Evolution

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Evolution is considered in a manner similar to Cosmology and as such includes the 'Origin of Life' (analogous to the Big Bang) and the evolution of complexity (the expansion of the Universe). We review several scenarios that are compatible with the existing fossil records and pay particular attention to some far reaching ideas.

I. Introduction

Two of the most riveting and thought provoking scientific questions have been addressed by almost all cultures and civilizations: the Origin of the Universe and the Origin of Life. In most cases they have been assumed to be two nearly simultaneous events - although the Origin of the Universe has preceded the Origin of Life (see for example Genesis [1], and [2] for alternative views). In recent times we have again become focused on the question of the Origin of the Universe with the introduction of the General Theory of Relativity[3,4] and it's prediction of an expanding Universe several years before Hubble's observations. It is also becoming respectable to address the question of the Origin of Life[5-10]. It seems, however, that we have a much better understanding of the early stages of the Universe, at least after $time > 10^{-35} secs$, than we have of the necessary conditions for the onset of complex biological molecules.

I will give a brief review of our present understanding of the Evolution of Life and Organisms as determined from the fossil records and other data. One problem we face (the same as in Cosmology) is that the only evidence for life is found on planet Earth and thus our speculations, to a large extent, are limited by our particular set of data. There is, however, a better chance that there are living organisms on other planets in our galaxy or on planets in distant galaxies than that there are other Universes. There is hope that, we might at some time in the future, be in a position to test our conjectures, scenarios and theories on living organisms other than those found on Earth. The paucity of nearby planets supporting life forces us to read the 'tea leaves' of our data with perhaps too high a magnification and too much emphasis on what may later turn out to be insignificant elements. Thus there is the everpresent danger that we are over reaching and extrapolating into areas with scant evidence. This is the price, the rejection of ideas based on one example of a biosphere, that we should be willing to pay if our conjectures turn out to be in some manner testable or refutable.

General theories of Evolution which includes the Origin of Life will be reviewed and particular attention will be paid to the work of Kauffman, Tsallis and coworkers, Peliti, Bak and coworkers. It is obvious from this list of my prejudice but I hope to persuade you, the reader, that there are strong views which cannot be ignored in any complete work on Evolution.

II. Fossil legacy

The solar system is about 5 billion (10^9) years old and the Earth about **4.5** billion years. The earliest non-controversial sign of life is **3.5** billions years old[11], although there is some evidence that the oldest rocks show signs of life and that is about **3.8** billion years old. The data is in the form of biologically mediated carbon isotope fractionation from the Isua Group of Greenland[12]. If this is indeed true then we are faced with finding an adequate time window for the formation of life. Recent work on modelling the accretion of Earth from the dust cloud with the associated meteoritic impacts suggest that even if life originated earlier than **4** billion years it is unlikely that it would have survived the inhospitable bombardments and impacts

from comets and meteorites on the protoearth [see recent events on Jupiter for a dramatic demonstration]. The window for the creation of life may be as small as 200 million years - from 4 billion years ago to 3.8. This window has been considered as too small by some[13] and they have postulated the theory of panspermia where life originated elsewhere and the spores or seeds have been propagated in space. The above discussion is based on the premise that life was found primarily in the upper regions of the oceans. The interval may be longer if life had a foothold, as it does today, at the thermal vents on the ocean floor. The Earth would then be repopulated after catastrophic events destroying most living creatures but not, off course, those at the thermal vents. There is no evidence for this scenario and according to Sleep et al, this seems unlikely[14]. The earliest living organisms were simple cells referred to as prokaryote cells - cells without a well defined nucleus. It seems that these unicellular organisms were the only living creatures for about 2 billion years. A major by-product or pollutant for these anaeorobic cells is oxygen which is found in large quantities in the atmosphere for the first time about 2 billion years ago after the ferrous oxides and other chemical sinks had been exhausted.

Blue-green algae metabolic strategy involved the production of oxygen from photosynthesis. Most of the earliest produced oxygen was removed by the formation of oxides with the reduced minerals present in soluble form in the oceans and lakes. This kept the environment relatively stable for about 2 billion years until there were no further minerals or rocks in the reduced state and the excess oxygen found its way into the atmosphere. At about this time we have the appearance of eucaryotes - cells with a well defined nucleus and also other organelles such as mitochondria. After a further 0.9 billion years, about 0.9 billion years ago there is some evidence for multicellular plants and other complex organisms. It is believed that sexual reproduction appeared at this stage. Multicellular animals however only appear in the fossil records about 0.6 billion years ago. About this time plants began to form on the fringes of lakes and swamps, the first evidence for life on land. This evolutionary development was the gateway for special animals to take advantage of various niches opened up by the vanguard of plants.

I will not discuss the interesting area of adaptive systems that evolve on rough fitness landscapes. These studies lead to a better understanding of adaptive evolution as 'hill climbing' towards fitness peaks. I refer the reader who would like to follow recent developments to [21] and references therein, and also to the proceedings volume of the Santa Fe Institute[23].

This Cambrian period at about 0.55 billion years marks the onset of an explosion of a large variety of animals - the fossil records indicate an exponential proliferation of species. The rich development which took place at this period is vividly told in the book 'Wonderful Life' by Stephen J. Gould[15]. This is one of the most fascinating period in the Earth's history as there is a richness of diversity in the fossil record which is stunning and its surprising appearance was expressed as 'a highway originating in the dessert'[16]. Note that the rich diversity encountered here is not due to massive extinctions but reflects the new niche on land for animals and plants and the complex multicellular organisms were more or less populating an ecological vacuum. This is reflected by an exponential like increase in species during this period. Some have theorised that the evolution of 'sex' might be responsible for this rich diversity. There have also been catastrophic events reflecting major demise of species - e.g the end of the Permian Period about 250 million years ago which saw the removal of about 90 percent of species. About 65 million years ago about 50 percent of the species of animals and plants became extinct - this was the demise of the dinosaurs at the end of the Cretaceous period. I will not continue the reporting on the fossil records of recent times as we have touched on most of the elements we will require for an understanding of Evolution.

III. Evolution

A good theory of evolution should include insights into the Origin of Life, the role of the environment, the interplay between diversity and complexity, the creation and extinction of species, the role of punctuated equilibria which is the apparent long periods of stasis or quiesence in the ecology followed by rapid changes in existing species or the appearance of new species, coevolution of species and their interdependence, the role of sex, etc. One may also add other features but it seems that any theory that shed insights into these diverse features will be robust. We now briefly comment

on models that attempt to shed light on some of the above elements.

Most theories that attempt to explain the origin of life assume implicitly or explicitly a chemical generous environment. By this we mean that there is a generous supply of monomers, a fairly stable environment and a rich catalytic source. In some theories the catalyst is an external agent like clay[17] or iron-sulphide[18] while in others the evolving polymers themselves are the catalytic agents. An extremely good example of a generous environment is a cell, which is well protected from external influences and is to some extent controlled. Some have focused on existing mechanisms such as DNA and RNA and have explored scenarios which will make the evolution of these structures or their prototypes likely. Our present understanding of the working of the cell pays primary importance to the roles played by DNA. One aspect is the encoding of information by the base sequences and the other role is the ability of DNA to separate into two strands where each has the ability to template its missing partner. Others have focused on more general scenarios where the evolving polymers themselves act as catalysts. This is in some sense an extreme form of chemical generosity and we may be excused from feeling somewhat uncomfortable in that the assumptions contain the solution. Essential elements of models include open systems - monomers, input energy etc.; catalytic activities; limited niche in that there is some form of competition for resources or representation in the succeeding generation.

IV. Autocatalytic sets

Kauffman and co-workers[19-21] have attempted to explore a general approach where templating appears somewhere later in the living organisms. The essential elements are a supply of monomers, protocell environments, autocatalytic activities provided by the existing polymers and finally closure of the autocatalytic set. This I have interpreted to mean that all members of the polymer population evolve from catalytic activities involving other existing members and are formed from the smaller chains which themselves have been formed in the same manner, all the way down to the input monomers. This approach is not too dissimilar to the work of Dyson[6] although it is more specific. The generation of polymers in Kauffman's studies is mapped onto random graphs. Each polymer which can be constructed from sequence of a given number of monomers is represented by a node in phase space, and where the parameters Edges (E) and Nodes (N) play an important role via $\frac{E}{N}$. For $\frac{E}{N}$ of a value 1.0 we find a spanning cluster of graphs connecting most of the nodes. This is interpreted by Kauffman as indicating a phase transition and also sufficient complexity such that protocells will all have more or less the same set of polymers without templating. In this scenario we may imagine that a protocell divides into two daughter cells and the nutrients of monomers diffuse through the walls and the existing polymers are sufficient to continue the catalysing process so eventually the set of polymers in both daughter cells are more or less the same as the set of polymers in the parent cell.

DNA templating evolves somewhat later, as a more complex polymer which stores the information associated with the random graph and each daughter cell will now have exactly the same ingredients as the parent cell. Thus the encoding of information is an evolved complexity wheras the catalytic properties is the equivalent of the 'background radiation' of cosmology in that it was present at the onset. We may assume that in this approach the autocatalytic set of polymers are not all identical - in that there must be variation and some polymers will have better catalytic properties than others. This type of fitness might express itself in more daughter cells or faster growing daughter cell etc. DNA or DNA prototypes store the information of the random graphs. Once this element is present we have the Darwinian mechanism for richer and richer complexity. However Farrner et al[20] suggest that RNA autocatalytic network may have coexisted with a peptide-like network although this seems not essential.

V. Spin glass

Following earlier ideas by Anderson, Peliti and co-workers[22-24] have considered evolution and the origin of life as a random walk on a rugged landscape using Ising models. They considered a fixed population of size M, where each member of the population has a genome of fixed length N. The label for each member of the population is α and s_i is a binary variable describing

the state of gene, i.

$$s^\alpha = (s_1^\alpha, ..., s_N^\alpha), s_i^\alpha = \pm 1; \alpha = 1, ..., M; i = 1, ..., N \tag{1}$$

There is a fitness function associated with each member of the population which is determined by the function $H(s)$ defined in the genome space. Two types of $H(s)$ were explicitly considered (a) a Random Energy Model (REM), which is completely uncorrelated and where $H(s)$ assumes a value between -1 and 1 independent of s; (b) a spin glass function where $H(s)$ is an energy function with an interaction between each pair of spins. $H(s) = \sum_{ij} J_{ij} s_i s_j$. A selection mechanism is now introduced in the form of a death function, p(H):

$$p(H) = \frac{1}{1 + e^{\beta(H(s) - H_o)}} \tag{2}$$

The coefficient β is a sharpness parameter which plays a role similar to reciprocal temperature in a Fermi function and H, is a threshold. As $\beta \to \infty$, the function $p(H)$ is 1 for all values of $H(s) <$ H, and 0 otherwise. The survival shows a sharp cut-off. Finite values of β lead to a more tolerant environment. If $\beta = 0$ the survival probability is $\frac{1}{2}$ for all members of the population.

The population evolves in the following manner: A random population is created at the onset. Each member of the population fitness is evaluated by means of equation 2 and with this probability selected for replication. This process is continued until we have as many members in the subsequent generation as there were at the onset. A fraction of the genomes are flipped from s_i^α to $-s_i^\alpha$. We have now created a new generation.

We now review some of the results. We consider first the $\beta \to 0$ case. Now the death probability is $\frac{1}{2}$ independent of the genome. In this case half the population is randomly decimated at each generation and within a relatively short period we find that all the present generation may be traced to a single individual of the primordial population. This property appears to be quite common and is in keeping with recent observations that all present day homo sapiens may be traced to a single mother about 200,000 years ago. One also observes after a long time that the population occupies a small *region* of genome space and this is descibed as a *quasi-species*[7]. The loci of the quasi species drifts in space with time. Next consider the limit $\beta \to \infty$ and $H(s)$ is the REM model of Derrida[25]. The genome

space of 2^N hypercube consists of allowed and forbidden sites dependent on H,. Thus for a fairly forgiving enviroment there are many connected regions of allowed sites but as the environment becomes more demanding this space shrinks to disconnected clusters whose average size becomes smaller and smaller. Thus stringent conditions (large H_o) keep the population within a restricted genome space - the system has a long lived memory.

There are elements of this approach which is very close to the Genetic Algorithm[26,27] which is used to find optimal solutions to complex problems. Let us briefly review the adaptation by Sutton et al[28] to find the ground state energy of the $\pm$J spin glass. We start with an initial population of random spin configurations and the given random arrangement of bonds. The fitness is now evaluated - this is simply the energy of the configuration of spins for the given bonds. The new generation of configurations are selected from the spins - those which are more fit have a higher probability of being selected as potential parents. The parents are selected in pairs and with a probability of $\frac{1}{2}$ there is genetic mixing - so-called sex. This is done by randomly selecting a site in the systems (which are considered as one dimensional arrays) and all spins on the left of this position come from one parent and all on the right come from the other parent. There is not an equal sharing of genetic material as there is in typical biological systems. In addition a finite fraction of the spins of the new population are flipped to the opposite state - random mutation. We next sweep through the lattice and all spins are flipped which lower the energy of that configuration. All favourable mutations are accepted. We have now completed one generation. We observe a general increase of the average energy of the ensemble with time and also within a relatively short period we find the ground state energy for that particular arrangement of bonds. We have checked this in two ways - for small systems we have actually enumerated all the 2^N configurations and determined the groundstate energy while for the larger systems we have repeated the search with different random numbers and for the same bond arrangement. *In all* cases we found the same ground state energy and its value agreed with the known ground state energy in both two and three dimensions. We see that an algorithm with some of the

elements of evolution, is capable of an efficient search in the complex landscape of the spin glass to find the ground state energy.

We may conclude from the above that the evolutinary strategy is quite robust and is efficient in locating optimal features in complex landscapes. From observing the evolution of the population, we note that diversity is somewhat reduced with time and there is more or less a general increase in the average fitness of the population. Unless we impose a very sharp and demanding fitness function, the evolving population forms a cloud about the optimal solution.

VI. Biopolymers

Tsallis and Ferreira[29-31] have proposed a rather simple mechanism of autocatalytic activity of the type proposed by Kauffman based on the observed behaviour of catalytic activity in present day cells. Again implicit in this scenario there is a rich supply of DNA type monomers or their precursors. The initial set of monomers consisted of A(denine), T(hymine), C(ytosine) and G(uanine) and dimers $A - T, A - C$ etc. Hydrogen bonds occured between complimentary pairs, i.e. A and T or C and G with probabilities P_{AT} and P_{CG} whenever these pairs are situated in close proximity to each other i.e. on nearest-neighbour sites. The system is autocatalytic with the growth of covalent bonds with probabilities depending on the existente of the appropriate hydrogen bonds. The probabilities of forming a covalent bond between the ends of chains or monomers and that of cleavage of a long chain into two sub-chains were selected to satisfy detailed balance. The main conclusions are: random sequences of monomers along the chain; the polymer chains were relatively short apart from the critical point at $P_{AT} = P_{CG} = 1$; the system reached equilibrium, i.e. the distribution of chains remained constant, after an initial growth period.

Herrmann and Tsallis[32] developed a computer algorithm based on this model. They considered two two dimensional lattices, one above the other. These two systems were populated with monomers and dimers, which are allowed to diffuse. Monomers, dimers or polymers which are placed on one lattice are constrained to stay there. A hydrogen bond is created with probability P_{AT} if the monomers at equivalent sites are A

and T. The similar arrangement is allowed for C and G. Two monomers are allowed to form a bond between them in a particular lattice if the corresponding hydrogen bonds have been formed. Note that the hydrogen bonds are formed between the two lattices and the permanent bond that is formed is between two monomers on the same lattice. Existing covalent bonds between monomers are allowed to break in the same manner. Detailed balance is satisfied and therefore the system is in equilibrium. The chains were allowed to grow only in the y-direction. These polymers were essentially stiff rods. Relatively short polymers were grown apart from at the critical point. The monomers on the polymer chains appeared to be random.

Kelly and Jan[33] extended the computer model of Herrmann and Tsallis to the semi-dilute regime. Only one lattice was necessary to store the system and each site either contained a monorner or polymer, irrespective of its length. Now the polymers diffuse quite easily in both directions and all the catalytic features of Herrmann and Tsallis are retained. The simulation showed that it was possible to grow relatively long chains away from the above mentioned critical values of 1. There appeared only random sequences along the chains - as far as one was able to measure. However if one assumed that certain sequences along a chain led to enhanced catalytic features then these sequences soon appeared in all members of the population. This usually accurred within a relatively small number of generations. The net effect after this occurs is that there is more or less a random drift until another favourable sequence occurs - and again there will be another fast takeover of the population. This may be a rudimentary form of punctuated equilibria.

VII. Coevolution

There have been musings that somehow life should evolve near the edge of chaos. This point of view has been the primary focus of the Santa Fe group and to some extent was motivated by developments in Chaos Theory. In a somewhat naive manner we may consider an ordered system such as a crystal with its repetitive unit cell as limited in encoding information. On the other hand a completely random system cannot encode information. Thus the onset of chaos might be a prime region for rich behaviour with maximum information.

Bak's interest in Self Organised Criticality (SOC)[34] had profound impact on this scenario - he realised that this event belongs to the category of SOC.

A model that realised these elements of SOC is the Bak-Sneppen model[35−39]. Consider a one dimensional lattice of sites where each lattice site is seeded with a random number uniformly distributed between 0 and 1. Each site represents a species and the value of the random number at the site represents the fitness of the species. Bak makes the plausible assertion that the least fit species is the one most likely to be susceptible to successful mutations and hence a change in its fitness. This feature is incorporated by searching through the random sequence and finding the site with the smallest random number. This random number is now replaced by another random number. This represent a successful mutation and since in some sense the immediate neighbours are immediately effected - they are now also given new random values. As Bak explains - a mutation of a co-dependent species may lead to a particular species becoming unfit through no 'fault' of the species. This is the model. The evolution is continued by searching for the species (site) with the lowest number and replacing it and its two neighbours with new values randomly selected between 0 and 1.

This process is continued until the steady state is achieved. The following properties of this model are observed: intermittency of evolution, i.e. long periods of stasis followed by bursts of activity or 'avalanches', power law in the size distribution of avalanches, the steady state characterised by most species having a fitness greater than 0.667 for the one dimensional system, catastrophic extinction is a natural consequence of the SOC, anomalous relaxation to the SOC state is observed without critical slowing down[38].

In this Bak-Sneppen model the association is made between intense mutational activity - in the form of creation of new species and modifications of existing species and extinctions including massive extinctions. Massive extinctions may be triggered by an external catastrophic event and then there will be major niches awaiting new or modified life forms, but there is no need to associate massive extinctions with external catastrophes. A slight change may trigger a mutation in a particular species and this in turn might trigger changes in the codependent species and so on etc. Therefore extinctions are a SOC phenomenon and the frequency of extinctions of size, s, should follow a power law. This appears to be the case from the fossil records[40]. It also appears that there are long periods of stasis - periods where there appear to be small changes taking place. This is observed from observing a single species over an extended period of time - one observes intermittent bursts of mutational activity or from looking at the fossil records and observing that there are short periods when there is massive creation of mutational activity. The main conclusion from the Bak-Sneppen model is that life (the set of all species) is at a self organised critical state and that there is always the potential for changes at all length scales from small perturbations. This is indeed insightful and in keeping with comparison with Cosmology may be compared to the observation that galaxies form clusters on all length scales - it is a fractal.

VIII. Discussion and conclusion

Since we do not have an ensemble of life on different planets we are forced to extract as much information as possible from this one biosphere. We may, e.g. consider the time taken for certain events to occur as a measure of the complexity of the event. From this perspective it seems that the creation of life from inorganic or simple organic precursors such as produced in a Urey and Miller[41] type experiment is by far the easiest task. The transition from procaryotes to eucaryotes took about half of life's history, 2 billion years and from single cell eucaryotes to multicellular organisms took a further billion years. Multicellular animals only appeared in the fossil record about 0.5 billion years, life on land about 0.4 billion years ago and what we might consider to be difficult for evolution (from simple multicellular to complex homo sapiens) appears easy. I find it perplexing and one of the great mysteries that life appeared so early in Earth's history.

It is popular to consider the two sister planets of Earth, Venus and Mars, as slightly beyond the hospitable range for the evolution of life. Today Venus may be considered in a state of arrested development. The carbon dioxide in its atmosphere is similar to the quantities calculated from the abiotic Earth's environment but its runaway greenhouse effect has made the surface temperature extremely inhospitable. Mars on

the other hand is far too cold and is almost devoid of atmosphere and water. There is evidence that at some time in Mars history there was abundant water on its surface. One may speculate that 'there but for Life goes Earth': these are the possible scenarios for Earth if life had not evolved. We may also speculate that had life evolved on these planets their fates might have been different. If this was possible then the problem of life originating only on Earth takes on subtle features which makes this difficult problem even more challenging. We pose the following: Was life possible on Mars and Venus? If the answer is yes, then why did it not evolve on these planets? if no, then why not.

Simple models and determination of the molecular structure of DNA are leading to an understanding of the mechanisms of evolution. The structure of DNA allows for the encoding of information and also the twin strands comprising DNA are each capable of templating the other. We have the mechanisms for cell division and genetic mutations which enables variability in the fitness of individuals. The finite lifetime of individuals and restrictions on the size of the population of a species within a niche are critical factors which may at times be overloolted. If the protopolymers were not biodegradable, then evolution is severly restricted. Also if the biological niches supported infinite populations, again evolution is meaningless. In addition to autocatalytic activities or other mechanisms leading to the creation of polymers one has to postulate a continuous process for the generation of these polymers with finite niches and also finite lifetimes for the polymers or the smallest biological entity.

The work of Bak, Kauffman and others clearly focus on a surprising aspect of evolution - that all of life exists at Self Organised Criticality. This has never to my knowledge been clearly expressed as an element of evolution in the pre-1980's literature and if further confirmation is forthcoming, will have far reaching consequences. Note also that the autocatalytic theory of Kauffman is closely related to the model of Ferreira and Tsallis. It would be useful to merge the approach of Bak to systems of spin glasses where the fitness of species take place via random mutations, in this way combining the spin glass approach of Peliti with the SOC of Bak. In this manner one is adding complexity to the fitness of the various species instead of representing fitness by a variable between 0 and 1.

Evolution is as challenging to the physicist as Cosmology. The problems are perplexing and they also share several similarities. We still need to make major advancements in Evolution before we are able have the same degree of confidence as we have with Cosmological theories.

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