

Systems Biology

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A systemic approach to the origin of biological organization

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SUMMARY

I present here an analysis of the core of biological organization from a genealogical perspective, trying to show which could be the driving forces or principles of organization leading from the physico-chemical world to the biological one. From this perspective the essential issue is to understand how new principles of generation and preservation of complexity could appear. At the beginning, the driving force towards complexity was nothing but the confluence of several principles of ordering, such as self-assembly, template replication, or self-organization, merged in the framework of what I have called a nontrivial self-maintaining organization. The key of this process is functional recursivity, namely, the fact that every novelty capable of contributing to a more efficient form of maintenance will be recruited. This leads us to the central concept of autonomy, defined as a form of self-constructing organization, which maintains its identity through its interactions with its environment. As such, autonomy grasps the idea of (minimal) metabolic organization, which, in turn, is at the basis of what we mean by (minimal) organism. Finally, from the concept of autonomy, I try to show how it has generated a new and more encompassing system in which evolution by natural selection takes over, generating in turn a new form of individual organization (genetically instructed metabolism) erasing the previous ones.

1. INTRODUCTION

Living systems appear as highly complex integrated units formed out of many different and complex chemical aggregates. Nothing similar in degree of complexity exists in the inorganic world, neither among human-made artifacts, where systems lack the deep integration and autonomy characteristic of living organisms. This organization is an intricate web of chemical reactions organized spatiotemporally. Organisms share the property that the functional molecules of their material make-up (DNA, proteins, fatty acids, etc.) are fabricated by internal processes. One could say that the functional hardware of living systems is continuously changing as new proteins are constructed and other molecules synthesized. The first conclusion, then, is that those components that make up the system as a whole are, in their turn, generated through the web of interactions of the whole system (in the sense that each process depends on several others within the system). This apparent causal circularity – along with the deep integration and high complexity of their components – makes the understanding of biological systems extremely difficult. Thus, the explanation of biological systems requires many different principles: physical and chemical laws, self-organization, and even informational constraints.

Already, certain philosophers acknowledged the problem of deep integration and holism, which are so characteristic of biological systems. More than 200 years ago, I. Kant (1790:1987) remarked that living systems are beings that organize themselves; they are systems whose parts depend on each other so that, taken as a whole, a living being is both the cause and effect of itself. Scientists, however, have begun to see living organisms from a holistic perspective only more recently.¹ In the 1950s Rashevsky (1954) defended the idea that living organization can only be explained in relational terms, i.e., every component in a biological organism will have an explanation in which the other components of the system are involved. R. Rosen, a disciple of Rashevsky, has held a similar view, defining organisms as ‘systems closed under efficient causation’ (1991). In contrast to any man-made machine, living organisms are self-made machines, in the sense that all the complex components are made within the system. In other words, the complex organization of living systems is a consequence of itself. To consider the whole network as a result of a former (lower) level made up of simpler isolable components whose properties determine their interactions would be partial, and ultimately, useless. The reason is that many of these components can only exist as such, as a consequence of the recursive maintenance of the whole network. In other words, complex components depend on the whole system.

¹ With the important exception of Developmental Biology at the end of nineteenth century and the beginning of the twentieth century.

01 However, this holistic view of living organization is at odds with the standard
02 evolutionary perspective, which sees organisms as the result of changes in genes
03 that have taken place at the populational level. Modern molecular biology has
04 grounded this view, presenting a highly hierarchical approach of cellular orga-
05 nization. According to this view, the extreme precision of cellular organization
06 relies on the fact that practically all biological reactions are controlled by one
07 kind of macromolecule: catalytic proteins, i.e., enzymes. If we inquire about
08 the cause that produces a given protein we will find a rather peculiar situation.
09 In the first place, we can answer that, as any other component of the cell, a
10 protein is the result of the action of a set of components (which will constitute,
11 in Aristotelian terms, the efficient cause of this particular protein). Concretely,
12 the synthesis of any protein is a direct consequence of the action of tRNAs
13 and peptidyltransferase protein molecules, both involved in the formation of the
14 string of amino acids. Another answer to the question is that the cause of a pro-
15 tein is the smaller molecular aggregates of which it is made of (this constitutes
16 in Aristotelian terms its material cause). Then, amino acids would be considered
17 to be the material cause of proteins.

18 Unlike other components, proteins are highly specific and complex. As is
19 well known, the specific sequences of amino acids that constitute the proteins
20 of a particular organism are related ultimately to the specific sequences of the
21 nucleotides of DNA molecules. DNA (and RNA) acts, then, as an 'informa-
22 tional' template for the synthesis of proteins, because it contains the necessary
23 instructions for guiding the construction of primary sequence of proteins. Hence,
24 we can say, in Aristotelian terms, that DNA molecules are the formal cause
25 of proteins in biological cells, because their specific sequence of nucleotides
26 conveys the 'form' of the latter.

27 If we finally ask which is the cause of the specific form that DNA molecules
28 carry, the answer would send us to a more encompassing framework than that
29 of the individual cell. There is a fundamental difference between DNA and
30 the remaining components of the cell. Although materially speaking, DNA is
31 made up of building blocks as any other component, the specific order of
32 the nucleotide sequence of a given DNA is ultimately a consequence of the
33 evolutionary process, which leads us beyond the level of the cell. DNA represents
34 a material connection between the evolutionary and the organismic levels, the
35 collective/historical dimension and the individual organization. This is why DNA
36 'escapes' in a certain sense the causal closure that characterizes the organization
37 of individual living beings.

38 This seems to give the final word to (Darwinian) evolution. But what is
39 in fact evolution? Biological evolution, as we know it, requires the existence
40 of certain types of systems: self-reproducing discrete entities based on a full
41 Geno-Phenotype separation (namely, a code-based organization), which compete
42 among each other in a noninterbreeding way. Then, if Darwinian evolution does

01 not exist without organisms (or something almost likewise complex) how to
02 explain the appearance of organisms by evolutionary mechanisms?

03 The solution to this dilemma leads us to the question of the origins. If evolution
04 requires a certain threshold of organizational complexity, we have to search
05 what kind of principles would explain the appearance of such organization.
06 Which kind of properties/features that could have appeared in a purely physico-
07 chemical scenario (and that, despite such initial simplicity, could be capable
08 of generating a sequence of steps of increasing complexity) should the early –
09 necessarily simple – prebiotic organizations possess? How can such an intricately
10 holistic and complex organization appear from the much more ‘simple’ and
11 understandable physico-chemical world?

12 As has been mentioned at the beginning, the understanding of biological
13 organization will require many different principles. I am convinced that, unless
14 we understand how all these organizational principles have become entangled
15 together, we will not achieve a full understanding of life.

16 2. THE ORGANIZATIONAL PERSPECTIVE

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19 The process by which living organization originated may probably be a sequence
20 of different forms of organization, progressing from relative simple to more
21 complex stages. In a general sense, the term organization means the activity
22 (or result) of distributing or disposing a set of elements properly or methodically.
23 Namely, in an organization there is a nonrandom arrangement of parts, generally
24 serving a purpose or function. However, for obvious reasons, in our case, we
25 have to discard any form of external design and/or purpose. That is why, in a
26 prebiotic context, the idea of organization is rather associated with the formation
27 of dynamical systems in which the random interaction of their parts generates
28 the ‘emergence’ of a global order.

29 The spontaneous emergence of order could take two different forms: self-
30 assembly (SA) and self-organization (SO). Unlike evolution, both SA and SO
31 are widespread phenomena, which do not require very complex elements or
32 systems. Self-assembly is a process in which a set of (randomly distributed)
33 elements group together, forming a stable structure (an order), e.g., a crystal.
34 This process is due to the material properties of the elements, namely, to the
35 forces acting among them. Thermodynamically, self-assembly can be described
36 as a process towards equilibrium, ending in a stable structure.

37 In both SA and SO there is the emergence of order from a set of randomly
38 interrelated elements. However, in the case of SO this order is not a conse-
39 quence of the structure of the constitutive elements,² but of certain boundary
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42 ² However, as we shall see, complex forms of SO will require the introduction of a variety of specific constraints in the constitutive elements.

01 conditions in far-from-equilibrium (FFE) conditions: the emergent order is essen-
02 tially dissipative. Given certain specific boundary conditions in FFE a set of
03 local interactions becomes nonlinear, and a collective behavior – a macroscopic
04 pattern – emerges. Now, the maintenance of this pattern is not only a con-
05 sequence of the given boundary conditions, but also a result of the inherent
06 recursivity of the process: once it appears, the pattern constraints the dynamics
07 of the system components so that the produced pattern in turn produces itself.
08 For instance, in the case of Bénard convection cells, the emergent pattern (the
09 creation of hexagonal cells) contributes to the self-maintenance, because the fact
10 of belonging to a certain cell is what makes a molecule turn to the left or the
11 right. Thus, recursivity and removal from thermodynamic equilibrium is the key
12 feature of this concept of organization.

13 Though very different in nature, both SA and SO are important sources
14 of order. In fact, many systems show both forms. However, only SO really
15 holds the dynamical and functional senses of the idea of organization. The term
16 ‘organization’ implies not only order, but also the usefulness of this order that
17 it effectively does something. And for this ‘doing’, a continuous process is
18 implicitly necessary. SO is therefore the ground of any organization as it is a
19 dynamical form of order that contributes to the creation and *maintenance* of itself.
20 The minimal (because self-sustaining) meaning of the terms *task* and *function*
21 is that something is contributing to the maintenance of the very organization in
22 which it appears. As we shall see, this internal sense of usefulness that appears
23 in SO is the key for allowing a process of increase in complexity.

24 25 26 **3. THE STARTING POINT: NONTRIVIAL SELF-MAINTENANCE**

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28 Now, within this idea of organization, what is of interest for our purpose? As the
29 process by which life originated was probably a sequence of different forms of
30 *organization* going from relative simple to progressively more complex stages,
31 we have to look for a kind of organization fulfilling two basic conditions: on the
32 one hand, such an organization has to be, in principle, simple enough for it to be
33 likely to appear from sets of material aggregates formed spontaneously; on the
34 other hand, it has to have the capacity, at least in principle, to further generate
35 other, more complex forms of organization³ (and so on, until new organizational
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38 ³ Here I will use the term complexity in an organizational frame. This means that by an increase of organiza-
39 tional complexity I am not considering a mere increase in the ‘complicatedness’ (i. e., more number and variety
40 of components) of the system, but rather a functional re-arrangement of this complicatedness. In this sense,
41 an increase in complexity is linked to the generation within a system of new functional levels of organization.
42 Thus, an increase of organizational complexity can take the paradoxical form of an apparent ‘simplification’
of the underlying complicatedness when a system creates a new hierarchical level (Simon, 1969) through a
functional loss of details (Pattee, 1973).

01 principles would appear). Accordingly, the fundamental problem can be stated
02 this way: ‘How can a system be organized such that (given certain specific but
03 probable conditions⁴) it can generate higher degrees of complexity, and, at the
04 same time, is capable of retaining this new complexity?’

05 As for the first requirement, we should conceive a set of prebiotically plausible
06 boundary conditions capable of driving a variety of chemical (see next point)
07 systems where the maintenance of the process is (at least in a very simple sense)
08 a consequence of the very organization of the system, namely, a self-maintaining
09 system (SMS). Although such systems had to be probably preceded by many
10 other systems whose maintenance was essentially driven by boundary conditions
11 much more complex than themselves, the appearance of SMS is the fundamental
12 starting point for a sustainable process of increase in complexity. For, if the
13 retention of new complexity in a SMS were mainly dependent on an increasingly
14 complex set of external conditions, we would be only transferring our problem
15 (namely, the natural, prebiotic origin and maintenance of increasingly complex
16 forms of organization) to the external environment. Accordingly, the starting
17 point should be a self-maintaining (SM⁵) organization, namely, a system in
18 which it is the organization itself (rather than external conditions) that explains
19 the maintenance of the process. This leads us to the second requirement.

20 As for the second condition, the way in which the system realizes its own
21 maintenance has to be nontrivial. By a nontrivial form of self-maintenance
22 (henceforth, NTSM), I mean those systems where there are many simple inter-
23 actions involved in its realization and (also many) ways to achieve it. In other
24 words, the system has to be capable of increasing the number of different func-
25 tional relations (within an integrated whole). In the next section we will see how
26 this can be done.

27 These two requirements should be entangled, namely, the very organization
28 plays some role on itself, such that it creates new internal differences; and some
29 of these organizational differences may later play a new functional role. For
30 instance, a new form of organization (say, a self-enclosing autocatalytic network)
31 might be preserved because it allows a more stable form of maintenance.

32 But what kind of self-maintaining organization is at the same time minimal
33 (i.e., the simplest) and capable to increase in complexity? This is the kind of
34 organization that I call ‘nontrivial SM’. Let us examine this question in several
35 steps. First, I shall characterize what is a trivial form of SM. Second, I will
36 consider the necessary (but not sufficient) condition for an NTSM. And finally,
37 I will discuss the (minimal) organizational requirements for NTSM.

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39 ⁴ In terms of what the physical and chemical evolution of the universe can create in certain places during
40 reasonable temporal periods.

41 ⁵ The term SM is usually referred to in studies of the organization of chemical systems (because of the
42 constructive character of these systems), whereas in physical systems the usual term is self-organization. But
here, I am using the term SM generically, as equivalent to SO.

3.1. From self-organization to NTSM

We now want to address the relation between SO and complexity. Ordinary forms of SO – those which can appear in relatively simple conditions, be they in natural ones, like thunderstorms, or in artificial ones, like Belousov–Zabotinskii reactions – may show in certain cases significant degrees of robustness, but they seem unable to achieve further increases in complexity. Let us take the example of the so-called dissipative structures. A Dissipative Structure (DS) is a phenomenon by which a set of nonlinear microscopic processes generates a macroscopic-collective pattern in a situation of distance from thermodynamic equilibrium⁶ maintained by the continuous action of a group of constraints, one of which is the very pattern generated by the global dynamics. Now, although in classical DSs (either physical or chemical) the emergent pattern may be very complicated, its contribution to the maintenance of the process is always ‘simple’, in the sense that such global pattern cannot exert a variety of selective local constraints on the microscopic dynamics. In Bénard’s Convection Cells, for example, the pattern only makes a molecule turn to the left or the right. Thus, the generation of new complexity is only possible if the dissipative organization of the system develops a remarkable degree of internal plasticity, so that certain elements (and/or patterns) will be recruited to serve different roles in the system, thus producing a new form of SM. But how?

The answer is a SM organization that produces local and selective constraints (instead of only one or few global patterns). In other words, it has to be a chemical organization, for physical systems in general do not have the capacity to create a wide enough variety of dynamical constraints. On the contrary, the chemical domain is based on relations among elements that generate new elements, and these new elements may in turn give rise to different interactions, which may produce new elements, and so on, bringing about a potentially unlimited set. From the thermodynamic perspective, chemical systems are a special kind of organization in which the construction of new molecular variety through dissipative processes creates new conservative constraints (molecular shapes), which in turn can modify the whole organization, and so on. A chemical organization creates many local, selective constraints (new components) and its global maintenance relies on many of them. Interestingly, some elements – called catalysts – can modify the relations among elements, and therefore a chemical system is potentially a domain where components can become rules and vice versa.

In other words, the jump from physics to chemistry seems necessary for material systems to reach a diverse enough spectrum of dynamic, constructive, and

⁶ Unlike the case of self-assembling structures, which keep their order in thermodynamic equilibrium.

01 emergent behavior.⁷ Chemistry allows accumulative construction, a process of
02 interactive feedback between the organization of components and the accumula-
03 tive assembly of increasingly complex components, which is a consequence of
04 the combinatorial – chemical – nature of molecules. This way, chemical networks
05 can reach a special plasticity or potential for diversification. This does not mean
06 that chemistry is enough for this process of increase in complexity. As we see in
07 biological systems self-assembly is also an important factor of the construction
08 of their complex organization, and once a high level of molecular complexity is
09 reached, there are even constructive processes of mechanical nature. But what I
10 want to stress here is that all these processes are possible due to the establishment
11 of a NTSM chemical organization.⁸

12 Now, what does SM mean in this context? The basic idea is that of auto-
13 catalysis: molecule A could catalyze the formation of B, B of C, and C of A
14 (but of course many more reactions and side reactions can occur). Given a set
15 of specific initial conditions, a process of production of components may be
16 triggered, creating new components and catalysts, which in turn will produce
17 new ones, and so on, until the initial set of components is produced and the
18 whole process becomes recursively regenerated.⁹ The key feature of a SM orga-
19 nization capable of increasing its complexity is that the circular loop involves
20 the generation of many (some of them stable) components that may act as local
21 and selective constraints (molecules and supramolecular structures). In other
22 words, an increasing part of the dynamical order is recorded in complex stable
23 structures/components (which in turn will allow more complex forms of orga-
24 nization). However, the maintenance of the system depends on the whole set
25 of relations, and is therefore a distributed, holistic phenomenon. The interesting
26 point here is that, once a certain threshold of complexity is crossed, the main-
27 tenance of an autocatalytic organization lies in the entire network, instead of in
28 single reactions (see footnote 12). Thus, the main characteristic of a system of
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31 ⁷ It is necessary but not sufficient. In fact, a chemical DS like a BZ system is a type of organization in which
32 the emergent pattern depends on dynamical factors, such as (the behavior of) concentrations or diffusion of
33 the components of the system, but not on changes of the relations of production (catalytic reaction rates)
34 among components. Thus, the emergent pattern is (like in purely physical DSs) nothing more than a global
35 correlation of billions of molecules allowing a different (according to some authors, more efficient) way to
36 dissipate energy but not a selective re-organization of the component–production relations that may change
37 the identity of the system. For example, a burning candle is a self-maintaining chemical system, in which the
38 macroscopic pattern—the flame itself—contributes to maintaining the organization of the system (by vaporizing
39 wax). However, the flame as a macroscopic, global constraint only plays this action, and therefore it is a trivial
40 form of SM.

41 ⁸ This process, however, would be similar to what Evelyn Fox Keller (this issue) refers to as ‘the iterative
42 processes of self-organization that occur in heterogeneous systems over time’, because she considers the
43 formation of composite systems rather than composite structures (components).

44 ⁹ Autocatalysis constitutes a simple example of the entangled relation between construction and organization
45 maintenance. A dissipative process is maintained through the construction of certain aggregates (catalysts)
46 that in turn modify the interactions in such a way that the organization will again produce such components.

01 this kind is that some components are products of reactions catalyzed by other
02 components whose formation depends recursively on the action of the whole
03 network.

04 A NTSM organization constitutes a special case of the general principle of
05 self-maintenance. Whereas the common feature of all forms of SM is a more
06 or less robust but simple form of recursivity, what is specific in our case is
07 that the whole organization is a potentially self-modifying form of SM.¹⁰ This
08 organization is potentially capable of generating open forms of recursivity, as
09 a change in the initial conditions can bring about new molecular structures,
10 which in turn may produce new forms of organization indefinitely. Such an
11 organization can explore an unlimited¹¹ variety of new molecular combinations
12 and transformation processes leading to new, more complex forms of organiza-
13 tion in the context of reaction webs where a reaction can directly or indirectly
14 influence another, until a certain recursivity (closure) property is reached. The
15 system is self-maintaining because of the recursive and holistic form of its orga-
16 nization: the global dynamics is necessary for the maintenance of (many of)
17 the reactions of the system and these reactions are in turn necessary for the
18 maintenance of the whole system ('metabolic' closure¹²). This is the basic idea
19 behind Rosen's (1971, 1973) 'M, R. systems' or Kampis's (1991) 'component
20 production systems'. A NTSM organization is in fact the core of a metabolic
21 organization.

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23 Along with this capacity to generate internal variety, a sustainable process
24 of increase in complexity requires ways of preserving it. Only those novel
25 forms of complexity contributing to the maintenance of—or being functional in—
26 the organization that generated them can be preserved. Typically, the way to
27 retain complexity is by stabilizing it. There are several ways to create stability
28 within a dissipative organization: from the production of certain structurally
29 complex components that are thermodynamically stable and 'localize' degrees
30 of complexity to functional reorganization in hierarchical levels.¹³ To sum up,
31 a SM organization has the capacity to preserve the generated complexity if it
32 is able to recruit it for a further, more efficient (ultimately, more stable), form
33 of SM. In other words, by 'jumping' to another more efficient form a SM can
34 preserve generated complexity.

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37 ¹⁰ M. Bickhard (2000) uses the term 'recursive SM' with a very similar meaning.

38 ¹¹ This limitless is only potential, because, as we shall see, as the complexity of the organization increases, its
39 brittleness also increases.

40 ¹² As has recently been pointed out by Letelier et al. (submitted, pp. 20–21), a nontrivial idea of 'metabolic
41 closure' is more demanding than that of autocatalytic closure, such that in the former the circularity is a
42 property of the global connectivity in the entire network, not a property of a single reaction.

¹³ Fast and reliable reproduction is also an indirect way to increase the stability of a given organization. We
shall further discuss the origin and consequences of this mechanism.

01 As a consequence, a NTSM organization is capable of a true complexity
02 'bootstrapping', in the sense that (some of) the new organizational varieties
03 (that can be generated) can in turn create new levels of functionality and SM.
04 The creation of increasingly larger and richer chemical networks can even bring
05 forth functionally hierarchical organizations, as for instance, cellular organiza-
06 tions, which in turn generate new forms of SM, increasingly autonomous of the
07 environmental conditions.

10 3.2. The problem of the origin of NTSMs

11 So far the conditions of possibility for the appearance of a prebiotic evolution
12 were analyzed, concluding that the key step is the appearance of certain kind of
13 chemical systems based on what we have called an NTSM organization.

14 We do not know how these kinds of systems could have appeared, neither what
15 the threshold is of complexity of the chemical aggregates necessary to generate
16 them, nor under which set of boundary conditions. These are questions whose
17 answers depend largely on empirical research. Unlike ordinary examples of DS
18 that appear spontaneously, present-day life has created a wide organizational
19 'no-mans-land' (because life has changed primitive conditions and also because
20 of its capacity to eliminate less efficient competitors). This space has probably
21 been occupied by a long sequence of increasingly complex systems (which must
22 in turn have eliminated their precursors). Thus, the appearance of a NTSM
23 organization is nowadays only possible in lab experimental conditions.

24 We may imagine that a great variety of chemical systems appeared on spe-
25 cial places of the Earth (or other similar planets) during the period of chemical
26 prebiotic evolution that took place when the planet cooled down. Among these
27 systems, some would constitute autocatalytic cycles, leading to increasingly large
28 self-maintaining networks, namely, systems where all components and compo-
29 nent aggregates (directly involved in their organizational dynamics) must be
30 products of a reaction network that constructs itself. As Kauffman (1993) has
31 pointed out, 'The origin of life was a quite probable consequence of the collec-
32 tive properties of catalytic polymers. More probably (. . .) many properties of
33 organisms may be probably emergent collective properties of their constituents.
34 The origins of such properties then find their explanation in principles of self-
35 organization rather than sufficiency of time.' In support of this claim, Kauffman
36 (Farmer et al., 1986) and more recently, also other authors (Fontana, 1992, Steel,
37 2000, Hordjik & Steel, 2004) have presented different computer simulations
38 showing the emergence of this kind of systems from a small set of relatively
39 simple components.¹⁴ However, most of these simulations ignore or neglect the
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42 ¹⁴ By now the only evidence of the spontaneous appearance of NTSM systems is computational simulations.

01 thermodynamic requirements for self-maintenance. From a physically realistic
02 perspective, an NTSMSs cannot have appeared unless there exists a set of condi-
03 tions ensuring both the adequate concentrations of its fundamental components
04 and a specific order among their constitutive reactions (endergonic reactions
05 have to be adequately coupled with exergonic ones). As F. Harold has pointed
06 out (2001, p. 251) ‘a credible biopoietic theory will be one that generates mount-
07 ing levels of complexity naturally, by providing the means to convert the flux
08 of energy into organization’.

09 Given the deep interdependence between the degree of complexity of an orga-
10 nization and its capacity for developing real self-maintenance, it is hard to imag-
11 ine the early steps of the process. In the absence of self-generated mechanisms
12 for maintaining the conditions of functioning, the earlier SMSs were probably
13 fragile or/and dependent on highly specific external conditions. A good example
14 is the hypothetical protometabolism proposed by G. Wächtershäuser (1988).
15 This author argues that certain mineral surfaces could have created the adequate
16 conditions for the appearance of a kind of what he considers a protometabolic
17 organization. He defends that the first ‘surface metabolic network’ was estab-
18 lished on the interface of solid/liquid phase (mineral surface/water). Under these
19 conditions the system could ‘act’ on the environment only establishing a buffer-
20 ing of pH or bringing down the tendency towards hydrolysis in its surroundings.
21 Other authors (Harold, 1986, Morowitz, 1992, Deamer, 1997, Segré et al., 2001),
22 however, consider very unlikely the possibility of a metabolic organization,
23 however primitive it may be, in the absence of any enclosure. Such scenario
24 would imply the necessity to elaborate models that integrate metabolism and
25 compartmentation simultaneously (Penny, 2005).

26 Be it as it may, it is likely that the earlier SM systems were highly dependent
27 on a set of external conditions upon which they did have few (if any) control.
28 Thus, their degree of robustness would be seriously restricted, and the accessible
29 level of complexity would also be low. In consequence, the appearance of NTSM
30 systems is linked to crossing a frontier between those organizations whose
31 identity was more dependent on a set of external conditions (let us call them
32 ‘predominantly passive SM systems’) and those whose maintenance depends
33 more on their own organization (let us call them ‘predominantly active SM
34 systems’). This frontier is precisely what defines the *autonomy* of the system.

35 36 37 **4. NTSM ORGANIZATION AND AUTONOMY**

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39 The question of whether the earlier NTSMSs appeared in certain mineral sur-
40 faces, enclosed in primitive compartments or otherwise, is an empirical issue.
41 However, what in any case is essential is that the organization of the primitive
42 NTSMSs could control the external constraints necessary for their maintenance.

01 Then, how can a NTSMS reinforce its own self-maintenance? This question
02 is strongly related with the problem of the increase in the complexity. Let us
03 see why.

04 In a scenario populated by primitive SM chemical systems the appearance
05 of new systems based on new components is very likely, therefore allowing
06 different forms of SM. Some of these new forms of SM may be simpler, but
07 others will probably create larger and more diverse networks. The interesting
08 point is that, within this variety of systems, some of them can generate new,
09 more efficient ways to achieve SM – for instance, increasing both internal
10 diversity and stability. In other words, a more complex organization may be
11 reached and preserved if it increases the capacity of self-maintenance of the
12 whole system. This fact is important because, in general, as the complexity of a
13 FFE organization increases, its maintenance becomes harder.

14 These considerations point to a key question. We have seen that the condi-
15 tion to preserve the new complexity generated is that it is functional for the
16 maintenance of the system. This can take place if the system becomes less
17 dependent on (the presence of) certain external conditions and, consequently,
18 more dependent on itself. Thus, the possibility of any significant increase in
19 complexity of the primitive SM chemical organizations implies a progressive
20 takeover of the external conditions necessary for their viability; and the only way
21 for this to happen is that the system recruits its own organization for the active
22 reconstruction of the necessary conditions of its maintenance. In other words, by
23 increasing their degree of autonomy with respect to the earlier minimal case. By
24 this, I mean a progressive takeover by the NTSM systems of the environmental
25 conditions necessary for their viability. Accordingly, a system can be considered
26 autonomous if its maintenance is more the consequence of its own organization
27 than of the structure of its external environment.

28 A crucial step in the evolution towards autonomy was the appearance of
29 systems whose organization includes the construction of a selective and func-
30 tionally active membrane.¹⁵ Such organizational change allows the components
31 of the system to be produced in much more favorable and stable conditions
32 (regulation of concentrations, selection of kinds of components, etc.). In this
33 way the generation and stability of more complex systems becomes possible.
34 Now the (internal) organization will appear much more integrated and complex
35 in respect to its environment than either the primitive autocatalytic networks
36 without physical border or the primitive micelles or vesicles.¹⁶

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¹⁵ The incorporation of a membrane is a process that transcends the chemical frame, as it implies the recruitment of certain independent processes of self-assembly.

¹⁶ It is likely that cellularity integrated with the inner organization was preceded by more primitive cellular systems (like micelles or vesicles enclosing independent SM organizations).

01 Self-encapsulation will sharply differentiate the organization of the system
02 (the set of relations that constitute it as a distinct unity) from the environment,
03 where different interactions occur. In this way, a clearly distinct inner medium
04 is created: a space where not just concentrations, but even components will be
05 different from those of the “external” medium. However, the most important
06 issue is that the boundary is produced by the very organization of the system
07 (as it is an integral and integrated part of the metabolic network, not a mere
08 ‘wall’ whose properties are externally defined). This entanglement, between the
09 physical border and the recursive process of production of components consti-
10 tuting the system as an autonomous unit, is basically the idea of an autopoietic
11 system (AS), as has been explained by Maturana and Varela (1973) 30 years ago.

12 However, the idea of autopoiesis has been formulated in a rather abstract
13 way. If we take into account the thermodynamic requirements, an AS should
14 also manage autonomously the flows of matter and energy necessary for its
15 maintenance. To be autonomous, a primitive SM system should be capable of
16 constraining the flows of energy (and matter) to ensure the TD realization of
17 the processes that constitute it as a system. In other words, the constructive
18 logic (the recursiveness of the relations among the components of the system)
19 should be entangled with the energetic logic (Moreno & Ruiz-Mirazo, 1999,
20 Ruiz Mirazo & Moreno, 2000, 2004). This implies that the membrane is not
21 only a physical border ensuring adequate concentrations, but also a key element
22 in the energetical maintenance of the system¹⁷ (Pereto, 2005). In any known
23 living system a phospholipid membrane and its molecular machines actively
24 control the flows of energy between the inside and the outside. The essence of
25 the energetic self-maintenance of the cells lies in the asymmetric disposition of
26 molecular machines on the cell membrane allowing efficient coupling between
27 primary energy sources and metabolic networks.

28 This thermodynamic view of autonomy goes far beyond the idea of logical
29 closure of autopoiesis. As a FFE organization, the constitutive processes, the
30 recursive network of production of components, of an autonomous system is
31 essentially entangled with a set of interactive processes. Thus, an autonomous
32 system is an agent, namely, a system that maintains its own identity by per-
33 forming functional processes on its environment (Moreno & Etxeberría, 2005,
34 Moreno & Barandiarán, 2005) (see Fig. 1).

35 These interactive processes are different from mere physico-chemical reac-
36 tions constantly taking place in both directions (and which, in fact, occur in all
37 kinds of systems, from the simplest to the most complex). As the interactive
38 processes are embedded in the self-constructing dynamics of the system, they
39

40 ¹⁷ Thus, such an interface needs to be a semi-permeable structure where coupling mechanisms (particularly
41 energetic transduction and active transport mechanisms), which are basic for the complete self-construction,
42 are anchored.

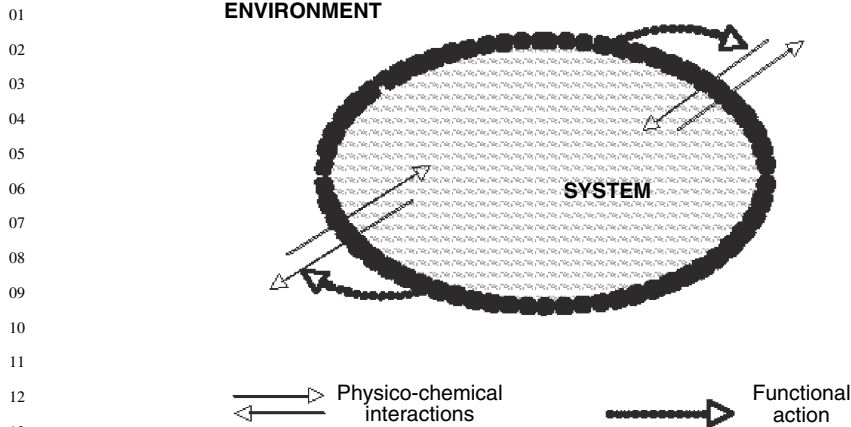


Figure 1 Agency in a basic autonomous system

will constitute a functional loop of the system itself, i.e., agency constitutes an environmentally mediated process, but clearly asymmetric.¹⁸ The interactive processes are driven by the internal organization of the system. An example of a very basic form of agency (universally present in all cellular life) is the mechanism of active transport, which is an in/out flow of matter against a concentration gradient driven by a free energy source.¹⁹ Agency involves a functional action on the environment, modifying (and later controlling) certain environmental conditions for the system's dynamics. In short, seen from a thermodynamic perspective, autonomy is the necessary expression of nontrivial self-maintenance. Without autonomy, either the organization of a system is extremely simple or, if complex, it is dependent on another more complex one (whose origin requires explanation).

Let us summarize. Starting from simple dissipative chemical organizations, with maintenance highly dependent on a set of specific external conditions, a process of exploration of new organizational forms and retention of the functional ones leads to progressively more complex organizations. As this process takes place in a chemical scenario, the increase in complexity of the systems creates an accumulative process of construction of bigger, more complex components, which in turn are the necessary elements for the creation of more complex organizations.

The progress occurs when certain specific form of the former collateral complexity is recruited. Thus, in every step, the new organization achieves SM

¹⁸ Asymmetric in the sense that the environment cannot establish such recursive interaction processes with the agent, unless we are speaking of an interactive coupling between two agents.

¹⁹ This mechanism must have appeared in early forms of cellular organizations because it is required for avoiding an osmotic crisis, which would lead to the bursting of the cell.

01 in a different, more efficient, and robust way, so that it increases its efficiency
02 (in capturing the material and energetical resources necessary for its maintenance).
03 This way, certain systems became capable of using their own organization for
04 their self-maintenance. In other words, they became autonomous systems.

05 It is frequently argued that a metabolic-like organization – what we char-
06 acterize as basic autonomy – is the result of evolution by Natural Selection,
07 which, understood in a more simplified way, would only require a scenario of
08 self-replicating molecules, provided that they are able to introduce and transmit
09 variations and generate themselves (along with its environment) a selective pres-
10 sure, leading to the survival of the “fittest”. However, this argument fails. For,
11 on the one hand, an evolutionary process of hereditary self-replicating molecules
12 is hard to conceive in the absence of a functional organization of the energy
13 necessary to keep the process going (i.e., a rudimentary metabolic organization).
14 On the other hand, an evolutionary process leading to higher forms of com-
15 plexity would require self-replicating entities that could in principle produce an
16 open space for functional variations. Now, an open space for functional varia-
17 tions requires in turn a scenario capable of translating sequential variations into
18 different functional properties (catalytic, for instance) which ultimately influ-
19 ence the way of realization of self-maintenance: more or less capacity to gather
20 external energetical resources; resistance to perturbations; endurance (through
21 either recursive self-production or self-reproduction). Thus, only an organiza-
22 tional framework allows an open space of (“phenotypical”) functions.²⁰ Last, but
23 not least, without a form of enclosure it is hard to conceive a workable process
24 of selection. The conclusion is therefore that basic autonomy is the precondition
25 for the appearance of a (Darwinian) evolutionary system (and not the contrary).
26

27 **5. THE EMERGENCE OF A HISTORICAL–COLLECTIVE** 28 **DIMENSION**

30 **5.1. Autonomous systems with memory**

31
32 The basic form of autonomy that we have analyzed in the previous section implies
33 a primitive form of metabolic organization, but not necessarily an instructed one
34 (Ruiz-Mirazo & Moreno, 2004). We can conceive such systems as capable of a
35 nonreliable form of self-reproduction. Thus, it is likely that the maintenance of
36 populations of these primitive autonomous systems permitted that some of them
37 increased the efficiency of their metabolic machinery, allowing the production
38 of more complex components.
39

40
41 ²⁰ This is the core of the argument presented by Wicken (1987) against the evolutionary possibilities of
42 populations of self-replicating modular templates (like RNA-type molecules) in the absence of metabolic
organizations.

01 However, as complexity grows, so does fragility. The organization of basic
02 autonomy, just by itself, does not solve the problem of preserving (for long-
03 term periods) the new complexity that it can generate, and therefore, neither
04 the problem of how this complexity could grow indefinitely. Of course, the
05 productive and reproductive dynamics of a scenario of basic autonomous systems
06 would allow the maintenance of certain level of complexity. But this – still
07 rudimentary – functional dynamics cannot ensure that the components (together
08 with their way of organization) remain unaltered for much longer than their
09 typical life spans (or the one of the whole organization), and the system faces a
10 bottleneck: as complexity rises, its preservation becomes more and more difficult.
11 Therefore, only those autonomous systems that developed specific mechanisms
12 to stabilize and retain the increasing structural and organizational complexity
13 with a fairly high degree of reliability could begin to unfold new, subsequent
14 levels of complexity and, furthermore, set up the first pillars to ensure their
15 *long-term* maintenance.

16 Now, how to do that? As Szathmáry and Maynard-Smith (1997) have pointed
17 out, the way to preserve the specificity of an increasingly complex organization
18 is through what they call a mechanism of ‘unlimited memory’. This mechanism
19 consists in linking the sequential structure of certain stable and self-replicating
20 components (to be more precise, the specific sequence of modular templates²¹)
21 with the most complex structural–functional properties. This allows a ‘storage’
22 or ‘recording’ of these complex (and highly specific) functions, which in turn
23 permits – if these material records become replicated – a reliable form of
24 reproduction (regardless of how complex the organization of the system is).
25 Thus, the requirement for the start of an unlimited hereditary memory is the
26 generation by (and integration within) the organization of autonomous systems
27 of suitable components for this storage.

28 There are two important aspects here. The first is that with the introduction of
29 these components the maintenance of the specific structure of the organization
30 changes: Instead of a mechanism in which the specific order of the system lies in
31 the dynamically dissipative maintenance of the whole organization, an important
32 part of such order is now frozen in the linear sequence of some components
33 (as this linear sequence will specify increasingly complex key catalytic functions
34 of the system, and therefore it will help to stabilize it). The second is that,
35 because such components have template capacities, they can transmit the specific

36
37
38 ²¹ A ‘modular’ molecule is a big structure made of a sequence (a small set) of subunits. In this component, the
39 global shape is a consequence of the particular order of the subunits. A molecule is considered a (catalytic)
40 template when its structure acts as blueprint, inducing the formation of copies of such structure. Although
41 modular templates are considerably complex molecules that hardly must have appeared before the evolution of
42 autonomous systems simple kinds of templates also probably played an important role in previous stages. For
instance, certain mineral surfaces would probably have played a role as catalysts in noncellular protometabolic
systems, or the very membrane in encapsulated systems.

01 order they store by direct replication. This way the renewal of the increasingly
02 complex structure of certain components does not depend any more only on
03 the maintenance of an increasingly complex and holistic process, but on the
04 template-directed replication (which relies in a specific sequential order of their
05 building blocks). The robustness of the system may also significantly increase
06 because of the possibility to reliably produce new highly functional components
07 (despite their increased structural complexity). The so-far distributed dissipative
08 organization becomes this way preserved by means of a local conservative order
09 stored in modular template-like components. In other words, the maintenance
10 and reproduction of the organization becomes instructed.

11 Interestingly, the introduction of modular templates specifying the most
12 complex part of the functional organization of the system conveys an important
13 change: the formerly highly distributed and holistic organization opens the way
14 to a much more modular organization. This is an advantage, as in a modular
15 system the organization as a whole is less likely to be disrupted by a localized
16 failure. Thus, seen in an evolutionary perspective, modularity increases flexi-
17 bility and minimizes cascading malfunctions (Harold, 2001, p. 212). In total,
18 the introduction of this mechanism of unlimited memory changes so deeply the
19 organization and capacities of the primitive autonomous systems that it seems
20 convenient to give them a specific name. We have elsewhere (Ruiz-Mirazo et al.,
21 2004) used the term of hereditary autonomous systems (HAS).

22 Let us go now to the more fundamental question. Given that modular tem-
23 plates now control both the maintenance and reproduction of the system, all
24 random changes in these components (allowing viable reproduction) will lead to
25 a process of exploration of the sequential space linked to a correlative selective
26 retention of the more efficient organizational forms.²² This allows the recruit-
27 ment by the individual autonomous systems of the results (end-products: selected
28 patterns) of a slow process of natural selection, which is much more encom-
29 passing as it takes place beyond these individual autonomous systems. Thus
30 the evolutionary process in which the whole population and its environment
31 are involved largely determines the changes that take place at the level of the
32 sequences of the templates. These templates become a kind of material memory,
33 which can reliably transfer organizational changes from one system to another.
34 In this way, the systems endowed with modular templates can combine coher-
35 ently and consistently the individual dimension of their activity (related to the
36 self-construction/self-maintenance of each of them) with a progressively more
37 important temporal and spatial dimension (related to their long-term maintenance
38 and evolution as a whole population). But the most important consequence is
39 the increase in the complexity of the metabolic organization that this insertion
40 in a historical and collective dimension allows.

41 _____
42 ²² Provided there exist certain additional constraints, like competition for resources in a limited space.

01 The beginning of a process of evolution based on the transmission of modular
02 templates probably inaugurated a stage of both vertical and horizontal exchanges
03 of hereditary components (as suggested by Woese²³). As a consequence, indi-
04 vidual organisms crucially depend on the (long-term) selection of the functional
05 hereditary components; and in turn this global process of selection of func-
06 tional hereditary components from a random process of variation will depend
07 on the performances of the individual organisms they instruct. From now on
08 the maintenance of the autonomous systems will depend on the maintenance
09 of this global historical–collective structure of relations. Furthermore, even the
10 structure of the autonomous systems will progressively depend on these larger
11 and wider relations that we know with the term “biological evolution” (recall
12 Dobzhansky famous dictum: “nothing in biology makes sense except in the
13 light of evolution”).
14

15 5.2. The origin of an informational organization

16 Hereditary autonomous systems must have been the immediate precursors of
17 present-day living organization. As has been mentioned in the previous section,
18 the organization of HAS was likely based on one single type of polymer to sup-
19 port at the same time template and catalytic functions.²⁴ Now, this organization
20 cannot yield to an unlimited increase in complexity, and therefore the evolu-
21 tionary possibilities of HAS are blocked. The reason is the following: there is
22 a trade-off between the realization of catalytic and storage/replicative functions;
23 the better a given type of polymer is suited for template tasks, the worse it is
24 for exploring the catalytic space, and vice versa.²⁵ Accordingly, the only way
25 for an unlimited increase in complexity is by introducing two different types
26 of polymers, devoted, respectively, to template and catalytic tasks (Ruiz-Mirazo
27 et al. 2004). This way, the systems that start to produce two different – and
28
29

30 ²³ Such modular organization should have helped the exploration of new, more efficient forms of organization.
31 As Woese (2002) has pointed out, the beginning of cellular evolution was necessarily a collective process,
32 where different cellular designs evolved simultaneously, systematically exchanging genetic material (what
33 he calls ‘horizontal gene transfer’). So, this early (pre) Darwinian evolution would allow an exploration of
34 different forms of organization, until a ‘modern design’ was reached.

35 ²⁴ The current view of the origin of life postulates a stage of prebiotic systems based on certain type of
36 bi-functional polymers (like RNAs) capable of performing both template and catalytic functions, although in
37 a much less suitable way than DNA and proteins. Hence, despite its evident limitation in the exploitation of
38 both template and catalytic functions, this solution is organizationally much more simple (because it allows
39 the direct conversion of a specific sequence into a specific catalytic task) and therefore more likely to have
40 occurred. This is in fact the hypothesis of the so-called RNA world.

41 ²⁵ This problem has a rather simple chemical interpretation. Template activity requires a stable, uniform
42 morphology, suitable to be linearly copied (i.e., a monotonous spatial arrangement that favors low reactivity
and is not altered by sequence changes), whereas catalytic diversity requires precisely the opposite: a very
wide range of 3D shapes (configuration of catalytic sites), which are highly sensitive to variations in the
sequence (Moreno & Fernández, 1990, Benner, 1999).

01 complementary – polymers create two new ‘operational subsystems’: one in
02 charge of the reliable recording, storage, and replication of certain sequences
03 (which are crucial for the correct functioning of the system and that of similar
04 systems in future generations) and the other strictly in charge of carrying out –
05 with increasing efficiency – these metabolic tasks required for the continuous
06 realization of the individual autonomous system (mainly contributing to the gener-
07 ation of more and more sophisticated mechanisms of catalysis). Then, these
08 former template–catalytic components (RNA) can be substituted by two others:
09 pure templates now completely free of any catalytic task will become tools
10 for an unlimited memory (as we know them in present-day DNA), and pure
11 catalysts, optimally suited for translating sequential variations into 3D diversity
12 (as happens in present-day proteins).

13 It must be stressed at this point that the emergence of these two new types of
14 processes cannot occur but from a common metabolic platform (i.e., from the
15 characteristic organization of the previous stage), which now becomes respon-
16 sible for keeping a constant bond between the two, and enables their comple-
17 mentary development as generations flow. Now, as these two new types of
18 macromolecular components (the new templates and the new catalysts) cannot
19 be made of the same kind of monomers or the same kind of chain bonds, an
20 indirect, mediated connection turns to be a requisite in order to achieve an
21 effective functioning between the two operational levels of the system. Thus,
22 the connection becomes a mechanism of a contingent nature (which does not
23 mean that it will be established randomly or free from any constraint). This
24 mechanism, known as the genetic code, is what underlies the duality between
25 genotype and phenotype.²⁶

26 The scenario that this transition brings about is a new form of organization
27 based on two quite different – but complementary – forms of operation: one
28 involved in the fundamental productive-metabolic processes (i.e., dynamic, rate-
29 dependent processes) and the other (constituted by the genetic processes), partly
30 decoupled from all that muddle of on-line chemical reactions, puts together a
31 group of special processes and components (rate-independent processes), with
32 particular rules of composition and functioning (Pattee, 1977). Now, despite
33 their dynamical decoupling, both forms of operation in the system are so deeply
34 linked that none of them can work without the other, and therefore, the whole
35 system depends on their causal connection. However, as the genetic strings are
36 dynamically decoupled from the metabolic processes, their causal action is of a

37
38 ²⁶ The genetic code, rather than a mechanism, is in fact the expression of an organization, which Pattee (1982)
39 has called Semantic Closure. The basic idea is that gene strings are self-interpreting symbols because their
40 action – specific but arbitrary as it is mediated by the recognition of certain functional components – is
41 the synthesis of those components (tRNAs and synthetases) that allow the causal action of the very genes.
42 Thus, by contributing to the maintenance of the whole cellular organization, genes in fact achieve their own
interpretation.

01 quite different nature: In fact the causal action of the DNA is the transmission
02 of a specific order or form. DNA ‘selects’ certain specific sequences for the
03 different amino acids building up proteins. Therefore, the causal role of DNA
04 is to instruct the synthesis of otherwise highly improbable proteins.²⁷ On the
05 other hand, the almost inert character of DNA molecules and the dynamical
06 decoupling from the metabolic processes permit to see the changes in the DNA
07 strings as practically independent of the metabolic organization (as if they were
08 ‘compositional’ changes). This dynamical decoupling along with its causal role
09 expresses the informational nature of the genetic material in living organization.
10 Thus, in this new form of organization, causal action is structured in different
11 levels: within the dynamics of the metabolic process and between the dynami-
12 cally decoupled operational levels of genes and proteins.

13 Ultimately, this decoupling of the genetic material from the metabolic dynam-
14 ics is the expression of the radical insertion of organisms, as autonomous systems,
15 into a historical–collective (meta)system, where the ‘slow’ processes of creation
16 and modification of informational patterns take place and where an additional
17 circular relation of cause and effect is established between individual organi-
18 zations and the eco-evolutionary global dimension. The origin of information
19 (of genetic information) takes place precisely when the link between both dimen-
20 sions is articulated. As a consequence, the appearance of information opens a
21 new scenario incorporating continuously new causal relations in the individual
22 organization. Each time a new genetic component, linked to the production of a
23 new functional protein, enters into the organization of a cell, and if this modifi-
24 cation turns out to be viable and advantageous for that cell, a new causal link
25 becomes stabilized.

26 Thus, in functional terms, the causal action of information allows, on the
27 one hand, the robustness of the processes associated with self-maintenance in
28 the early living systems and, on the other, the increase in the complexity of
29 living systems. The informational components, shaped through a collective and
30 historical process, re-arrange material subsets of structures so that highly orga-
31 nized systems are generated and preserved. One important feature of this new
32 organization is that the specification for the maintenance of the system is hierar-
33 chically organized: an important part of these specifications is stored/recorded in
34 the informational sequences of the genetic components. This allows the robust
35 maintenance of much more complex networks (which in turn will support more
36 specifications in their connectivity). So, the informational organization will allow
37

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39 _____
40 ²⁷ However, the final result of the DNA – the function of the proteins – is also due to the very materiality
41 of the protein. In fact, one of the key aspects of this process is an ‘opportunistic’ use of the self-assembling
42 properties of the material properties of components. Protein folding is largely a tacit process where the explicit
information contained in the linear sequence is only a short part of the causes that govern the process of
folding, and therefore the expression of its function. Thus, the specific materiality of the protein is crucial.

01 a self-sustained feedback between records and metabolic networks, allowing
02 further increases in complexity.

03 This organization, which we can now call living organization (LO), will permit
04 a limitless exploration of a potentially huge sequence space (of the modular
05 templates) that can also be matched with an unlimited space of functions.
06

07 **6. THE OPEN STRUCTURE OF DARWINIAN EVOLUTION**

08
09 Unlike the limited world of HAS, the appearance of informational organization
10 generates a new form of self-preservation: it generates a process in which (a set
11 of) individual organizations reproduce their basic functional dynamics, bringing
12 about an unlimited variety of equivalent systems, of ways of manifesting that
13 dynamics, which are not subject to any predetermined upper bound of organiza-
14 tional complexity (even if they are, indeed, to the energetic-material restrictions
15 imposed by a finite environment and by the universal physico-chemical laws)
16 (Ruiz-Mirazo, Moreno & Umerez, in preparation). Thus, the key of this form of
17 self-preservation is the following: On the one hand, any of these systems can
18 adopt a particular, hereditary, form of organization. On the other hand, all of
19 them, however different they may be, share a basic common organizational form
20 (as has been described) whose long-term preservation depends precisely on this
21 capacity of continuous, unlimited variation.
22

23 Let us examine the different elements and relations underlying this new form
24 of preservation through open-ended evolution. First, we need a set²⁸ of certain
25 individual ‘units’, which have to be autonomous agents (organisms) capable of
26 template reproduction and whose organization is based in two complementary
27 polymers (which implies a full Geno-Phenotype duality: the genetic level is
28 separated from the organization of the agent). We shall call this organization, as
29 has been described, a basic informational organization (BIO). Second, these units
30 will constitute a web of recursive interactions. Third, this web is a populational
31 and ecological system. Populational: it requires a critical mass of individuals
32 sharing the same specific form of SM (phenotype); a certain degree of variability
33 with buffering (within which selection, namely, differential reproduction with
34 conservation of form, is generated) is also necessary; Ecological: it requires
35 the existence of different kinds (species) of individual components (organisms).
36 However, from an initial unique type a diversity of kinds will be generated,
37 so that the boundary conditions for the SM of a given type start to depend on
38 the interactions with other types (ecological relations). As a consequence, the
39 different reproductive rates will depend on the recursive relations between types
40 (and between individuals of the same type).
41

42 ²⁸ The system has to include certain degree of redundancy: A unique individual component is not enough.

01 Accordingly, the specific way in which the units achieve self-maintenance
02 and self-reproduction is deeply entangled with the recursive relations among
03 them. Given all that, the temporal unfolding (evolution) of this system is such
04 that the kinds (species) change according to the transformations of the boundary
05 conditions of the self-maintenance and self-reproduction of their units (individual
06 organisms), which in turn are the result of the recursive interactions at the
07 populational and ecological level. The variation possibilities of (both) individual
08 components and populations are, in principle, open, but the whole evolutionary
09 system is not.²⁹

10 This set of relations would constitute the nucleus of the form of evolution
11 that we know in current life, namely, Darwinian evolution. Let us summarize
12 the requirements for a Darwinian system.

- 13
- 14 (1) At the level of the individual components: They have to possess an internal
15 organization such that (a) they can reliably self-reproduce the common basic
16 informational organization (CBIO) that characterizes them as individual
17 agents; (b) this CBIO has to admit an unlimited variety of forms, which
18 (c) they will indefinitely and reliably reproduce.
 - 19 (2) At the global level, the populationally and ecologically generated boundary
20 conditions will act on a particular variety of forms (but never on the CBIO).
21 The effective variability of these forms (unfolded in time) depends on these
22 boundary conditions, and in turn, these ones ultimately depend on the way
23 the former interact with each other, recursively, so that the whole system
24 achieves long-term SM.
 - 25 (3) This long-term SM of the whole system is (as a consequence of these
26 two previous requirements) necessarily an open process not subject to any
27 pre-determined upper bound of organizational complexity³⁰ (except to the
28 energetic-material restrictions imposed by a finite environment and by the
29 universal physico-chemical laws³¹). (See Fig. 2)

30 Notice that we have used the term “system” instead of “organization” for this
31 set of relations. The reason is the following: Whereas in any of the cases where
32 we have used the term organization there is a form of closure, the evolution-
33 ary ‘self-maintenance’ never closes. It is essentially an open-ended process.
34

35

36 ²⁹ Until new properties of the components giving rise to new forms of interaction capable to generate new
37 forms of SM (societies, technologies, etc . . .) emerge, and this way, the fundamental biological organization
38 would be transcended.

39 ³⁰ As any more complex form would not be preserved unless it were compatible with this organizational
40 structure.

41 ³¹ This implies an endless process of creation of new organizational forms. There are, however, certain
42 restrictions in this huge unlimited space (body plans, internal SO laws, etc.) but, on the other hand, these
restrictions can act as a set of new rules that create new primitives and relations allowing new forms of
increasingly complex organizations.

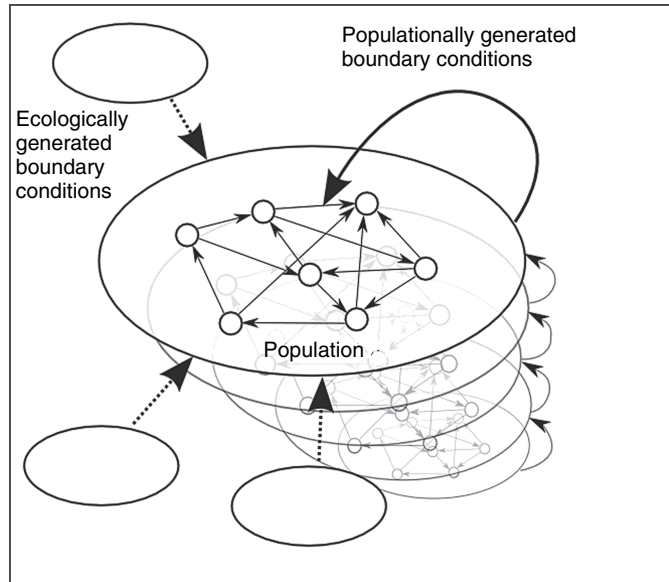
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Figure 2 The evolutionary system

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This open-endedness constitutes the main difference between the concept of organization based on the principle of nontrivial closure/SM and that of Natural Selection. This latter, by its nature, tends to generate processes that never close,³² and, with the invention of the informational organization, this potential openness of NS may finally unfold.

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Therefore, the invention of the basic living organization was qualitatively different from any other precedent invention in terms of long-term preservation, admitting ever new increases of complexity. Once the first form of living organization appears, not only will it be preserved, but it also becomes the condition of possibility for any further and more complex organizational steps. All further forms of organization that have appeared in the course of evolution not only have retained the basic organization of early life, but also crucially depend on it (just think on how bacterial life is the condition of possibility of the emergence of more complex living systems).

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7. CONCLUDING REMARKS

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The origin of living organization occurred through a long-term process involving different steps. During this process each new form of organization erased these

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42

³² Although these processes may hit a ceiling, as we have seen for those HAS based on a unique type of polymer.

01 previous ones that brought them forth. Hence, the origin of life is a set of
02 self-erasing increasingly complex organizational steps leading to a ratchet-like
03 form of organization that is able to increase its complexity only by preserving
04 its basic form. However, once the first form of living organization appeared,
05 it was not only preserved, but also became the condition of possibility for
06 further and more complex organizational steps. Therefore the invention of the
07 basic living organization was qualitatively different from any other precedent
08 invention in terms of long-term preservation, regardless of the eventual increases
09 of complexity.

10 At the beginning, the 'driving force' was nothing but the confluence of
11 several principles of ordering, like self-assembly, template replication, or self-
12 organization, merged in the framework of what I have called a nontrivial
13 self-maintaining organization. Given this special form of self-maintenance, and
14 provided a long and wide enough scenario, the complementary action of these
15 principles will lead to a process of increase in complexity.

16 The key to the beginning of this process is functional recursivity. Every
17 novelty capable of contributing to a more efficient form of maintenance will
18 be recruited. This process makes possible the appearance of new, increasingly
19 complex forms of organization. But the key to their stability and capacity of
20 preservation is the achievement of a basic autonomy. Only autonomous systems
21 could attain the threshold of complexity necessary for the appearance of the new
22 driving force of Natural Selection.

23 Natural selection brings about a mechanism for exploring new causal relations
24 in a much wider dimension, which will progressively make the organization
25 of autonomous systems more complex. But the increase in their complexity
26 will also produce deep changes, integrating them in a historical and collective
27 dimension. Self-maintenance transcends the level of the individual, autonomous
28 organization.

29 The basic organization of living systems is what generates the mechanism
30 of Darwinian evolution, which is in turn the driving force that ensures their
31 long-term maintenance and increase in complexity. But, ultimately, the open-
32 endedness of the evolutionary process has its roots in that organization.

36 **ACKNOWLEDGMENTS**

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