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Chemical selection, diversity, teleonomy and the second law of thermodynamics

Reflections on Eigen's theory of self-organization of matter

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Two fundamental properties of animate matter, specific complexity and purposeful organization (teleonomy), are traced to their origin, applying Eigen's theory of self-organization of matter. Template-replicating copolymers possess the three dynamic properties that are essential for prebiotic evolution: autocatalysis, diversification and selection. By autocatalysis, even a single microscopic molecule replicates exponentially to macroscopic quantities. By diversification, it extends to a divergent distribution of such molecules. By selection, the distribution converges to a '*quasi-species*' that possesses properties like 'survival' and 'adaptation' to its environment. These are teleonomic properties that evolved from a nonteleonomic distribution by selection. Alternating divergent and convergent courses of chemical evolution lead such distributions to ever-growing complexity, including mutual catalytic interactions between the template-replicating copolymers and their chemical environment. Thus, chemical evolution may have started from even a single step, a de novo synthesis of a template-replicating copolymer, and arrived at a primordial living cell, just as biological evolution has started from a primordial cell and arrived at the biological world of today.

1. Introduction

Molecular biology has dealt a final death blow to vitalistic theories of the functioning of animate matter, in whatever disguise they may appear. It has proven definitely that animate matter functions by the same laws of physics (including chemistry) as inanimate matter, all based on the fundamental laws of quantum mechanics and thermodynamics.

Therefore, these laws must have governed the transition from an inanimate, 'prebiotic' planet to a 'biotic' one. One of the objectives of the study of the origin of life is to understand how this transition actually did happen. It is now generally recognized that the appearance of animate matter several billion years ago has modified drastically the structure and composition of the earth's crust and atmosphere. Precious information on the origin of life has been lost, perhaps forever. Therefore, the historical questions of how the transition from inanimate to animate matter actually occurred may never be answered in sufficient details to satisfy scientific curiosity.

The fundamental question of the origin of life is, however, not historical. The question is, can one conceive a possible transition from inanimate to animate matter that would be compatible with the laws of physics and chemistry? The crux of this problem is how to avoid violation of the second law of thermodynamics. The complexity of

Dedicated to Professor Manfred Eigen on the occasion of his 60th birthday.

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even the simplest forms of life has been proven by the discoveries of molecular biology to be so enormous that the occurrence by chance of any 'first' form of life would be a most improbable event. What is a 'most improbable' molecular event? The age of our globe is of the order of 10 billion years. An event that may occur only once in a billion years is very improbable but cannot be excluded. However, what if the chance of its occurrence is once in a billion-billion years? Somewhere along the sequence of decreasing probabilities, invoking too improbable events to explain the origin of life becomes incompatible with the second law of thermodynamics. Therefore, a scientific understanding of the origin of life must indicate a way by which the transition from inanimate to animate matter avoids this trap of 'improbable events'. Some of the greatest minds of our time stumbled on this issue. Eugene Wigner [1] posed this question, and his conclusion was that the present laws of physics will have to undergo modifications before they can be applied to the problem of life. Jacques Monod was reluctantly reconciled to accept violation of the second law of thermodynamics as a way out of this dilemma. In his fascinating book '*Chance and Necessity*' [3] he says:

"When one ponders on the tremendous journey of evolution over the past three billion years or so... one may well find oneself begining to doubt again whether all this could conceivably be the product of an enormous lottery presided over by natural selection, blindly picking the rare winners from among numbers drawn at utter random. While one's conviction may be restored by a detailed review of the accumulated modern evidence that this conception alone is compatible with the facts (notably with the molecular mechanisms of replication, mutation, and translation), it affords no synthetic, intuitive and immediate grasp of the vast sweep of evolution" [4]. And after pondering over the riddle of the genetic code's origin, he adds: "Life appeared on earth: what, *before the event*, were the chances that this would occur? The present structure of the biosphere far from excludes the possibility that the decisive event occurred *only once*. Which would mean that its *a priori* probability was virtually zero. This idea is distasteful to most scientists. Science can neither say nor do anything about a unique occurrence. It can only consider occurrences that form a class, whose *a priori* probability, however faint, is yet definite" [5]. Thus, Monod concludes that the origin of life may be a unique event, not impossible but improbable to the extent as to be beyond the range of validity of the second law of thermodynamics, or in Monod's inimitable style: "The miracle stands "explained"; it does not strike us any less miraculous" [4].

On this background Manfred Eigen's study of self-organization of matter [2] is a most significant landmark. He showed that a set of self-reproducing macromolecules must undergo processes that have the characteristics of Darwinian selection, and that such processes generate information. Eigen elevated Darwinian selection from the status of a law governing the evolution of biological species, namely, a biological law, to the status of a general law, physico-chemical as well as biological, governing all self-reproducing systems, whether animate or inanimate. He showed that chemical evolution must have preceded biological evolution, and that Darwinian selection must have governed not only the evolution of the species but also the evolution of inanimate matter towards the acquisition of animate properties.

Eigen's theory leads to two major conclusions that require special emphasis. First, it resolves the difficulty of the apparent violation of the second law of thermodynamics that bothered Wigner and Monod. Darwinian selection among self-reproducing copolymers leads to the formation of a 'quasispecies' comprised of a best-adapted 'wild-type' copolymer together with its closest mutants. Thus, an event that is most improbable a priori becomes probable if it is arrived at by the way of selection.

Second, Eigen's theory offers a physico-chemical explanation for the development of purpose-like, or teleonomic, properties in inanimate matter. (*Teleonomy* is purposeful organization and behavior, characteristic of living organisms and life processes. *Teleology*, the quality of having an ultimate purpose, is distinguished from *teleonomy* by having a theological, or metaphysical, connotation. See the appendix for a more detailed discussion of the term and its origin.) Teleonomic behavior is the most fundamental property of life.

According to Darwinian theory, the evolution of teleonomic properties by living systems is the result of the survival of the fittest by natural selection. According to Eigen's theory, the gradual maximization of a 'selective-value function' in self-reproducing macromolecules as they evolve towards a quasi-species well-adapted to its environment is the most elementary manifestation of teleonomic behavior by inanimate matter.

In the present communication I wish to shed some more light on these two issues, namely, the compatibility of the transition from inanimate to animate matter with the second law of thermodynamics, and the acquisition of teleonomic properties by inanimate matter. I shall outline a variant of Eigen's theory, starting with a primitive self-replicating copolymer as the first step on the road of transition from inanimate to animate matter. This variant, I believe, is particularly suited to highlight the role of *imperfect self-replication* in initiating diversity on the one hand and chemical selection on the other, in creating systems that are otherwise a priori highly improbable, and in endowing such systems with teleonomic properties.

2. Chemical selection and diversity

In setting the scene for transition from inanimate to animate matter, one must take for granted the existence of a prebiotic world where multitudes of various chemical compounds interact with each other in all possible ways according to the laws of chemistry and physics, continuously forming and breaking structures that contain covalent bonds, ion complexes, as well as weak interactions such as hydrogen bonds. Also granted is an eletromagnetic source of solar energy that catalyses various reactions by creating free radicals and other forms of excited molecules. From the numerous structures and processes that must have occurred in such an environment let us single out those of interest in our present context. These may be grouped in three sections, according to their share in explaining the gradual onset of teleonomic properties in inanimate matter.

2.1. Linear copolymer chains

Many monomer compounds could polymerize to form various structures, among them also linear copolymers of various chain lengths. Two microscopically distinguishable properties of linear copolymer chains (namely, properties of the individual chain, not of the macroscopic, bulk material of copolymers) are relevant to the origin of animate matter. The first is that as chains become longer, the number of different sequences of monomers grows so fast, that any particular sequence that may have occurred by chance, if long enough, is a '*one-time event*'. That is to say, it will most probably never again occur by chance within a time scale much larger than that of the age of the earth or indeed of the whole universe. To see this, note how m^n, the number of microscopically distinguishable sequences in a copolymer that is n monomer residues long and is made of m monomer species randomly distributed along the copolymer chain, increases incredibly with chain length. For $m = 4$ monomer species, as in nucleotides or $m = 20$ as in amino acids, and for chain lengths $n = 50$–100, one obtains $10^{30} < m^n < 10^{130}$. Since the age of the universe is 'only' approx. 10^{18} s and the surface of the earth is only approx. 10^{18} cm^2, random synthesis of particular sequences must indeed be a one-time event.

The second microscopic property of linear copolymers that is relevant to the present discussion is that each member of the set of m^n possible individual sequences can exist in an enormous number of temporary states, or conformations. These conformations maintain in general a dynamic equilibrium, where their relative probabilities of occurrence are determined by their relative energies, according to the Boltzmann law of distribution of microscopic states in a thermodynamic system. The physico-chemical properties of each sequence are averages over the ensemble of all its available conformations, and may vary widely from one sequence to another.

Since it is impossible to separate a single sequence from the bulk of copolymers obtained by random polymerization, only the macroscopic properties of such a copolymeric material, averaged over all the conformations of all the sequences, can be observed. While particular sequences may possess exceptional properties, these are unobservable. Since long copolymers are in general, as we have seen, one-time events, their individual properties disappear forever without being noticed, once the chain is decomposed.

This situation is analogous to the thermal motion of molecules in a gas, where some molecules are temporarily much faster than others. Maxwell suggested that if there were a 'demon' that could select all fast molecules and direct them to one corner of the room, he would create a macroscopic temperature difference out of a dynamic equilibration distribution of microscopic velocities, i.e., out of a macroscopically uniform temperature. The nonexistence of Maxwell's Demon is, according to Maxwell, equivalent to the second law of thermodynamics. By analogy, the separation of microscopically distinguishable copolymers of exceptional properties from a bulk of randomly distributed copolymer sequences would also require a Maxwell's Demon, in violation of the second law of thermodynamics.

Biological copolymers such as nucleic acids and proteins are all microscopically distinguishable one-time events each possessing some exceptional property, that together constitute the living cell. Therefore their creation or arrival *by chance* at the same time and space would obviously be a glaring violation of the second law of thermodynamics. The question can therefore be put metaphorically: Who is this relative of Maxwell's demon that created animate matter, and how did he perform this tricks?

2.2. *Autocatalysis and selection among chemical compounds*

Autocatalysis is rare in our present environment except inside living cells, but in prebiotic environments, not yet overwhelmed by animate matter, a whole variety of autocatalytic processes may have occurred. Template replication of copolymers is special among autocatalytic processes and its uniqueness, that might have led eventually to molecular evolution and the onset of teleonomy, is the subject of section 2.3. This section focuses attention on two preliminary issues of major importance. One is the power of autocatalysis to modify the probability of occurrence of events, the other being the introduction, through autocatalysis, of chemical selection as distinct from chemical competition.

Any autocatalytic process must start with the synthesis of a first autocatalytic molecule that is obtained 'de novo' by some other chemical process when a 'substrate', namely, a starting material, is available and other appropriate conditions prevail. The de novo synthesis of an autocatalytic molecule may be an improbable, rare event, even to the extent of being a one-time event in the sense discussed above. However, *once an autocatalytic molecule occurs by chance as a microscopic event, the probability of other such molecules reoccurring is radically changed.* This radical change endows autocatalytic molecules with the 'demonic' potential, using Maxwell's metaphor, of growing from a microscopic event of low probability to a macroscopically observable object, and is the key to the solution of the Wigner-Monod puzzle about the a priori improbability of the transition from inanimate to animate matter. Once a first autocatalytic molecule occurs de novo, a second one has obviously a larger probability of occurrence than the original, since it can be synthesized either de novo or autocatalytically. The occurrence of further replicas doubles from generation to generation provided the original conditions (including availability of substrate) prevail. This is the so-called exponential growth, typical of all autocatalytic processes. Explosive reactions, chemical as well as nuclear, are in this respect autocatalytic processes.

Considering that molecules possess a finite rate of decomposition, it may be noted that autocatalytic molecules either grow exponentially, if their rate of synthesis is faster than that of decomposition (positive rate of net growth) or decay exponentially, if it is slower (negative rate of net growth).

Exponential, positive net growth of autocatalytic reactions cannot prevail for long at a constant rate, since it must gradually deplete the substrate on which it depends. Thus, the rate of net growth decreases gradually, eventually reaching the state of zero rate of net growth, where decomposition matches growth.

Zero net growth may be a stable steady state when substrate molecules are continuously supplied to a single autocatalytic compound. In such a steady state the rates of composition and decomposition are precisely equal to each other and depend on the rate of supply of substrate. The point of zero growth may also be transient rather than stable. For example, if there is no continuous supply of substrate, the system moves on from the state of positive net growth to a negative one. Ultimately it becomes extinct, the information for autocatalysis is lost, and only de novo synthesis can restore it. If the molecule is of the kind described as one-time events, the information is lost forever.

Consider now the case of two autocatalytic compounds 'feeding' on a continuous supply of the same substrate in the same environment. A steady state in such circumstances is inherently unstable. As the consumption of the substrate by the two autocatalytic compounds proceeds towards balancing its supply, one autocatalytic compound may still be in the net exponential growth phase, while the other may have already crossed the sharp demarkation line of zero growth into the phase of net exponential decay, which must lead to its extinction. Thus, under such circumstances, competition between two autocatalytic compounds for the same substrate leads necessarily to 'survival' of one and 'death' of the other. The one whose net growth rate is larger reaches a stable steady state whereas the other becomes extinct.

Quite obviously, similar considerations are valid when any finite number of autocatalytic compounds depend on the same substrate. The compound with the smallest net growth rate is the first to fall into negative net growth rate leading to its extinction. The others follow suit one after the other, until the one with the fastest net growth rate remains the single survivor.

Such competition between autocatalytic compounds deserves the name chemical selection. It is inherently similar to Darwinian selection between biological species. It may therefore be appropriate and even illuminating to include both chemical selection and biological selection in natural selection, referring to both inanimate and animate nature.

Chemical selection is inherently different from other forms of chemical competition where two nonautocatalytic simultaneous reactions compete for the same substrate. There the competing reactions may proceed at different rates, but no single reaction is eliminated by the other.

However, chemical selection in itself does not necessarily imply evolution. Evolution depends on the dynamics of diversification of the ensemble of systems on which chemical selection acts, and that is where template replication of copolymers enters.

2.3. Template replication

Template replication of copolymers is a particular autocatalytic mechanism based on 'microscopic recognition', which is a physico-chemical interaction, where each one among the several types of monomer residues binds preferentially to its corresponding type of monomer substrate.

Template-replicating copolymers share with other copolymers all the properties discussed in section 2.1, namely, that the number of microscopically distinguishable sequences as well as the number of conformations of each sequence, and consequently the diversity of properties of the microscopically distinguishable sequences, all increase exponentially with the copolymer's chain length.

Template-replicating copolymers share with other autocatalytic systems all the properties discussed in section 2.2, viz., that their exponential growth is limited by the supply of monomer substrates, so that they must approach a steady state where copolymers with positive net growth are selected against copolymers with negative net growth.

In addition to these characteristic properties, template-replicating copolymers possess a singular property: they can generate new copolymers whose microscopically distinguishable sequences have never occurred before. New copolymers are generated either by errors in the microscopic recognition of the substrate monomers or by various mechanisms of modifying the chain length of the copolymers. As a consequence of this property, self-replicating copolymers have an unlimited capacity for *diversification*. It is sufficient that sometime somewhere under some favorable environmental conditions a single, short, self-replicating copolymer be synthesized de novo by chance, and the ensuing self-replications and diversifications repeated on and on may form a vast *distribution of self-replicating copolymers*.

Chemical selection among template-replicating copolymers differs from that described in section 2.2 in two important ways. First, copolymers are selected not only for faster replication and slower decomposition but also for fidelity of replication. Those that make less errors in replication have a better chance of positive net replication. Second, new members of the distribution are continuously formed while the existing members compete for survival. Consequently, the copolymers that are at any given moment the best fit for survival need not be the survivors, since the composition of the distribution may change while selection goes on.

Distributions of template-replicating copolymers are thus driven by two opposing 'forces': *selection* and *diversification*. Chemical selection tends to set the distribution on a *convergent course* towards a select distribution that Eigen called a 'quasi-species', since it shares with biological species the most fundamental property of being well-adapted to its environment. The quasi-species is composed of a '*wild-type*' copolymer, the chief survivor of the chemical selection, and its '*mutants*', derived from the wild type by errors in replication.

Chemical diversification, on the other hand, tends to set the distribution on a *divergent course*, where new copolymers are continuously generated while old ones become extinct. If the copolymers in such a '*drifting distribution*' are long enough to constitute one-time events as defined in section 2.1, they may appear once in the distribution and then mostly disappear, never to appear again.

Eigen set the conditions that determine the boundary between divergent and convergent courses of a distribution. He showed that the maximum degree of polymerization (chain length) of a stable quasi-species is inversely proportional to the percentage of errors in the microscopic recognition, and directly proportional to a quantity that measures the selective superiority of the wild type over its mutants. He also showed that the closer the chain lengths of the members of a distribution are to the maximum length set by the stability condition, the faster the evolution towards a stable quasi-species, while if the chain lengths extend beyond this maximum, the distribution diverges.

3. Teleonomy and the second law of thermodynamics

A quasi-species as defined by Eigen is the most elementary system that possesses a purpose-like, or teleonomic, character. It is most elementary because it originates from a nonteleonomic system, a distribution of template-replicating copolymers, by a nonteleonomic process, chemical selection. It is teleonomic because it has acquired the property of survival, namely, of keeping its identity while the wild type and its mutants continue to replicate. The quality of being best-fitted, or well-adapted to its environment may be viewed as a purposeful property that is required for survival.

However, teleonomy as a property of animate matter that distinguishes it from inanimate matter implies more than a passive fitness of a distribution of template-replicating copolymers to its environment. The template-replicating copolymers in biological species actively direct the construction of their own environment within the boundaries of the living cell. Through the elaborate machinery of the genetic code they conduct the construction of cell walls, synthesis of substrate monomers, speed and accuracy of replication and supply of chemicals and energy across the cell walls. In short, they exhibit purposeful, teleonomic properties on a much higher level of sophistication and complexity.

Is the evolution of higher levels of teleonomy based on the same principles that directed template-replicating copolymers towards either quasi-species or drifting distributions? Eigen's theory of self-organization of matter [2] and its extension to the model of 'the hypercycle' [6] answers this question in the affirmative. From the point of view of '*chemical evolution*', namely, of long-range dynamic changes, both the quasi-species and the drifting distributions are only transient states. Distributions of template-replicating copolymers are in the long run inherently unstable, not only because the environmental conditions change on such a time scale. More importantly, any rare occurrence of a single template-replicating copolymer with a strong selective advantage may destabilize the system, converting a rare event to a dominant phenomenon through fast exponential, positive net growth. A drifting distribution generates continuously new copolymers, thus scanning the enormously large '*sequence space*' of all possible sequences for rare events of selective advantage. Each time such an event is met, the distribution may be set on a convergent course towards a new quasi-species. On the other hand, an existing quasi-species may be destabilized, either by a rare large error in replication or by some mechanisms of chain elongation that may form longer copolymers than allowed by Eigen's stability condition. Such copolymers may initiate a drifting distribution if they compete successfully with the quasi-species distribution for substrates.

Among the various factors that determine the selective advantage of microscopically distinguishable template-replicating copolymers, interaction with the chemical environment may play a major role. Compounds in contact with the copolymers may inhibit or promote the processes of microscopic recognition, template replication and decomposition, in some sequences more efficiently than in others. Conversely, some microscopically distinguishable copolymers may play an active role in catalysing such inhibitors or promoters. Thus, both passive and active interactions of template-replicating copolymers with their environment affect the chemical evolution of their distributions. Any copolymer that uses compounds in its vicinity as chemical promotors to enhance its selective advantage or that catalyses such promoters may grow by selection to form the wild type in a quasi-species. Among the teleonomic properties of such a quasi-species one may then count active response or modification of its environment in ways that serve the 'purpose' of its being well-adapted to it.

There is a very long distance between a mentally constructed quasi-species that modifies teleonomically its environment in as yet unknown and supposedly primitive ways at one end, and a live and functioning cell at the other. However, the long road that connects these two ends must have been paved by the chemical evolution of template-replicating copolymers. This is in essence Eigen's theory of chemical evolution, and as such it is seen to be an extension of Darwin's theory of biological evolution, since it recognizes in template-replicating copolymers the same properties that Darwin recognized in biologically replicating species, namely, diversification and natural selection.

The Wigner-Monod puzzle of the apparent violation of the second law of thermodynamics by the appearance of life on earth can now be resolved in the light of the theory of chemical evolution. The appearance of life on earth *by chance*, even in its most primitive forms, is indeed so improbable as to be inconsistent with the second law of thermodynamics. Chemical structures and processes that convert improbable or less probable events to more probable ones are therefore necessary in order to circumvent the probability barrier. Such structures and processes lie indeed at the roots of the theory of chemical evolution. The structures are template-replicating copolymers, and the processes are autocatalysis, diversification and selection. *Autocatalysis* converts a microscopic single event, de novo synthesis of an autocatalytic molecule, to a macroscopically observable phenomenon. *Diversification* converts a single template-replicating copolymer to an ever-growing distribution of such copolymers. *Selection* singles out from the distribution the copolymers that fit best to their environment. Chemical evolution thus paves the road to a primordial living cell without violation of the laws of physics and chemistry just as biological evolution extended this road from the primordial cell to the biological world of today.

In concluding these reflections on Eigen's theory of self-organization of matter, I wish to return to the metaphor of Maxwell's Demon. This demon, a creation of the mind, was supposed to play the trick of converting improbable microscopic events into observable macroscopic phenomena, but failed, of course, to do so. Three demons are required to play the trick of converting inanimate matter into self-organized matter: autocatalysis, diversification and selection. They seem to have been more successful. They deserve to be named *Eigen's Demons*.

Appendix: Purpose as a physico-chemical property of matter

Teleonomy, namely, purposeful organization and behavior, may be considered to be the most significant property of animate matter. It seems therefore appropriate to devote a few comments to the legitimacy of teleonomy as a physico-chemical concept. The fundamental laws of nature are universal. Yet, there are properties and modes of behavior, with their associated laws, that belong solely to animate matter, just as other properties are typical of other classes of matter. The unity of science excludes neither the existence of particular modes of behavior of particular systems nor particular laws that govern such behavior. On the contrary, science as a whole is based on a hierarchy of complexities in nature, from quarks to nucleons, to atoms, to molecules; from single particles to thermodynamic systems, to animate matter; from single cells to multicellular organisms to societies and ecosystems. As science addresses itself to higher levels of complexity, it requires new concepts and new laws to represent the new phenomena observed. Thus, temperature, pressure and chemical potentials are applicable to macroscopic systems but are useless to meaningless for single particles. However, they are related to the microscopic properties of single particles through statistical mechanics. Similarly, the 230 groups of space symmetry represent the symmetry properties of crystals and are useless or meaningless for other states of matter. However, their existence can be derived from the symmetry properties of single molecules and the intermolecular forces between neighboring molecules. In the same way teleonomic, namely, purpose-like behavior, is a biological property of animate matter, meaningless or useless in the study of inanimate matter. However, it is related to the physico-chemical properties of matter by being the result of Darwinian selection.

Linked with teleonomy is a huge collection of semantic concepts. Animate, and only animate, matter can be said to be *organized*, meaning that it is a system made of elements, each one having a *function* to *fulfill* as a necessary *contribution* to the *functioning* of the system as a whole. There is, or it seems as if there is, a *purpose* built into any living system, as well as in its *functioning* elements. (Note that all terms emphasized in italics have teleonomic connotation.) Using philosophical terminology, it is often said that living matter exhibits *teleological* behavior. However, attributing *teleological* properties to animate matter may be interpreted, and often rightly so, as sneaking-in *vitalism* through the back door.

It is for this reason that Jacques Monod [3] has adopted the term teleonomy instead of teleology, the one being related to the other like *astronomy* is related to *astrology*, *chemistry* to *alchemy*, or *physics* to *metaphysics*. Monod defines teleonomy as follows: "All the structures, all the performances, all the activities contributing to the success of the essential project will hence be called "teleonomic" [7]. One may note that this definition is circular, as it uses terms like 'success' and 'project' which are themselves teleonomic, and that it does not draw a clear demarkation line between teleonomy and teleology. One may similarly criticise as circular my above reference to an organized system as one that has a function and is made of functional elements, since function in this sense is as teleonomic a concept as organization. Such relations, like definitions in general, are tautological. They leave open the big question, what makes the concept teleonomy a scientific necessity, what is the origin of teleonomic systems, how did they come into existence in a prebiotic environment?

It is of some interest to trace back the term *teleonomy* to its origin. Bernie D. Davis [8], in his opening lecture at a symposium on cellular regulatory mechanisms, refers to teleonomy and its relation to teleology as follows:

"Most biologists, of course, in using the term teleology to denote the development of valuable structures and mechanisms, understand implicitly that they have in mind natural selection as the responsible agent, rather than the divine foresight of the original definition. However, the term still raises uneasy doubts concerning the theological bias of its user, and so I would like to support the recent proposal by Pittendrigh (1958) of the term *teleonomy* to make explicit the shift in the meaning of teleology as used by the modern biologist. I am reminded of the statement, ascribed to von Bruecke, that teleology is a lady without whom no biologist can live – but he is ashamed to be seen with her in public. If the change in name means that the lady's alliance with biology has acquired legitimate marital status, perhaps her numerous offspring will be more readily subject to confirmation".

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