrace all the great discoveries of "reductionistic" branches of modern biology, molecular biology and genetics. The structure and function of DNA and proteins, the mechanisms of heredity and the role of mutations (random changes in DNA created by environmental factors or by intrinsic infidelity of molecular recognition processes), all these were thought to be compatible with the general concept of "the survival of the fittest". But the discussions on the meaning and implications of the general notions of the theory of natural selection remained the domain of naturalists.

Among the general notions of the Darwinian theory the term that focused the most controversies and discussions was that of adaptation. A detailed analysis of the meaning of this term was, for example, provided by Richard C. Lewontin, Professor of Zoology at Harvard University. At the beginning of his 1978 article[11] he wrote: "The modern view of adaptation is that the external world sets certain 'problems' that organisms need to 'solve', and that evolution by means of natural selection is the mechanism for creating these solutions. Adaptation is the process of evolutionary change by which the organism provides a better and better 'solution' to the 'problem', and the end result is the state of being adapted (...) Yet there is no end to adaptation." Later on he modified the definition as follows: "When adaptation is considered to be the result of natural selection under the pressure of the struggle for existence, it is seen to be a relative condition rather than an absolute one (...) The concept of relative adaptation removes the apparent tautology in the theory of natural selection (...) An analysis in which problems of design are posed and characters are understood as being design solutions breaks through this tautology by predicting in advance which individuals will be fitter". However, "evolution cannot be described as a process of adaptation, because organisms are already adapted. Then what is happening in evolution?" In this context Lewontin recalls the concept known as the "Red Queen" hypothesis, or "the hypothesis of environmental tracking". According to this concept "environment is constantly decaying with respect to existing organisms, so that natural selection operates essentially to enable the organisms to maintain their state of adaptation rather than to improve it." This is, indeed, an interesting idea, but it implies that if the environment were to remain unchanged, no evolution would be necessary.

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[11] R.C. Lewontin, Adaptation, in: Evolution. A Scientific American book, San Francisco 1978 Freeman, p. 115-125.

Later on he says: "The current procedure for judging the adaptation of traits is an engineering analysis of the organism and its environment", and his meaning of "engineering analysis" is purely naturalistic. An example is the shape of a sponge optimized for both maximal feeding efficiency and the greatest resistance to predators. How such an optimization could have occurred on the basis of random changes in the genetic material, remains somewhat perplexing.

Let's recall one more fragment from Lewontin's paper: "The diversity that is generated by various mechanisms of reproduction and mutation is in principle random, but the diversity that is observed in the real world is nodal: organisms have a finite number of morphologies, physiologies and behaviors and occupy a finite number of niches. It is natural selection, operating under the pressures of the struggle for existence, that creates the nodes. The nodes are 'adaptative peaks', and the species or other form occupying a peak is said to be adapted". The explanation of this "nodality" in terms of random generation of genetic variability would require assumption that several different mutations should occur simultaneously to make it possible to jump from one node to the other. Had the "living matter" enough time to create the known diversity of species by testing all randomly generated combinations of mutations?

Lewontin's paper shows the kind of problems "naturalists" encounter with the term "adaptation". Apparently they all agree that some state of adaptation is a general attribute of life (or "living matter"). But are there organisms "better" or "worse" adapted? Can adaptation be quantified? Does better (higher, tighter) adaptation guarantee the evolutionary success? Can one predict which organisms are better (higher, tighter) adapted to a given environment? Is there any "reference" that would make it possible to judge *a priori* which modification will be successful? Or is there some "inner reality" that we have not yet visited?

5. EVOLUTION OF THE BIOLOGICAL EVOLUTION

Let's take a short look at the history of life on Earth. Life originated on Earth some 3,5 billion years ago. Then it took 2 billion years until the first eukaryotic cells appeared. Multicellular plants and animals emerged only some 600 million years ago. From that time on, with relatively short periods of abrupt reduction of diversity due to great extinction episodes, the number of species inhabiting the Earth increased in time, the growth in some stretches of time being exponential. The first exponential diversification is known to have occurred during Ordovician, the second started in Triassic and is evident until the present time[12]. Why did it took so long to design *Eucaryota*? Why did diversification proceed at the accelerated pace despite the organisms becoming more complex? One can intuitively predict that in complex organisms single mutations would very rarely be adaptative. The more specialized and optimised the organisms are, the more complicated sets of simultaneously occurring mutations would be required to cause a jump from one adaptative node to the other. If mutations occur randomly, the likelihood of creating an adaptive set of mutations will decrease.

Let's look again to the concepts emerging from modern "reductionistic" branches of biology. It has been determined that the structures of some proteins playing critical role in the maintenance of biological order are conserved for millions, or even billions of years. An example is the gene of triosephosphate isomerase, which internal structure (including five introns, i.e., non-coding sequences) suggests that it was preserved for 3 billion years[13]. The explanation is that almost any mutation in this important gene was lethal. Apparently some fundamental biological inventions were so fit that they could have never been changed. Others, however, were apparently "less ingenious" inventions and could have been changed more frequently. But were these changes really random?

The number of proteins with different primary structures (amino acid sequences) is unimaginably high. From 20 types of amino acid residues more than 10^{390} different proteins can be formed. However, only a small fraction of polypeptide chains would adopt a stable conformation while the others would have many different conformations (none of them preferred) and their chemical (catalytic) properties would remain undefined and useless from the point of view of creation of "biological order". For this reason new proteins usually evolved by alterations of the old ones. One of the new protein generation mechanism is that of recombination of the pre-existing polypeptide domains of proven stability and "biological usefulness". This is achieved by multiplying and combining the coding sequences of genes (exons)[14]. The genomes of *Eucaryota* generally contain many types of the so-called "transposable elements", DNA sequences which can increase genome diversity by causing

[12] M. Benton, Diversification and extinction in the history of life, "Science" 1984, v. 268, p. 52-58.
[13] W. Gilbert, M. Marchionni, G. McKnight, On the antiquity of introns, "Cell" 1987, v. 46, p. 151-154.
[14] C. Blake, Exons and the evolution of proteins, "Trends in Biochemical Science" 1983, v. 8, p. 11-13.

duplication and movement of exons (exon shuffling)[15]. It is highly possible that the appearance and evolution of transposable elements of the genome provided the means for randomly exchanging the pre-selected exons encoding the polypeptides of proven usefulness in creating biological order. Interestingly, 10% of the human genome consists of only two kinds of transposable elements (the L1 sequence which encodes reverse transcriptase, and the Alu sequence). Their emergence and multiplication, of relatively recent vintage, could have contributed to the accelerated evolution leading to the creation of the hominids and humans[16].

As mentioned above, the ability of organisms to evolve was not constant over time. According to paleobiological data, the rate of diversification of "living matter" more or less continuously increased. The plausible explanation provided by molecular biology is that the genome of the *Eucaryota* evolved not only as the genetic determinant of the state of adaptation, or the level of fitness. Apparently its ability to evolve, or in other words its ability to generate – in ever shorter periods of time – more tight adaptation to increasingly sharply defined ecological niches also evolved. Thus, the biological evolution is a multi-dimentional phenomenon. It operates at many different levels.

Procaryota "learned" how to evolve to remain fit in the changing environments and preselected a class of genes encoding polypeptide chains that are useful in maintaining "biological order". Their evolution was probably driven by purely random mutations, and this is the reason why it took so long to create *Eucaryota*. *Eucaryota* learned how to evolve more efficiently and in shorter time probably by "inventing" the transposable elements facilitating exon shuffling. This is why they were able to create, in the relatively short time, the unprecedented diversity of species tightly adapted to the narrowly defined ecological niches. Most recently, the rate of evolutionary change speeded up in primates, leading to the origin of hominids and, finally, humans. The difference in the protein makeup between humans and some primates is approximately 3%, but the adaptative difference is enormous. It is highly unlikely that this enormous evolutionary progress resulted from random mutations and the mechanism of natural selection.

6. *HOMO SAPIENS* – NEW PERSPECTIVES FOR EVOLUTION

At the beginning of the present article I mentioned a rather important fact that human beings are also living organisms. We certainly share with other

[15] J.D. Finnegan, Eukaryotic transposable elements and genome evolution, "Trends in Genetics" 1989, v. 5, p. 103-107.
[16] P.L. Deininger, G.R. Daniels, The recent evolution of mammalian repetitive DNA elements, "Trends in Genetics" 1986, v. 2, p. 76-80.

species of living organisms the similarity of chemical composition and design, we also operate on the basis of the same thermodynamic principles as self-organizing dissipative structures. But are we, humans, subjects of the process of biological evolution? This is a highly controversial point and will be touched upon only very briefly. Evolutionists, by and large, try to avoid giving definitive answers to such a question. The opinions of those few who dared to discuss this problem were extremely diverse. Some authors were and are trying to prove that human populations are subject to natural selection in the Darwinian sense (meaning "survival of the fittest"). Others say that, as far as contemporary populations of *Homo sapiens* in the well developed countries are concerned, the evolutionary process either has stopped, or is about to stop. An example of this way of thinking is given by the Polish microbiologist Władysław Goldfinger-Kunicki, who wrote: "Humans are specialized species, although in principle the specialization concerns only one function – thinking (...) Biological evolution of the humans, as it seems, is therefore closed for very long, if not forever"[17]. Is it really?

If we assume, along the line of reasoning put forth in the preceding chapters, that the real subject of the evolutionary process by natural selection is the efficiency of communication between organisms and their environment, we will easily comprehend the very basic difference between the non-human species and humans. The mechanism of natural selection operates as if the environmental conditions and their change were given a *priori*, or at most were being influenced (changed) by the evolving species in a purposeless, unpredictive manner. Purposeful interventions (such as creation of artificial environment by nest formation, etc.) are of negligibly small magnitude compared to the powers of Nature. At the same time the only source of adaptative variability are mutational changes in the genetic material. *Homo sapiens*, thanks to several unique properties (such as abstract thinking and language, complicated social structuring of populations, spatial and temporal accumulation of knowledge and technology, etc.) attained the ability to purposefully reshape its external environment. The actions of human species are already global in scope and its powers begin to commensurate with those of Nature. It may be debated whether the environmental reshaping is really purposely executed, but the prerequisites of such "adroit" actions, i.e., technological potential to create artificial but "biologically friendly" external "Nature-independent" environments do, indeed, exist. Furthermore, technical means of deeply influencing the workings of the human body on the cellular level, including first at-

[17] W. Kunicki-Goldfinger, Dziedzictwo i przyszłość [Heredity and future], Warszawa 1976 PWN.

tempts to purposefully change (or, rather, repair) the genetic material, seem to be a matter of not too distant future.

All these seem to give credence to the notion that *Homo sapiens* ceased to be a subject of natural selection, at least in the Darwinian sense. Human survival shall not be restricted to the "fittest", the "less fit" individuals shall be medically treated and cured including having their genes repaired. However, this will, by no means, be the end of evolution. Even if we assume that the genetic pool of *Homo sapiens* will be somehow purposefully stabilized, so that the evolutionary process defined in terms of population genetics (i.e., as the frequency of genes in the population genetic pool) will be terminated, many other aspects of the very complex relationship between human populations and their environments will, out of necessity, continue to change at an ever-increasing expenses of energy and resources. While this seems to hail the advent of a new strategy of evolution, it certainly does not imply the end of the evolutionary process itself.

Table I

The attributes of "living matter"	
I. Chemical composition	
1. Elementary analysis	Biogenic elements: C,H,O,N,S,P Other necessary: Cl,Ca,K,Na,Fe,Mg Microelements: B,Mn,Zn,Cu,Mo,Co,J,F (Altogether only < 25 % of elements abundant on earth
2. Molecular Structure	Carbon chains and rings. Macromolecules: Proteins built of aminoacids Nucleic acids built of nucleotides
3. Molecules and supramolecular structures dissolved or dispersed in water	
II. Spatial design of molecules	Macromolecular aggregates Compartmentation by unit membranes Cell as the unit structure generating biological order
III. Temporal design of cells	Biological order is made possible by the relaese of heat energy from cells Cells obtain energy by the oxidation of reduced polycarbon molecules and conserve it in the from of ATP The hydrolysis of ATP generates biological order through molecular recognition processes Enzyme-catalysed reactions are linked in sequences (chains or cycles) which are tightly regulated