

The origin of species by means of natural drift

El origen de las especies por medio de la deriva natural

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ABSTRACT

In this article we propose that the mechanism that gave rise to the diversity of living systems that we find today, as well as to the biosphere as coherent system of interrelated autonomous living systems, is natural drift. And we also propose that that which we biologists connote with the expression natural selection is a consequence of the history of the constitution of the biosphere through natural drift, and not the mechanism that generates that history. Moreover, we do this by proposing: a) that the history of living systems on earth is the history of the arising, conservation, and diversification of lineages through reproduction, and not of populations; b) that biological reproduction is a systemic process of conservation of a particular ontogenic-phenotype/ontogenic-niche relation, and not a genetic process of conservation of some genetic constitution; c) that a lineage arises in the systemic reproductive conservation of an ontogenic-phenotype/ontogenic-niche relation, and not in the conservation of a particular genotype; d) that although nothing can happen in the life history of a living system that is not permitted by its total genotype, whatever happens in it arises in an epigenetic manner, and it is not possible to properly claim that any features that arises in the life history of an organism is genetically determined; e) that it is behavior what guides the course of the history of living systems, not genetics; and f) that that which a taxonomist distinguishes when he or she claims that an organism belongs to a particular species, is a particular ontogenic phenotype/ontogenic niche relation that occupies a nodal position in the historical diversification of lineages.

Key Words: evolution, natural drift, natural selection, lineage, organism, species.

RESUMEN

En éste ensayo proponemos que el mecanismo que ha originado la diversidad de seres vivos que encontramos hoy día, y que también ha originado a la biosfera como un sistema coherente de seres vivos autónomos e interrelacionados, es la deriva natural. Y también proponemos que aquello que los biólogos connotamos con la expresión selección natural, es una consecuencia de la historia de la constitución de la biosfera por medio de la deriva natural, y no el mecanismo que genera esta historia. Además, en el desarrollo de estas nociones, proponemos: a) que la historia de los seres vivos en la Tierra es la historia del surgimiento, conservación y diversificación de linajes, y no de poblaciones; b) que la reproducción biológica es un proceso sistémico de conservación de una particular relación fenotipo ontogénico/nicho ontogénico, y no un proceso genético de conservación de algún particular genotipo o constitución genética; c) que un linaje surge en la conservación sistémica reproductiva de una relación fenotipo ontogénico/nicho ontogénico, y no en la conservación de un genotipo particular; d) que aunque en la ontogenia de un ser vivo no pueda ocurrir nada que no esté permitido por su genotipo total, cualquier cosa que ocurra surge de un modo epigenético, de manera que no es posible sostener que las características estructurales que surgen en la ontogenia de un organismo están genéticamente determinadas; e) que es la conducta, y no la genética, el factor central que guía el curso de la historia de los sistemas vivos; y f) que aquello que un taxónomo distingue cuando él o ella afirma que un organismo pertenece a una especie particular, es una particular relación fenotipo ontogénico/nicho ontogénico, que ocupa una posición nodal en la historia de diversificación del linaje.

Palabras Clave: evolución, deriva natural, selección natural, linaje, organismo, especie.

FOREWORD

This essay is an English version of the article "Origen de las especies por medio de la deriva natural, o la diversificación de los linajes a través de la conservación y el cambio de los fenotipos

ontogénicos", published in Spanish in 1992, as the 46th special issue of the journal "Revista del Museo de Historia Natural de Chile". We are in great debt to the insight and courage of two distinguish Chilean biologists, Luis F. Capurro S. and José Yañez V., who though that the ideas

here presented deserved to be known and considered by the community of biologists in general, and of those concerned with the understanding of the history of living systems in particular, even though they were to a great extent contrary to most of the modern evolutionary views as they are based in genetic thinking. We want to thank them. We want also thank to the Direccion de Bibliotecas, Archivos y Museos de Chile, who published the original article in full trust of its quality in 1992.

We say that this is the English version of that article and not just its translation, because it became expanded as we rewrote it in English and we attempted to make more explicit our thinking in relation to some key concepts like those that refer to the epigenesis and the ontogenic and phylogenic drift of the relation organism/niche. There was a first translation made by Cristina Magro that provided us with a vision of how it would appear in English, and which we used to some extent when making the present one, but which eventually we did not use fully because we changed much of the contents of the article. Nonetheless we want to thank Cristina for the effort and appreciation for our work, as well as Julia Tetel Andersen and Barbara Herrstein Smith who collaborated with her.

In writing this essay we concentrated our attention on the presentation of our ideas and notions on natural drift, and we have not attempted to exemplify what we say with particular cases in which one could more easily see it. Of course we think that to see natural drift in action only implies a shift in attention, but to illustrate that would no doubt require an independent work that we shall also do.

I. INTRODUCTION

The main purposes of this essay are to reconsider some of the fundamental biological questions that according to us were the explicit or implicit

central concerns of Darwin as he developed his evolutionary theory, and to propose a new manner of answering them. As we do so from the conceptual perspective that we will propose here, we shall find ourselves resorting the participation of behavior as a central factor in the history of diversification of living systems. Let us proceed.

We think that the fundamental biological questions that were the basic concerns of Darwin as he was developing his evolutionary thinking can be presently expressed under the form of the following four questions:

i) how can we explain the diversity and similarity we observe among living beings?

ii) how can we explain that the different types of presently existing living systems live in their natural medium in a way that is totally congruent to their circumstances, and that when this congruence is broken, they die?

iii) how can we explain that taxonomists, who frequently classify living systems considering only a few dimensions of their ongoing existence, can classify them in systematic categories that order and relate them in a way that makes biological significance?

iv) what is it that the taxonomist distinguishes when he or she classifies a living being and in doing so he or she specifies a systematic category with biological significance?

We also think that, in answering these questions, modern evolutionary theory use, as a conceptual background of basic notions, the following four assumptions that delimit and specify what can be said within that framework:

1. That adaptation as a relation of operational congruence of the living system with the medium is variable, and that it is possible to speak, with biological meaning, about organisms as if some of them were better adapted than others, as well as to talk about adaptive processes and adaptive strategies.¹

2. That the features of the medium that the different living beings encounter in the course of their respective particular ontogenic and

¹ A conceptual use of this assumption is revealed, for example, by the claim that organisms can only attain a sub-perfect degree of adaptation, due to developmental constraints and ecological trade-offs (Seeger & Stubblefield 1996). A more operational use of this assumption is revealed by the use, in many ecological and evolutive studies, of the differences in fertility and/or fecundity of the organisms that compose a population as an indicator of their different biological adequacies, or fitness (as in Medel 1999).

² The use of this notion is particularly clear in many modern paleontological studies and descriptions, where evolutionary novelties are envisaged as adaptative responses to environmental challenges. For example, it is claimed that the forelimbs of primitive amphibians arises as adaptative solutions to the problem of land locomotion (Benton 1990); that flowering plants evolve as an adaptative reponse of the ancestral flora to the predation of plant-eating dinosaurs (Bakker 1978); and that climatic and tectonic changes in the cenozoic era provide many opportunities for fast speciation of marine ostracoda fauna (Cronin & Ikeya 1990).

phylogenetic histories, are already there as such as they are encountered by the living systems, even though the same is not always assumed to be the case for the niche. Therefore, evolution occurs as a process of progressive or saltatory adaptation to a preexisting medium even when there is coadaptation.²

3. That, at a structural level, the evolutionary process is mainly a process of genetic change. These genetic changes takes place in the organisms, but appear expressed at the level of populations. Phenotypic changes are the results of the genetic changes, therefore, phenotypic changes follows historically the course of genetic changes.³

4. That every change requires the application of some sort of external force to be produced. Genetic changes, the structural substrate of organic evolution, are not an exception. The major force that guides the course of the genetic adaptative changes is the "selective pressure" imposed by the environment upon the organisms. It is claimed that there are a wide variety of selective agents and processes that can act upon an organism, either in a continuous or punctuated way.⁴

Under these conceptual assumptions, the differential survival observable among living systems, called "natural selection", is considered to be the mechanism that generates evolutionary change and adaptation. Moreover, under those assumption no question arises about the possibility that change and adaptation could be basic constitutive conditions of the living, and that differential survival could be the result of the evolutionary process and not the mechanism that generates it.

There is no doubt that the notion of natural selection as it presently stands has had great success in the deepening of our understanding of the history of living systems on earth. Yet, in spite of its apparent great coherence and explanatory power, the present state of evolutionary theory is not completely satisfactory because it leaves some serious gaps in several domains of Biology (Gould & Elredge 1977, Lewin 1980, Gould & Lewontin 1979, Brooks & Wiley 1986, Gould 1994). Thus, among the biological phenomena that modern evolutionary theory does not explain properly under the claim that every thing occurs in evolution in a process of progressive adapta-

tion through the natural selection of the best adapted, we can mention the following: a) the temporal dynamics of the phyletic change; b) the operational relation between phylogeny and ontogeny; c) The establishment of "phylogenetic trends" in lineages; d) the differences between the rhythms of molecular and organismic changes; e) the conservative character of the evolutionary process; f) the neutral aspect of much of the molecular evolution; and g) the presence of nonadaptive features or characters.

We think that this situation requires a direct reformulation of the questions presented above under a different conceptual approach. This is what we intend to do in what follows, and we shall do it based on the understanding that living systems as autopoietic systems (Maturana & Varela 1972) are structure determined systems, and that they exist as such only as long as in their operation and their interactions they conserve their organization (autopoiesis) and their operational congruence with the circumstances in which they live (adaptation). Accordingly, we shall reformulate these questions claiming that all biological phenomena, including those that take place in supra-individual relational domains, have to be explained and understood by taking into account what happens to living beings during the process of their realization as individuals that maintain their organization and adaptation as a condition of their existence. Furthermore, as we already said at the beginning of this essay, we shall develop our arguments showing how behavior is a guiding factor in the individual and evolutionary history of living beings.

Although this essay constitutes a coherent conceptual whole, we have divided it into several sections that can be read independently in different sequences according to the curiosity of the reader. Also, we have included at the end, as an appendix, a glossary that contains the meaning of the terms and notions that we introduce in this essay without a previous history, as well as clarifications about others that are in common use when we think that it is necessary to do so in relation to what we say. We invite the reader to look into this appendix for its own value, and to turn to it if the reading becomes obscure to him or her.

³ A contemporary and didactic exposition of this classic way of thinking can be found in Brandon (1990).

⁴ A detailed exposition of this way of thinking can be found in the book of Bell (1997). In the introduction (page xix), this author state:"there are many forces that hinder evolution - mutation, sampling errors, immigration and so forth- but selection is the only process that causes evolution".

II. EPISTEMOLOGICAL CONSIDERATIONS

II. 1. Structural determinism

Every explanatory argument, regardless of the domain in which it takes place, stands on the explicit or implicit acceptance of structural determinism. That is, all explanatory arguments stand on the explicit or implicit understanding that, both in its internal and in its external dynamics, every system operates at every instant in a manner determined by its structure at that instant. The notion of structural determinism is not an ontological assumption or an a priori notion. It is a descriptive abstraction that the observer makes of his or her experiential or operational coherences as he or she operates as such in his or her living, and that he or she makes when reflecting on the operational coherences of his or her experiences in the attempt to explain them. Even the notion of probability is valid only from the implicit or explicit acceptance by the observer that makes a probabilistic assessment that he or she operates in a domain of structural determinism that he or she cannot observe directly. The notions of system and mechanism imply structural determinism as a constitutive feature of what they connote (see appendix, "structure determined system"). Finally, explanations in general, and scientific explanations in particular, are possible only in a domain of structural determinism since they constitutively consist in the proposition of generative mechanisms or process that if allowed to operate according to the structural coherences that they entail, will give rise as a consequence to the experience that the observer wishes to explain (Maturana 1990) (we highly recommend to see the appendix, "organization" and "structure" at this point).

II.2. Living systems as structure determined systems

As biological entities living systems are structure determined systems. This means that they are such that everything that happens in them and to them, happens at every instant determined by their structure and structural dynamics at that instant, and that any external agent impinging on them only triggers in them structural changes determined in them. This implies that all the structural changes that a living system undergoes as it exists in interactions in the medium, are not and cannot be determined by the features of the medium, but arise in the living system as a result of its own structural dynamics in the realization

of its living as this flows modulated by the course of the structural changes triggered in it by its encounters in the medium (Maturana 1975). Moreover, as a structure determined system a living system only encounters those structural features of the medium that its own structure specifies. Therefore, the observer cannot see by him or herself such features of the medium, and has to use the structural changes triggered in the living system itself as an indicator or descriptor of them. Also, it is because the living system is a structure determined system that its structural changes follow a course that in a strict sense is indifferent to the way the observer describes the environment (surroundings) in which he or she sees the living system, but which is contingent to the course of its interactions with the part of the medium (niche) that it in fact encounters.

Furthermore, due to its structural determinism the living system cannot distinguish in its operation whether its structural changes are the result of its own internal structural dynamics or arise triggered in it by its encounters with the medium. In other words, the structural dynamics of a living system is indifferent to the distinction that an observer makes when speaking of what is internal and what is external to it. The distinction between what is internal and what is external to a living system, or to any structure determined system, is a distinction that an observer makes, and, therefore, does not participate in the operation of such systems. From all that we have said in relation to living systems as structure determined systems, it follows that the phenomena of the structural dynamics of a living system and the phenomena that occur in its interactions in the medium, are phenomena of different kind that occur in phenomenal domains that do not intersect, and cannot be expressed one in terms of the other. In general terms, this means, as we said already, that the medium cannot specify what happens to the living system as this interacts with it. The medium can only trigger in the living system structural changes determined in the living system, and vice versa, and all that can happen in the history of interactions of a living system and the medium that contains it, is that both undergo congruent structural changes that entail the conservation of adaptation or the living system as it remains in operational congruence with the medium, or it disintegrates.

II.3. Scientific explanations

What is peculiar or proper of scientific explanations is the epistemological procedure that de-

finer them and validate them as such. This procedure, that we call the “criterion of validation of scientific explanations”, consists in the coherent satisfaction of four operations, one of which is the proposition of a generative mechanism, that is, a mechanism or process that if allowed to operate gives rise, as a result of its operation, to the experience or phenomena to be explained. (Maturana 1990). Succinctly, these four operations are: a) the description of what an observer must do to live the experience to be explained; b) the proposition of a generative mechanism; c) the deduction from all the operational coherences implicit in (b), of other possible experiences for the observer, and of what he or she should do to live them; and d) the realization by the observer of what has been deduced in (c), and if the observer lives these additional experiences, then he or she accepts the generative mechanism proposed in (b) as a scientific explanation of the phenomenon to be explained as presented in (a). Furthermore, in as much scientific explanations consist in generative mechanisms, and the experience or phenomenon to be explained arises as a result of the operation of such generative mechanism, the experience to be explained and the generative mechanism pertain to different non-intersecting operational or phenomenal domains. It is because the experience to be explained and the generative mechanism that gives rise to it pertain to non-intersecting phenomenal (operational) domains, that explanations in general, and scientific explanations in particular, do not constitute phenomenal reductions. In other words, scientific explanations do not express the phenomena of one domain in the terms of another domain. Since our purpose is to answer the questions presented at the beginning of this essay giving a scientific explanation for the phenomena connoted by them, our task will be to present a generative mechanism that will give rise to those phenomena as a result of its operation.

III. BIOLOGICAL CONSIDERATIONS

III.1. Ontogenic structural drift

A living system is a first or second-order autopoietic system in the molecular space (Maturana & Varela 1984). That is, a living system is a dynamic structure determined molecular system, that exists as such only as long as the closed network of molecular productions and transformations that constitutes it courses in a way that its organization and operational congruence with the medium are conserved, or it

dies. In other words, what constitutes a living system as a living system is its uninterrupted operation in the continuous realization of its autopoietic organization (be this of primary or secondary order) in operational congruence with its circumstances of living (see appendix, “autopoiesis”). Still in other words, a living system remains a living system only insofar as its autopoietic organization is maintained in the flow of the structural changes it undergoes, independently of the origin of these changes (Maturana & Varela 1972, 1984), and as long as its operational congruence with the medium (adaptation) is also conserved (see 3.7. below, and also appendix, “adaptation”). Therefore, the individual history of a living being or ontogeny, constitutively takes place as a history of structural changes with conservation of autopoiesis and adaptation that follows a course that arises moment after moment, determined by the sequence of its interactions in the medium that contains it. The process of becoming in which a system follows a course of structural changes (or of change of position) through a history of interactions in which it conserves organization and adaptation (or relation of operational congruence with the medium) is denoted in English by the word “drift” (see appendix, “ontogeny” and “ontogenic drift”). Therefore we claim that:

a) the ontogeny of a living system is operationally a structural drift under conditions of conservation of its organization and adaptation;

b) the conservation of organization and adaptation in a medium is the condition for the existence of all living systems;

c) the conservation of organization and adaptation in the ongoing existence of a living system in continuous interactions in the medium is a general systemic phenomenon (see appendix, “systemic dynamics”), not a particular feature of the biological phenomenon; and

d) constitutively the ontogeny of a living system, that is, its individual structural drift, happens in its ongoing existence without any effort or intentionality or purpose.

Finally, it is according to all that we have said that when we speak of the structural changes that occur in a living system during its ontogeny, we speak of its structural ontogenic drift, and we do so insisting in that this is a spontaneous systemic process that as a constitutive feature of the realization of living systems does not need to be explained. And it is because all that we have said above, that we claim that any attempt to explain the history of living systems on earth must rest on those constitutive conditions (Fig. 1 and also Maturana & Varela 1984).

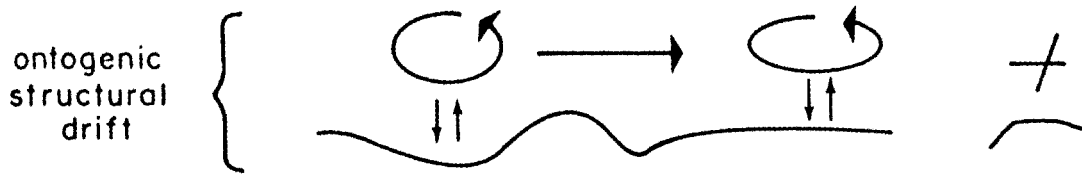


Fig. 1. This figure attempts to represent the congruent structural changes undergone by an organism and the medium along the ontogenic structural drift that takes place in the life history of an organism in the conservation of the ontogenic phenotype/ontogenic niche relation that defines its class identity. We show at the extreme right of the drawing the ultimate end of any ontogenic structural drift, namely, death. In this and successive figures, the closed arrow represents a living system; the curved line under the closed arrow represent the niche; the changing form of the closed arrow and the congruent changing form of the line that represents the niche, represent the conservation of dynamic structural congruence between organism and medium.

Esta figura representa los cambios estructurales congruentes sufridos por un organismo y su medio en el curso de la deriva estructural ontogénica del organismo. En ésta deriva, el organismo conserva y realiza la relación fenotipo ontogénico/nicho ontogénico que define su identidad de clase. En el extremo derecho de la figura se ilustra el resultado final de cualquier deriva estructural ontogénica, esto es, la muerte. En ésta y sucesivas figuras, la flecha curva cerrada representa al ser vivo; la línea curva bajo la flecha cerrada representa el nicho; la forma cambiante de la flecha cerrada, y el cambio congruente de la línea curva que representa al nicho, indican la conservación dinámica de la congruencia estructural entre organismo y medio.

III.2. The Living System and its Domain of Existence

During its ontogenic structural drift, the living system and its domain of existence change together congruently. Indeed, since a living system is a system that constitutively exists as such only in a continuous structural drift in the conservation of organization and adaptation in the medium, its domain of existence as that part of the medium in which it realizes its living necessarily arises with it in the realization of its living as an actual process, and changes with it. Under these circumstances the domain of existence of a living system does not preexist to the actual living of the living system in the domain in which it is distinguished by the observer. To be more accurate, we will make explicit the distinctions that an observer can make distinguishing a living being in the circumstance in which he or she distinguishes it:

a) The observer distinguishes the “medium” as the nameable or imaginable container in which he or she distinguishes the living system in the realization of its living. The medium, therefore, emerges with the distinction of the living system as everything that the observer sees and does not see, but that he or she conceives to surround and contain it.

b) The observer distinguishes as the “environment” of a living system all that he or she sees surrounding it when he or she distinguishes it as such. That is, the surroundings or environment in which a living system appears when distinguished

by the observer is not determined by the living system which only encounters the medium in those aspects or dimensions that constitute its domain of existence, and which henceforth we shall call the niche. The environment is which the observer sees or describes as surrounding the living system in the moment of its distinction.

c) The “niche”, or domain of existence of a living system is that part of the medium which the living system in fact encounters moment after moment in the realization of its living. The observer cannot see the niche directly, and he or she must induce it by observing the living system in its living. In other words, the niche or domain of existence of a living being cannot be characterized independently of the living being that lives it, and the only way the observer can know the niche of a living system is by using the operation living being itself to describe it or as a reference for its description.

Therefore, the living being appears in the distinction of the observer as it realizes its niche in the medium that contains it encircled or surrounded by the environment (Fig. 2). For the observer, who distinguishes the medium as containing the living being as well as including its niche, it may appear as if the medium or niche preexisted to the living system that he or she sees as occupying it. Yet, for the living system this is not and can not be so, since its domain of existence emerges with its operation in the actual realization of its living. For this reason, insofar as the medium includes the niche, and the niche does not preexist the living being, the medium does not

preexist the living system that occupies it either. The medium emerges with the distinction of the living system as a general domain of operational possibilities for the existence of the living system that the observer sees or imagines as possible through the operational coherences through which he or she distinguished the living system. As such, the medium appears to the observer as a background for the realization of the living of a living system and for the continuous emergence of the same or different niches according to the kind of being or beings that a living system becomes in the realization of its living. The niche or domain of existence of a living system corresponds substantially to what Von Euxküll (1957) calls its Umwelt (Fig. 2).

Given all that we have said above, we can not say that in its ontogenic structural drift the living being exists in the process of adapting to the medium, nor can we say that the medium selects the changes that the living systems undergo in their ontogenic and phylogenic histories. Such expressions entail the concept of preexistence of the medium to the living system that occupies it. What we can say, though, is that neither the medium nor the niche preexist to the living system that occupies them, and that during the structural drift of a living system the medium arises at the domain in which a living system can realize its niche, and that living system and niche necessarily change together congruently. Yet, we can

say that there is actually a costructural drift of living system and medium in the flow of their recursive interactions. At the same time, we can also say that whatever the observer sees as the environment of a living system, regardless of how valuable such vision may be for him or her to understand or imagine the niche of a living system, only reveals what the observer thinks. In these circumstances, and considering also what is expressed in II. 2., it is crucial for the understanding of the history of structural change of living systems and of the biosphere that they integrate, to make the distinction between the characterizations that the observer makes of the environment in which he or she finds a living system and what the living system finds in the medium as it realizes its niche in it. If we do not make this distinction we are led to confuse these two domains by assigning to the operation of the living systems phenomena that only belong to the descriptions made by the observers, and vice-versa, and thus mislead ourselves in the course of our explanations.

III. 3. Organisms

In Biology, we use the word organism as a generic expression that refers to a living system of first (unicellular) or second-order (multicellular), emphasizing its internal composition as a network

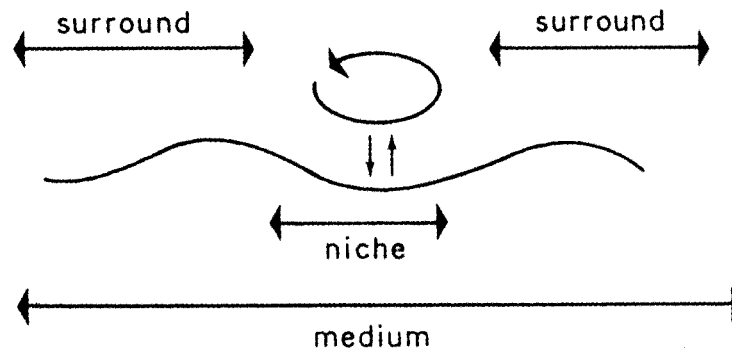


Fig. 2. This figure attempts to evoke the different views that an observer can have of a living system as he or she beholds it and reflects about its existence. As the observer beholds the living system from a distance: a) the medium appears to him or her as all that he or she may imagine as the great container in which it exists; b) the niche appears to him or her as that part of the medium with which the living system interacts and which it obscures, so that it can only be shown by the operation of the living system itself; and c) the ambient or that which surrounds the living system, appears to him or her as that which he or she sees around it but which being part of the medium is not part of its niche. Conceptually, the niche and the ambient together constitute the medium.

Esta figura ilustra las diferentes distinciones que un observador puede realizar respecto del dominio de relaciones de un organismo con su entorno. El medio es distinguido como todo aquello que, a juicio del observador, forma parte del gran continente o ámbito relacional y de interacciones en que el ser vivo existe. El nicho es distinguido como aquella parte del medio con la cual el ser vivo está interactuando, y que por tanto queda oculta al observador, el que puede inducirla solo a partir de las operaciones del propio ser vivo. El ambiente queda distinguido como toda aquella parte del medio que no forma parte del nicho. El nicho y el ambiente juntos constituyen el medio.

of processes associated to a particular subsystems that are considered to operate as the organs (instruments) that realize such processes. Moreover, the notion of organism connotes both the operational unity of the realization of the living as well as the unity of reproduction of the living systems.

An organism, therefore, can be characterized as a system of subsystems (organs, cells and systems of cells) which intersect in their structural realization, so that all the subsystems are part of the domain of realization of the niche of others. The various subsystems that are in structural intersection in an organism, however, exist in it as independent kinds of entities because their respective organizations do not intersect, and only their structures do. Due to these circumstances, the ontogenic conservation of an organism implies the simultaneous independent conservation of the different organizations of all the other systems (subsystems) that are in structural intersection in it. Thus, for example, and said explicitly, the ongoing existence of any particular organism entails the simultaneous conservation of: its autopoietic organization (either of first or second order, or both, according to the case), the organization proper to the organism under consideration, the different organizations of its different types of cells, and the different organizations of its different organs. Finally, in the reproduction of an organism, what is conserved is the initial structure that constitutes the possibility of the ontogenic realization of all the systems that intersect in its realization. That is, the reproduction of an organism involves or implies as a consequence the simultaneous reproduction of all the subsystems that through their structural intersection with it participate in its realization. It is because of this that the evolutionary history of living systems is a history of conservation and change not only of lineages of organisms (see 3.11 below and also appendix, "lineage" and "phylogeny"), but also of lineages of other kinds of systems that intersect with them in their structural realization. Accordingly, we shall speak of living systems when we refer to them in general terms, and of organisms when we want to refer to the ontogenic phenotypes (see 3.9 below and also appendix, "phenotype" and "ontogenic phenotype") as the ways of living that living beings conserve in their ontogenic or phylogenic becoming.

III.4. Ontogenic co-drifting

The recursive interactions between two or more organisms give rise to an ontogenic structural

codrift as a flow of congruent coherent structural changes in the conservation of their respective organizations and reciprocal adaptation as each one is part of the niche of the other. That is, in ontogenic codrift, the recursively interacting organisms follow reciprocally congruent structural drifts, and each one follows the path of the structural changes in which it conserves its organization and its adaptation in relation to the others, in an ongoing process that lasts until one of them separates or disintegrates. And, what is more, this is the fundament for the constitution of the biosphere as a system of structurally coherent recursively interacting systems that conserve their respective different organizations in a flow of continuous structural change, in an open dynamics of structural codrift that generates and conserves all and new systems in reciprocal structural coupling (see appendix, "structural coupling"). Furthermore, it is this condition what makes of ontogeny (and phylogeny) a processes that consists in the simultaneous conservation of both the organization of a system and its niche.

III.5. The intercrossing of identities.

As we have already said in point III.3. above, the structural realization of an organism as an autopoietic system entails the corealization of many other systems in structural intersection with it (subsystems), that, as they are defined by different organizations, exist as such in different relational domains. These different entities or subsystems in structural intersection have different structural dynamics, and undergo different ontogenic structural drifts in the conservation of their respective non-intersecting organizations even if they are not fully independent structurally, because their different structural dynamics participate in the realization of each other through their participation in the realization of the carrier system (the organism in this case) that they integrate. Therefore, although the subsystems in structural intersection in an organism exist in different non-intersecting relational domains, they affect each other through their different structural dynamics as the structural changes in one result in change in the structural realization of the others. As a general result, subsystems in structural intersection are in costructural drift in the system that carries them, but they can also disintegrate independently if their disintegration does not disintegrate the carrying system.

Any living system through the realization of its autopoiesis can be in the moment of its reproduc-

tion the phylogenic carrier of different organic subsystems that exist in structural intersection with it. Thus, for example, we as *Homo sapiens* operate as reproductive carriers of such different kinds of identities as vertebrate, mammal, and primate. We have called carrier system the system whose realization secures the phylogenic conservation of other systems that intersect with it. The same occurs with entities or systems of other kinds, such as organs or systems of organs that as particular subsystems also intersect in their realization with the realization of the living system that carries them. Such systems as organs are also conserved through the reproduction of the system that carries them. We do not usually consider organs as independently existing entities because we do not easily see the domain in which they exist as such. Yet, if we attend to the evolutionary history of organs, we can see that they form lineages defined by the conservation of some particular epigenic morphogenetic pattern through the successive generations of the carrier living system in the conservation of the realization of its niche. Indeed, the systems that intersect structurally with a carrier living system can themselves be carrier systems for other systems in structural intersection with them. Accordingly, when a carrier system disintegrates, all the subsystems that are in structural intersection with it also disintegrate. That is, and in general terms, although the different entities that realize themselves through the realization of a carrier system in the structural intersection with it depend for their realization on the realization of the carrier

system, all structurally intersecting entities exist individually in the realization of their respective niches in their respective domains of existence (Fig. 3; also Maturana 1988). Finally, what is conserved in the reproduction of a living system as a carrier of other subsystems that exist only in structural intersection with it, is an initial structure that allows in its epigenesis (see the two next sections) the epigenic realization of the different systems that intersect in it.

III.6. Epigenesis

A living system is a molecular autopoietic system of first or second order, and since it is as such a composite entity, its realization involves at every moment the participation of all its components, and it cannot be claimed that any of them can alone be by itself responsible for its characteristics. Indeed this is why it is not possible to speak with property of genetic determinism, or to say in a non-metaphorical way that certain features or traits that an organism exhibits as it operates as a whole are genetically determined, or to say in a non-metaphoric way that a particular trait of an organism as a whole is determined by the nuclear DNA of the cells of such an organism. What we can say, though, is that nothing happens in the ontogeny of an organism that is not allowed by its initial total genetic constitution, and that every trait, characteristic, or feature in an organism as a totality or in its components (cells, organs, or systemic relations between cells and between organs), emerges or results from an epigenic process (see appendix, "genetics"; "total genotype" and "genotype"). And we are also saying, that starting from its initial total structure, the life history of a living system courses as an ontogenic structural drift, and takes place as an epigenic process in which whatever happens in the organism at any moment arises in it in the interplay of its structural dynamics at that moment, modulated by the structural changes triggered in it by its interactions in the medium. So, the epigenesis is a process in which the initial total structure of a living system does not predetermine the structural changes that it will undergo in its ontogenic drift because these will arise moment after moment in the interactions of the structure of the living system and the medium in which it lives.

The initial structure of a living system constitutes a structural starting point that determines or specifies for that living system what an observer sees as the particular domain of all the possible ontogenetic transformations that that living sys-

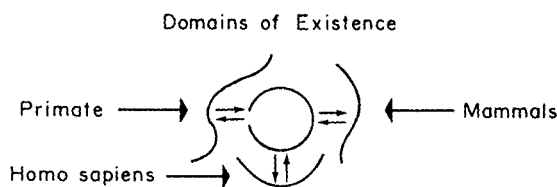


Fig. 3. This figure attempts to show the several identities that may exist in structural intersection in the realization any living system. Thus, a particular living system may be an *Homo sapiens*, a primate, or a mammal in different relational domains as different manners of realization of its living.

Esta figura muestra las varias identidades que pueden intersectarse estructuralmente en la realización de un ser vivo. Por ejemplo, un cierto ser vivo puede ser al mismo tiempo un *Homo sapiens*, un primate, o un mamífero, cada uno con su propio dominio relacional y su particular manera de realizar su vivir.

tem may live in an epigenic form. Yet, such a domain of ontogenetic epigenic possibilities (see appendix “epigenetic field”) is conceptual because only one of the ontogenies that the observer sees as possible in the epigenetic field will be actually realized in the epigenesis of the living system. Moreover, as we have already said, the actual ontogeny that a living system lives arises in the history of its interactions, and does not exist as such except in the course of that history as this happens as an epigenic process. Accordingly, only if the initial structure and the history of interactions are repeated during the epigenesis of the reproductive succession of living systems, the successive living systems will live the same ontogeny. It is only if an observer could affirm that a particular phenotype emerges independently of the course of the epigenic history of an organism, that he or she could say with operational meaning something similar to what one might want to say when speaking of genetic determination. A claim of genetic determination, then, can only be metaphorical because a phenotype, even at the cellular level, can only arise in an epigenic manner. That an observer can associate a trait of the structure of an organism in some instant of its ontogenic drift with some aspect of its initial structure, does not refute the fact that all the traits or characteristic of an organism arise in an epigenic manner from its initial structure. What can be claimed with proper biological operational meaning, though, is what we have already said, namely, that nothing will happen in the epigenesis of an organism that is not allowed by its initial structure as its total genetic constitution. The total initial structure of an organism determines the field of all the epigenic courses that it may follow in its ontogeny, but the epigenic path actually followed by the organism in its ontogeny, necessarily arises anew moment after moment in the course of its interactions as it lives in the conservation of organization and adaptation.

In synthesis, epigenesis is the manner of existing of living systems in the realization of living, and this is so regardless of whether they exist in the metabolic realization of their living as single cells, in the process of their embryonic development as they exist as multicellular organisms, in the constitution of symbiotic entities, or in their living as free autonomous beings. Moreover, in all cases, the internal dimensions of the living system are part of the relational domain in which its epigenesis takes place, and never can the features of the living system as such be claimed to be the sole result of the operation of any of its components (see also appendix “epigenesis”).

III.7. Medium, environment and niche again

It follows from what we said in section 3.2. above that as a living system lives, it in fact lives continuously realizing a niche that appears through its actual living. In this dynamics the living system does not encounter a preexisting niche because it appears with its living, and it does not see or relate to a preexisting medium because it does not encounter the medium beyond that which appears in the realization of its niche. It is in the explanation of the operation of living systems and their characteristics as they appear in their distinction by the observer, that the medium, the environment and the niche exist as operational relational dynamics that make the living of the living systems possible. Indeed, then, what the observer says is the following: a) as an observer distinguishes a living system he or she distinguishes it in a medium, and does so distinguishing it as a structure determined entity that lives realizing its niche in a medium that it does not see; b) in the flow of its living a living system does not interact or accommodate to the medium, the environment or its niche, it simply operates in its closed structural dynamics, and as it does so it realizes a niche that continuously arises *de novo*.

In the explanation of how living systems exist and diversify in history, then, it is not possible to argue with any operational sense that living systems diversify in a historical process of adaptation to a preexisting medium or environment. But to be aware of that, it is at the same time necessary to be aware that both in the ontogeny and the phylogeny of living systems, living system and niche change together, and that indeed, living system and medium change together in a continuous becoming of the biosphere as an interconnected network of living and not living systems that operationally arises at every instant as a novel present.

III.8. Reproduction and Heredity

The phenomenon of reproduction occurs in the very moment in which a system undergoes a division or fracture that conserves in the resulting fragments the organization of the original system, and gives rise in that way to two or more unities of the same kind as the first one. Something similar but in the reverse happens when two or more unities of the same class fuse together and give rise to another unity of that class. Reproduction as a process that conserves the organization of a progenitor system through the conservation of the particular structural dynamics that realizes that organization in the resulting fragments of a

reproductive division, constitutes the phenomenon of heredity (Maturana 1980, Maturana & Varela 1984). As such, reproduction involves the conservation in the progeny of the structure required for the realization of the organization conserved through it, as well as the conservation of the structural features of the medium that permits the realization of such organization. Due to its manner of occurrence reproduction occurs as a systemic phenomenon that takes place when the interplay of the structure of the reproducing living system and the structure of the medium results in the conservation of the organization of the progenitor in the offspring. Said other words, the phenomenon of heredity takes place as a phenomenon of conservation of an organization through a systemic reproductive division. Due to its manner of constitution through systemic reproduction, heredity in living beings does not depend on any special kind of molecules, nor even when there are special kinds of molecules that secure particular process of molecular production in the realization of the autopoiesis of the living system, as happens with nucleic acids. Moreover, we claim that reproduction is a systemic phenomenon that is possible when the realization of the organization of the system that reproduces (living system in our case) is not compartmentalized, but is distributed through its structural dynamics in a way such that the system admits at least one reproductive fracture. Indeed, it is the non-compartmentalized distribution of the components and processes that participate in the structural realization of a system what makes possible its reproduction, either directly by fracture or partition, or indirectly through the production of gametes, and not any particular kind of components. Reproduction is a common phenomenon in nature, and it is not in any particular manner proper to living beings, even though in them it currently occurs in many different ways that range from complex mitotic cell division, passing through meiosis and the production and fusion of gametes, to the fracture or separation of multicellular reproductive fragments as happens in various systematic and accidental ways in many different kinds of organisms.

From a structural point of view, what is inherited in the reproductive division of a living system, is what we have called below (see 3.6.) the “total genotype”, or “total initial structure” of the newly arising living system. But that total genotype does not specify the future of the living system, it only establishes a domain of possible epigenesis, only one of which will be realized in the internal and external structural dynamics that take place in the ontogeny of the new living system modulated by

the particular course of interactions that this undergoes in its particular life history. Accordingly, both reproduction and heredity are systemic phenomena not only because of the systemic character of the realization of the inner processes of the living system, but also because reproduction and heredity result as phenomena of the life history of living systems in the interplay between the internal structural dynamics of the living system and the structure of the medium. Therefore, what is conserved in reproduction is a manner of ontogenic becoming that involves in a systemic way the epigenesis of the living system and the conservation of the features of the medium that permit the realization of such ontogenic becoming. We have called the manner of epigenic becoming that a living system realizes in the course of its living from its inception to its death, “ontogenic phenotype”, and the ontogenic phenotype is conserved through systemic reproduction only if the possibility of the realization of the “ontogenic niche” is also conserved as part of the process of systemic reproduction. Accordingly, what is conserved in the systemic reproduction of any particular kind of organism, is an ontogenic phenotype that arises in an epigenic manner that entails the systemic conservation of both the initial structure that makes such ontogenic phenotype possible, and the conservation of the medium in which the history of interactions that results in that ontogenic phenotype may indeed occur in the realization of its corresponding ontogenic niche. Or, in other words, in the systemic reproduction of any particular ontogenic phenotype, what happens is the systemic reproductive conservation of the particular total initial structure and the particular features of the medium that result in the epigenic realization of the ontogenic phenotype reproductively conserved.

In summary, the main results of the systemic character of reproduction and heredity are three: one is that living systems and medium spontaneously change together congruently in the course of the generations of the living systems; two, that this occurs as a simple result of the history of recursive interactions between living systems and medium; and three, that whenever a group of living systems begin to live together, their living together becomes a feature of the medium that is conserved in their reproductive history, until they disintegrate independently or separate.

III.9. Ontogenic phenotype

We have called ontogenic phenotype the particular form of living that an organism realizes along its ontogeny from its inception to its death as the

manner it lives in its interactions in the medium. Therefore, the ontogenic phenotype that a living system lives arises in an epigenic manner in a process that involves the interplay of both the structural dynamics of the living system and the structural dynamics of the medium, so that the ontogenic phenotype that any living system realizes along its living, is not determined and cannot be determined by the particular total initial structure with which an organism begins its living. That is, the ontogenic phenotype that a living system realizes in its living as a particular kind of organism, is not and cannot be genetically determined, even though the total genetic constitution of any newly arising organism must permit the epigenic realization of the ontogenic phenotype that it actually realizes along its living. Therefore, no ontogenic phenotype can arise in the life history of a living system that is not made possible from the total initial structure of the newly arising organism and the structure of the medium in which it begins its living as a result of the systemic reproduction that gives origin to it. In other words, although neither the total initial structure of a newly arising organism, or the circumstances of the medium in which a living system lives, do not, and cannot determine what ontogenic phenotype a living system realizes in its living, both must be such that they allow for the realization of the ontogenic phenotype that the living system lives, whichever these may be. Therefore, the realization of the ontogenic phenotype that a living system lives occurs in the epigenic interplay of two dynamically independent systems as a particular historical occurrence, and the repetition or reenactment of an ontogenic phenotype requires the particular dynamic coincidence of those two independent systems that makes such a reenactment possible.

III.10. Lineage Formation

The total initial structure of a newly arising living system is not just any, it is some variation of the parental one. Similarly, the field of the possible epigenesis of a newly arising living system is not just any, it is some variation of the parental one. At the same time the structure of the medium in which a living system begins to live and lives, is not just any one, nor does not it change in a hazard way, it changes in a historical manner that depends on the course of living of the progenitor living systems. In these circumstances, the reproduction of a living system does not occur in just any place or circumstance, but it occurs in a particular place and under a particular set of circumstances that are

systemically determined by the particular course followed by the parental epigenesis. That is, the total initial structure of a new living being is not deposited by the reproducing organism just anywhere, but rather it is deposited in a particular place in a particular domain that is determined by the parent's particular life history. Consequently, what emerges in the reproduction of a living system, is another living system that realizes a particular ontogenic phenotype in the form of an organism that turns out to live one ontogenic phenotype or another depending on the epigenic path that it happens to follow in its life history starting under structural and interactional conditions in a medium brought forth by the contingencies of the life history of the progenitors. Accordingly, only if in the reproduction of a living system both the initial structure of the reproducing organism as well as the contingencies of its interactions in the medium are such that in the epigenesis of the new organism the parental ontogenic phenotype is repeated, the parental ontogenic phenotype is conserved through systemic reproduction in the new generation in the recursive interplay of those two conditions. Moreover, when that happens, and an ontogenic phenotype as well as the conditions of the medium that permits its realization are conserved generation after generation through systemic reproduction, a lineage arises as a particular history of phylogenetic structural drift in the conservation of an ontogenic phenotype/ontogenic niche relation (see appendix "Ontogenic phenotype / ontogenic niche relation").

No doubt that the reproductive conservation of an ontogenic phenotype can happen only if the particular systemic relations that make it possible occur as a historical coincidence in the recursive interactions between living systems and medium. But at the same time, that coincidence in the history of living systems is the result of its very occurrence in the systemic reproductive conservation of their organization and reciprocal adaptation in the constitution of a biosphere as a network of lineages in which all living systems participate as the medium of the others in the realization of their respective niches. Therefore, the constitution and conservation of a lineage of organisms and the constitution and conservation of the biosphere as a network of coadapted lineages of organisms, occurs only if a systemic dynamics of reciprocal structural coupling between living systems and medium occurs as a systemic result of their recursive interactions. Either the living of living systems contributes to the arising in the medium of the conditions for the realization of their living, or they disintegrate.

Moreover, as a result of the reproductive conservation of the parental ontogenic phenotype in

the constitution of a lineage, many subsystems that exist in structural intersection with it will be simultaneously conserved and form intersecting operationally independent lineages that can exist only as long as the lineage of the carrying ontogenic phenotype is conserved. Or, in other words, the conservation of the ontogenic phenotype that defines a lineage entails as part of its conservation the conservation of: a) the autopoietic organization of the living system reproduced as the carrier of all the subsystems that participate in its realization; b) the particular organization that defines the class identity of the reproducing living system as the particular kind of organism that it is; and c) the different organizations of all the subsystems or component entities that, as they intersect in their structural realization with the realization of the living system reproduced, reproduce with it.

If after a living system undergoes a reproductive fracture, the particular ontogenic phenotype that realized it as a particular kind of organism is not conserved in the progeny, one or several living systems appear that realize one or several ontogenic phenotypes different from the parental one. When this happens, a new type of living system appears under the form of a new kind of organism in the realization of a new ontogenic phenotype that is a variation of the kind of organism that the progenitor living system was. And, when the latter happens, the new organisms may or may not be the carriers of the same entities or subsystems that intersected in the structural realization of their progenitor. Furthermore, if the new living systems reproduce, two possibilities open for the constitution of new lineages: one is that a new ontogenic phenotype appears that begins henceforth to be conserved generation after generation, and a new lineage is immediately established; the other is that after a series of successive systemic reproductions with change in the ontogenic phenotype realized in each generation, one begins to be conserved through systemic reproduction in the conservation of the total initial structure and the configurations of the medium that make the systemic reproductive conservation of that ontogenic phenotype possible. We call this process "the phylogenetic shift of the ontogenic phenotype". When this process happens, what an observer that looks at the historical succession of lineages sees, is a phylogenetic saltation in the constitution of a new lineage.

The conservation of an ontogenic phenotype through the reproductive constitution of a lineage goes together with the conservation of the conditions of the medium that make the realization of that ontogenic phenotype possible as a spontane-

ous result of the systemic dynamics of conservation of the organization and adaptation of the reproducing organisms. As we have indicated above, when the constitution and conservation of lineages occurs in a group of living systems that interact with each other recursively in a way in which all operate as part of the medium of the others, what occurs is the history of conservation of the reciprocal adaptation of many structurally congruent ontogenic phenotypes in a non-living background, in a dynamic way that includes all together in the constitution of a biosphere or an ecosystem. The spontaneous systemic constitution of lineages and the spontaneous systemic phylogenetic shifting of the ontogenic phenotypes in the constitution of a biosphere, as a result of the conservation of living and adaptation, is what makes the biosphere and the ecological systems both resilient and fragile. They both can recover from disturbances within certain systemic limits, but when those systemic limits are trespassed, they disintegrate beyond recovery.

III.11. Behavior

The relational dynamics that we as observers call behavior when we distinguish a living system in interactions in the medium, occurs as the flow of the encounter of the living system and the medium, and is not something that the living system does by itself. That is, the behavior of an organism takes place as the flow of its interactions as it operates as a totality in its domain of existence, and involves both the structural dynamics of the organism and the structural dynamics of the medium. In other words, what we as observers see as the behavior of a living system is the interactional and relational dynamics through which a living system realizes its living as a particular kind of organism in its domain of existence. As such, behavior is not something that the living system does; instead, behavior takes place, and arises moment after moment, in the recursive encounters of the living system and the medium. At the same time, what an observer sees as the behavior of an organism is not the actual structural encounters of the organism and the medium, but what appears to him or her as the flow of the interactions and relations that take place in the course of those encounters. In these circumstances, if we look at a living system as it interacts in the medium in which it exists, we can distinguish three dynamic domains in relation to how it actually operates in its behavior, namely: a) the domain of the internal structural dynamics, of the living system as it operates in the realization

of its living, which is the structural domain that we usually connote when we speak of physiology; b) the domain of the structural dynamics of the medium, which we frequently do not see as we treat the medium as a container and the behavior as something that the organism does; c) the domain of the operation of the living system as a totality in the realization of its living as it relates and interacts as a whole with the medium, and which is what we usually call the behavioral domain of the living system (Fig. 4). As the physiological domain and the behavioral domain do not intersect, the phenomena of one cannot be deduced from the phenomena of the other, and the operations that take place in one of them cannot be expressed in terms of the operations that take place in the other. It follows from this that as the behavior takes place in the interactions of the living system as a totality and the medium in which it interacts, the behavior operates as a guide in the course of the interactions of the living system and the medium, and as such it operates coupling the course of the structural dynamics of the living system and the structural dynamics of the medium. What happens is the following: As the behavior takes place, the structural dynamics of the living systems triggers structural changes in the medium, and at the same time the structural changes that take place in the medium as behavior takes place trigger structural changes in the living system. As living takes place in the continuous conservation of autopoiesis and adaptation by the living system through its behavior, the behavior of the living system operates as the guide in the conservation or loss of the living through the coupling of the structural dynamics of the living system and the medium. That is, even though the two operational or phenomenal domains in which a living system exists do not intersect, there is a structural generative relation between them that couples the structural dynamics of the living system to the structural dynamics of the medium, namely: the course of behavior modulates the course of the structural changes of the living system, and the structural changes of the living system modulate the course of behavior, and this takes place in a flow of congruent changes of the living system and the medium along the path of the conservation of autopoiesis and adaptation in the living system.

In synthesis: Although the course of the behavior of a living system depends on the courses followed by both its internal structural dynamics and the independent structural dynamics of the medium, the internal structural dynamics of a living system and the structural dynamics of the medium, neither determines alone "its behavior" because this arises and occurs in the recursive

encounter of the living system and the medium, and hence, with the participation of both. That is, the internal structural dynamics of a living system does not determine its behavior, it only makes this possible. The converse situation is also the case. Accordingly, in the actual living of a living system, the flow of its behavior generates at every instant the circumstances under which it encounters the medium that contains it, and through that it determines which structural configurations of the medium, and in which sequence, trigger the structural changes that happen in the living system during the course of its recursive interactions with the medium without specifying them. Therefore, the continuous flow of behavior that a living system lives in its encounters with the medium constitutes the relational structural dynamics through which the living system and the medium change together congruently in a path in fact guided by the behavior of the living system. Or, in other words, as a living system and the medium have operationally independent structural dynamics, the structural changes of the living system and the structural changes of the medium remain in operational congruence only as long as the arising behavior of the living system continuously results in the conservation of the organization and adaptation of the behaving living system.

In these circumstances, four additional things also happen in the domain of behavior as consequences of the operation of a living system as a structure determined system:

a) That to the extent that the structural dynamics of a living system does not determine its behavior, but this arises and takes place in the interactions of the living system and the medium, the same behavior as the same interactional and relational dynamics seen by the observer that names it, can arise under many different internal structural dynamics of the living system.

b) That the internal structural dynamics of a living system and the behavior that arises in its interactions in the medium can vary independently along the structural drift of a living system.

c) That the domain of internal structural variability of any particular living system is potentially much greater than the domain of its behavioral variability.

d) That as the behavior of a living system realizes its manner of living in the recursive interactions between the living system and the medium while these two operate with independent structural dynamics that are only coupled through the behavior, conservation of organization (autopoiesis) and adaptation through behavior is what guides the ontogenic (and phylogenetic) structural drift of a living system (and of a lineage).

So, the part played by behavior in the ontogenic structural drift is fundamental in shaping the individual life history (and, hence, also the phylogenic history) of living systems. Indeed, to the extent that it is the behavior of the living system what guides the course of the structural changes triggered in it in the course of its interactions, it is the behavioral flow that arises in the interactions of the living system in the medium what channels and guides the flow of its ontogenic structural drift within the confines that permit the realization of an ontogenic phenotype in the conservation of autopoiesis and adaptation. In other words, the course of the behavioral flow of a living system guides the course of its epigenesis, so that the actual course of the epigenesis of a living system arises moment after moment in the interplay of the structure of the living system and the structure of the medium guided by the course of its behavioral dynamics along its ontogenic structural drift. But, at the same time, as the behavior of a living system arises in the interaction of the living system and the medium, a particular ontogenic phenotype can be repeated under the guidance of behavior only if the necessary dynamic structural conditions of the living system and the medium are repeated. Some of the systemic consequences of what we have said until now can be summarized as follows:

1. The behavioral flow of an organism in the course of its life history realizes its manner of living, and it is as such an aspect of its ontogenic phenotype.

2. The behavior that an observer sees as a configuration of dynamic relations that takes place in the recursive interactions of a living system and the medium, is part of the systemic relational dynamics that realizes a particular living system as a particular kind of organism. The inner structural dynamics of a living system does not determine its behavior, even though it participates in its generation because the behavior takes place in the organism-medium relations. At the same time, the behavioral dynamics that an observer distinguishes in the flow of the interactions of a living system in the medium does not specify or determine the structural changes that take place in the living system, it only guides the course of the structural changes triggered in it in its ontogenic structural drift. The same happens in relation to the structural changes of the medium.

3. Behavior as the dynamic realization of the living of a living system in the flow of its interactions in a medium is an aspect of the realization of its manner of living, and takes place at every moment as part of the realizations of its ontogenic phenotype as a feature of its epigenesis. Accord-

ingly, strictly speaking there is no genetic determination, nor can there be genetic determination of any character or feature of the behavior of an organism because the behavior occurs as a systemic relational dynamics in the recursive interactions of the living system and the medium, that operate under independent autonomous structural dynamics.

4. The reproductive conservation of any particular manner of behavior in a lineage, entails the satisfaction of three conditions: one, the reproductive conservation of the initial structure that makes possible that that behavior should arise in the epigenesis of the members of the lineage; two, the conservation in the structural dynamics of the medium of those features in it that make possible the realization of that behavior in the epigenesis of the members of the lineage; and three, the coincidence of the two previous conditions from one generation to the next.

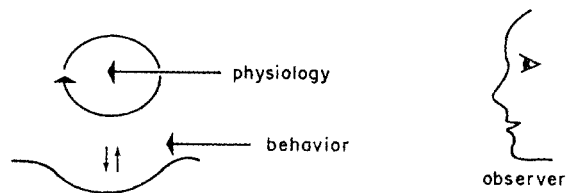


Fig. 4. This figure attempts to show the two domains in which a living system exists: the physiological domain and the behavioral domain. The physiological domain is the domain in which the living system exists in the operation of its components as a closed molecular autopoietic system. The behavioral domain is the domain in which the living system encounters the medium in the realization of its niche, and in which the behavior takes place in the interplay of the structural dynamic of the living system and the structural dynamics of the medium. So, the physiology involves the dynamic structure of living system only, while the behavior involves both the dynamic structure of the living system and the dynamic structure of the medium in the niche.

Esta figura ilustra los distintos dominios en que tiene lugar la existencia de un ser vivo: el dominio fisiológico y el dominio conductual. El dominio fisiológico es aquel en el cual ocurre la realización del ser vivo como sistema autopoietico, a través de la operación de sus componentes moleculares y celulares. El dominio conductual es aquel en el cual el ser vivo interactúa con su medio en la realización de su nicho, y en el cual la conducta (según la distingue un observador) toma lugar, como un continuo juego de encuentro estructural recíproco entre el ser vivo y el medio. Entonces, la realización fisiológica del ser vivo compromete solamente su dinámica estructural, en tanto la realización conductual de él compromete tanto su dinámica estructural como la dinámica estructural del medio en el nicho.

IV. OUR EXPLANATORY PROPOSITION

Now we shall make use of the operational and epistemological fundamentals that we have presented in the previous sections in order to propose a generative mechanism that would give rise directly or indirectly to the phenomena of the organic evolution.

We do not differ from Darwin and other evolutionists in what refers to accepting that the present diversity of living systems in the biosphere is the result of an evolutionary history based on phylogenetic differential survival. But we differ in that we claim that the generative mechanism of the evolutionary process is not natural selection but what we call "phylogenetic natural drift", as a process of spontaneous constitution, conservation, and diversification of lineages through the systemic reproductive conservation of organization and adaptation under the form of an ontogenic phenotype, as well as the spontaneous extinction of lineages when such systemic reproductive conservation does not occur. In other words, we claim that it is the process that we call phylogenetic natural drift what gives rise as a result of its operation to the diversification, conservation, and extinction of lineages that we modern biologists say is the consequence of natural selection. Let us repeat: we claim that natural selection is the consequence of evolution, not its generative mechanism, and that the generative mechanism of evolution is natural drift.

Indeed, we are proposing a basic conceptual change in dealing with the same fundamental questions that lead Darwin to the theory of evolution by means of natural selection. We claim that change occurs continuously as a spontaneous feature of the molecular existence of living system (and of all molecular systems), and that as an intrinsic condition of the existence of living systems it must not be explained. What must be explained is the course that change follows in the ontogeny and phylogeny of living systems. Moreover, as we accept change as an intrinsic condition of living systems, we do not have to think in terms of forces such as selective pressure to explain change or the course that change follows in the life history of living systems. It is a systemic condition that whenever in a system some relations begin to be conserved, every thing else is opened to change around them (see appendix, "systemic dynamics"). We claim that in the system living system/medium the relations conserved in the living of the living system are organization and adaptation as the relation of operational congruence between the living system and the medium in which it lives. Therefore, we claim that it

is the conservation of adaptation and organization while living system and medium are in continuous change, what defines moment after moment the courses that the continuous change of the living system and its circumstances follow, and what makes that those changes remain dynamically congruent in the conservation of the living of the living system while this lives. Obviously we do not think that such a conceptual shift with respect to the notion that natural selection is the generative mechanism of evolution is trivial because it will lead to the same final result, namely, differential survival. Quite on the contrary, we think that such conceptual shift will permit us to have a more complete understanding of the biological phenomena in general, and of history of the biosphere in particular.

Let us see now in detail the operation of the mechanism that we claim gave origin to the historical diversification of the living systems, through answering the basic questions that we presented at the beginning of this essay.

IV.1. Phylogenetic drift

What is conserved generation after generation in a lineage of systemically reproducing systems when that lineage is a lineage of living systems, is molecular autopoiesis and the conditions of the medium that make possible the conservation of the realization of autopoiesis in the reproducing systems. When a lineage of a particular kind of organisms is constituted, what is conserved generation after generation with every living system that appears as a member of this lineage, is the manner of realization of the ontogenic phenotype of that particular kind of organisms and the conditions of the medium that make that realization possible. When a mammal lineage is constituted, what is conserved generation after generation in every one of the living systems that appears as a member of that lineage, is the ontogenic phenotype "mammal" as well as the conditions of the medium in which that ontogenic phenotype can be realized. In general terms, what is conserved generation after generation in a lineage of systemically reproducing living systems is the ontogenic phenotype that defines the lineage and the conditions of the medium that make possible the realization of the niche of that ontogenic phenotype. Yet, since an ontogenic phenotype can be realized through many different total genotypes, the conservation of an ontogenic phenotype through systemic reproduction allows the total genotype to vary in the course of the generations as long as these variations do not

interfere with the realization of the ontogenic phenotype that is conserved. Similarly, since an ontogenic phenotype can be realized under many different configurations of the medium as long as this allows for the realization of the niche of the ontogenic phenotype, the conservation of an ontogenic phenotype through its systemic reproduction allows for medium to change around the conservation of the conditions of realization of its niche. Under these circumstances, if there is systemic reproduction, there is the possibility for variation in the conditions of realization of the ontogenic phenotype that is conserved in each reproductive step through variations in the total genotype of the reproducing living systems, as well as through variations in the configuration of the medium in which the niche of the reproducing living system is realized. Thus, if what is systemically reproduced is autopoiesis (that is, if what is conserved through systemic reproduction, is living and the configuration of the medium that makes living possible), then the possibility is open for a) variations in the way in which the newly arising living systems realize their autopoiesis; and b) the establishment of a new lineage or several new lineages of organisms as some of the new forms of realization of autopoiesis begin to be conserved in the living systems that arise in the course of their successive systemic reproductions.

Let us describe this dynamics differently: an ontogenic phenotype is repeated in the reproduction of a living system if a particular initial structure is conserved in it, and if a particular history of interactions, under the form of a particular configuration of encounters with the medium, is repeated in the epigenesis of the new living being during its ontogenic structural drift. Therefore, the conservation of an ontogenic phenotype along successive reproductions and, hence, the constitution of a lineage, are processes that imply in every generation the repetition of the particular relational dynamics between living being and medium that makes such repetition possible. Thus, for example, during the history of conservation of a particular lineage of mammals, what has to have been conserved in the succession of reproductions is a certain initial structure and a particular configuration of relations and interactions in the individual ontogeny of every new living system member of the lineage, so that in the interplay of these two conditions, the epigenesis proper to this particular kind of mammal would occur. In general terms then, a lineage arises in the systemic reproductive conservation generation after generation of an ontogenic phenotype/ontogenic niche relation.

We claim that the historical permanence of a lineage, that is, the continued conservation of an ontogenic phenotype/ontogenic niche relation through successive systemic reproductions, occurs in a systemic dynamics thanks to the systemic and not to the genetic nature of the realization of the ontogenic phenotype. In this process, the total genotype that supports and makes possible the realization of the ontogenic phenotype that defines a lineage without determining it, can vary while the lineage is conserved within a domain of possible changes determined through the conservation of the very same ontogenic phenotype that defines the lineage. At the same time, the structure of the medium is open to change according to its own dynamics of change and through its interactions with the organisms that it contains while a lineage is conserved, as long as the structural dynamic conditions in it that make possible the epigenesis that realize the ontogenic phenotype that defines that lineage are conserved. In these circumstances, a new lineage will be formed as a branching of an already existing one, whenever a new ontogenic phenotype that arises in the realization of one of the epigenic possibilities allowed by the total genotype of the progeny of one or more members of a "parental" lineage, begins to be conserved through systemic reproduction when the conditions of the medium that make the niche of that new ontogenic phenotype possible, are also conserved. That is, whether the branching of a new lineage takes place or not at a given moment in the history of some lineage, depends on whether the systemic relations between living systems and medium that make possible such a branching new lineage occur or not. The branching of a new lineage is a conservative phenomenon in which both the particular features of the new ontogenic phenotype conserved, and the particular features of the medium that permit the realization of the niche of the new ontogenic phenotype, arise as variations of conserved features of the epigenic dynamics of the realization of the ancestral ontogenic phenotype. In these circumstances, if the new lineages thus formed were to undergo in their turn one or more branching episodes, a ramified system of lineages connected by a common origin and a common epigenic history would be produced in which the new ontogenic phenotypes as well as the conditions for the realization of their respective niches will have changed together congruently. We call "natural phylogenetic drift" to this spontaneous process of generation and ramification of lineages of organisms through the systemic reproductive succession of living systems with conservation and change of the ontogenic phenotypes that define

the lineages, together with the conservation and change of the conditions of the medium that permit the realization of the respective niches of those ontogenic phenotypes. Natural phylogenetic drift, then, is a process that happens spontaneously whenever the conditions mentioned above prevail. Furthermore, in strict terms, what happens in natural phylogenetic drift in the codrifting of many lineages, is the constitution of a biosphere as a network of ontogenic phenotype / ontogenic niche relations, that arises as a historical wave front of codrifting living systems that are each part of the medium in which the others realize their respective niches.

Phylogenetic drift, therefore, is a historic systemic process that takes place in the reproductive succession of individuals as they constitute branching systems of lineages. Phylogenetic drift does not take place as a process of diversification of populations even though this is a historical consequence. Moreover, the process of phylogenetic drift occurs through lineages formed by systematically reproducing individual living systems, even when these depend for their existence on the conservation of the populations that they integrate. Furthermore, this is so even when some populations may themselves as a result of the particular manners of relating (such as sexuality or symbiosis) of the individual living systems that compose them, constitute unities that exist as such in some other relational domain. Multicellular organisms are an extreme case of this kind of composition as they constitute multicellular unities conserved through the systemic reproduction of some of their cellular components. Finally, in the lineages of organisms that interchange their genetic material and/or reproduce sexually, the phylogenetic drift takes the form of a network of conservation and change of ontogenic phenotype/ontogenic niche relations that change and stabilize within the dynamic boundaries set by the constraints produced by the different mechanisms that restrict gene flow between them.

The structural dynamics of the medium is operationally independent from the structural dynamics of the different kinds of organisms that arise in it in the process of phylogenetic drift, and these different kinds of organisms realize in the medium different niches that do not preexist to their actual operation as living systems in it. That is, the new niches corresponding to the new forms of living systems that arise in the natural phylogenetic drift, arise and change with the realization of the ontogenic phenotypes that appear and are conserved or change along the natural phylogenetic drift. Moreover, as structure determined systems the different organisms and the

medium interact recursively triggering in each other structural changes that they do not determine. Accordingly, in the natural phylogenetic drift both the ontogenic phenotypes and their corresponding niches arise and change together congruently following a path that arises moment after moment in the natural phylogenetic drift in the moment to moment transgenerational conservation of organization and adaptation. Indeed, this is what we connote when we speak of the conservation of the ontogenic phenotype/ontogenic niche relation in natural phylogenetic drift.

As a consequence, nothing occurs during the diversification of the lineages that occurs along the natural phylogenetic drift, that one can properly call a selective force or selective pressure. There is no doubt that an observer who sees a differential survival of some of the kinds of individuals that compose a changing population, can legitimately say that the survivors have been selected in the course of the history of the population. Yet, what the observer cannot say is that the mechanism that generated the differential survival observed, is a selective pressure or selection process, unless he or she claims that the phylogenetic drift is the selective mechanism. But to say the latter would only be a way of obscuring or hiding the process of phylogenetic drift as the actual generative mechanism of evolution. Selection in evolution is the result of the differential survival and, therefore, can not be its origin. Accordingly, and as we have already said, what evolutionary biologists call natural selection while observing differential survival when comparing populations in different moments of their history, is in fact the result of the process of production and conservation of lineages under conditions of systemic conservation of autopoiesis and adaptation through reproduction, that we have called natural phylogenetic drift, and not the result of the action of any force.

In these circumstances we can present as a general comment the following tautological statements: a) that all the structural changes that the members of a lineage undergo in the history of the lineage, occur coopted in the conservation of the ontogenic phenotype that defines the lineage following a path defined by the systemic reproductive conservation of that ontogenic phenotype as long as the lineage is conserved; b) that the constitution and conservation of a lineage occurs as an opening for the continuous variation of the total genetic constitution of the members of the lineage within the boundaries defined by the conservation in each systemic reproductive step of both the initial organic structure that can repeat the ontogenic phenotype of the lineage and the

conditions of the medium that make such repetition possible; and c) that for the conservation of a lineage there is no particular restriction on the initial total genetic constitution of the organisms that arise in it, or on the particular features of the circumstances of the medium in which these begin their living, other than those that permit the realization of the epigenesis that realizes the ontogenic phenotype that defines the lineage.

Finally, and as a synthesis of this point we propose:

1. That the history of diversification of living systems as well as the configuration of the biosphere, is the result of the spontaneous generation and diversification of lineages in the natural phylogenetic drift that begun with the systemic reproduction of living systems.

2. That the natural phylogenetic drift is a history of conservation of ontogenic phenotypes and of variation of the ontogenic phenotypes conserved through systemic reproduction, in a process in which the organisms and the medium change together in the conservation of some form of organism/medium relation.

IV.2. The participation of behavior

Living systems exist as totalities in a relational space, and it is their realization in that relational space what determines and constitutes their ontogenic and phylogenetic histories. Furthermore, as we said already, the realization of the living of a living system in a relational space appears to an observer as behavior, and the flow of living as the flow of behavior. In these circumstances, and according to what we said in section III. 11. behavior as the flow of the dynamic encounters between living system and medium, is the domain of the ontogenic realization of a living system as a particular kind of organism that determines moment after moment the course of its interactions, and specifies the path followed by its epigenesis. At the same time, behavior participates in the same manner in the systemic reproductive realization and conservation and of an ontogenic phenotype, and by determining the course of the interactions of the reproducing organisms, it determines the phylogenetic cooption of all the genetic variations that may occur in the history of a lineage in the conservation of that lineage.

Then, the flow of behavior, or in more general terms, the flow of the interactions of a living system along its living in its domain of existence, operates as a relational and interactional dynamics that channels the path followed by its structural drift during its ontogeny. That is, the behavior

of the members of a lineage through its participation in the systemic reproductive conservation of the manner of living that defines the lineage, acts through the succession of generations as a mechanism of cooption for the realization and conservation of the ontogenic phenotype/ ontogenic niche relation that defines the lineage of any variation of the total genotype of the members of the lineage. And it does so by setting a systemic operational boundary that separates what is conserved and what is not conserved from one generation to the next in each reproductive step. It follows that in the succession of generations that arise through systemic reproduction, it is the actual behavioral history lived by the reproducing organism in the course of their individual ontogenies what determines what variations in the total genotype are conserved from generation to generation and what determines the course of the phylogenetic drift in which those organisms participate. In particular, as in each organism the genotype remains hidden under the realization of the epigenesis that it happens to live in its ontogeny, the systemic reproductive conservation of any particular ontogenic phenotype/ ontogenic niche relation, operates as a mechanism that necessarily coopts all variation of the genotype for the conservation of the ontogenic phenotype/ontogenic niche relations that define the lineage (Figs. 5 and 6).

Let us now summarize what we have said in the next four statements.

1. We call behavior the flow of interactions of a living system in its niche in the realization of its living whatever its kind. As such, for an observer the behavior of an organism entails at any moment visible and invisible dimensions of interactions that can become apparent for him or her only in the course of his or her observation of the epigenesis of the organism. The behavior is the interactional aspect of the realization of the manner of living of a living system in the realization of the ontogenic phenotype/ ontogenic niche relation that it happens to live.

2. We propose that it is the behavior of the organisms as the flow of their interactions in their particular domains of living in their actual realization of their individual ontogenies, and not their genetic constitution, or any kind of directional external pressure on the course of the realization of their living, what guides through systemic reproduction the course followed by the phylogenetic structural drifts of living systems in evolution.

3. We propose that in general terms, the manner of living conserved through systemic reproduction is: a lineage sets an operational boundary to the genetic changes that are conserved through

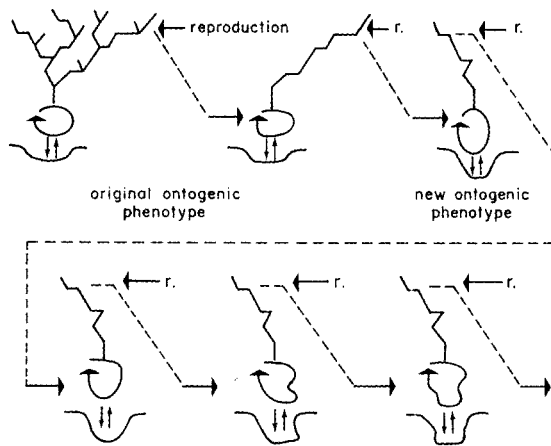


Fig. 5. This figure attempts to evoke a view of the progressive shifting of the genetic constitution in the successive members of a new lineage. The new lineage arises through the systemic reproductive conservation of a variation of the standard epigenetic realization proper to the parental lineage. The progressive shifting of the genetic constitution of the members of the new lineage gives rise to the progressive shifting of the epigenetic field of the new lineage as well as to the genetic stabilization of the organic conditions that make the conservation of the new lineage possible. In this figure and in figures 6 and 7, the branching design over the closed arrows (living systems) represents the field of the possible epigenetic courses that the ontogeny of a living system may follow in its individual life history; the zigzag in line over some living systems represents the particular epigenetic course that the life history of that living system actually follows; and the straight arrow and the small *r* indicate the moment of reproduction.

Esta figura ilustra el progresivo corrimiento de la constitución genética en los miembros sucesivos de un nuevo linaje. El nuevo linaje surge a través de la conservación reproductiva sistémica de una variación de la realización epigenética "standard" del linaje parental. El corrimiento sucesivo de la constitución genética de los miembros del nuevo linaje da lugar al corrimiento progresivo del campo epigenético del nuevo linaje, y también a la estabilización genética de las condiciones orgánicas que hacen posible la conservación de éste. En esta figura, y en la figuras 6 y 7, el diseño de ramas sobre las flechas cerradas (seres vivos) representa el campo de posibles cursos epigenéticos que un ser vivo podría seguir durante su ontogenia; la línea en zigzag sobre algunos de los seres vivos representa el curso epigenético particular seguido en la ontogenia de ese ser vivo; la pequeña flecha recta y la letra *r* indican el momento de la reproducción.

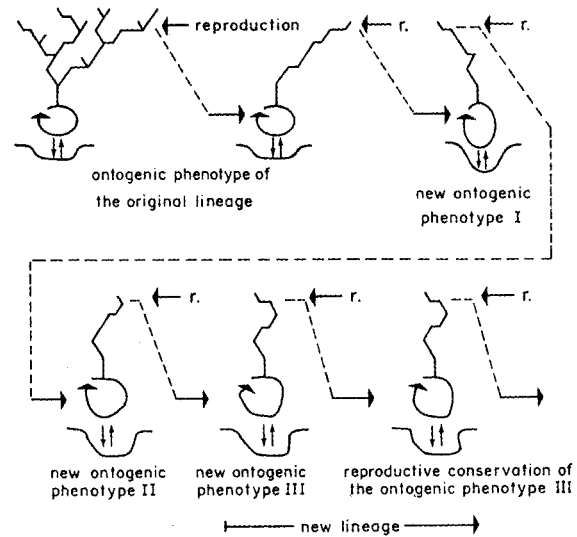


Fig. 6. This figure attempts to illustrate the change or shift of the ontogenic phenotype/ontogenic niche relation realized in each living system along a series of systemic reproduction steps in which organic living is conserved. When this occurs, the change or shifting of the ontogenic phenotype / ontogenic niche relation continues until some particular ontogenic phenotype/ontogenic niche relation arises that begins to be conserved from generation to generation through systemic reproduction (a new lineage is established), or the reproduction of the organic living comes to an end.

Esta figura ilustra el corrimiento de la relación fenotipo ontogénico/nicho ontogénico, realizada por cada ser vivo, a lo largo de una serie de etapas de reproducción sistémica, en cada una de las cuales el vivir orgánico es conservado. Cuando esto ocurre, el corrimiento de la relación fenotipo ontogénico/nicho ontogénico continúa, hasta que surge alguna particular relación fenotipo ontogénico/nicho ontogénico que comienza a ser conservada generación tras generación a través de la reproducción sistémica (un nuevo linaje es establecido), o esa sucesión de seres vivos se acaba.

systemic reproduction in the members of a lineage, and guides in that way the course of the phylogenetic genetic drift of the lineage without determining which genetic changes are produced in it (see appendix, genetic drift).

IV.3. Reproductive shift of the ontogenic phenotype

To the extent that in the epigenesis it is the behavior of the organism what guides the course of its interactions in the medium, and it is the

behavior of the organism what determines when and where reproduction takes place and the offspring appears, three different phenomena can occur after a reproductive event in which a basic ontogenic phenotype is conserved:

a) That the particular ontogenic phenotype of the progenitors that is carried by the basic one is conserved in the epigenesis of the offspring's of the successive generations. When this happens the lineage of the progenitors is conserved.

b) That the particular ontogenic phenotype of the progenitors is not conserved in the systemic reproduction of the basic ontogenic phenotype, and a new particular ontogenic phenotype is realized in the epigenesis of the progeny through the realization of the carrier basic ontogenic phenotype. If when this happens the resulting organisms reproduce depositing their offspring in a place in which these realize in their epigenesis, the new ontogenic phenotype giving rise from then on to the condition (a), a new lineage arises.

c) That the particular ontogenic phenotype of the progenitors is not conserved in the systemic reproduction of the basic ontogenic phenotype, and a new ontogenic phenotype appears such that at the moment of the reproduction of the organisms that realizes it yet another new particular ontogenic phenotype appears, and so successively until condition (b) occurs. When this happens what an observer sees is that a new lineage appears after a series saltatory shifts of the ontogenic phenotype realized in each generation.

When case (b) occurs, a new lineage arises in a single shift of the ontogenic phenotype/ontogenic niche relation conserved through systemic reproduction. If case (c) occurs, there arises a succession of saltatory shifts of the ontogenic phenotype/ontogenic niche relation realized generation after generation that lasts until a new particular lineage is established through its conservation through systemic reproduction. The successive changes of the ontogenic phenotypes produced through the process of saltatory shift of the ontogenic phenotypes may appear big or small to the observer, but in the actual process the magnitude of each saltatory change of the ontogenic phenotype is of no importance, what matters is that such a process takes place, and eventually may result in the appearance of a new lineage, or in the end of such series of saltatory shifts. We call this whole process "systemic reproductive shift of the ontogenic phenotype/ontogenic niche relation".

The process of reproductive shift of the ontogenic phenotype carries with it the systemic reproductive displacement of the field of possible epigenesis for each new organism in what we call "the systemic reproductive shift of the epigenetic

field" of the systemically reproducing organisms. The systemic reproductive displacement of the epigenetic field is the result of the shift in each generation of the total genotype of the members of the organisms that participate in the shift of the ontogenic phenotype. The arising of a new lineage in the conservation of a new ontogenic phenotype/ontogenic niche relation through systemic reproduction is not the end of the process of shift of the epigenetic field, and does not entail the necessary stabilization of a new total genotype. But it does show that in the relation living system/medium the systemic epigenetic dynamics that realizes in each new generation the ontogenic phenotype that defines the new lineage, is conserved, and that every other aspect of the genetic system of the members of the lineage is open to change. In other words, the establishment of a new lineage implies the arising of a systemic dynamic relation living system/medium that will be conserved only as long as the variations produced in the total genotype and in the medium do not interfere with the conservation of the epigenetic realization of the ontogenic phenotype/ontogenic niche relation that defines this lineage. That the arising of a new lineage is not a genetic process, but the result of the systemic conservation of adaptation in the relation organism/medium while both organism and medium are in continuous change, and that this is so even though the total genetic constitution of the participating organisms is what makes possible the new ontogenic phenotype from the perspective of the organisms, is what makes possible the diversification of lineages as a process that can occur in few generations in the interplay of conservation and change. At the same time, that this should be so is what makes possible the codrifting of different systems that have operationally independent dynamics of structural change, and the consequent constitution of ecosystems and biosphere's.

However, that is not all. We have said that behavior operates in fact as the systemic relational dynamics that involving the operational congruence between the organism and the medium, secures the reproductive conservation or the reproductive shift of the ontogenic phenotype/ontogenic niche relations or manners of living in the systemic reproductive history of living systems, and thus guides the course followed by their phylogenetic drifts. Thus, any new configuration of ontogenic behavior that begins to be conserved through systemic reproduction in a lineage of living systems, constitutes not only a change in the ontogenic phenotype conserved in the reproduction of these living systems but also the foundation of a new particular lineage of organ-

isms. In the history of this new lineage (as occurs in the history of any lineage), the systemic reproductive conservation generation after generation of the configuration of ontogenic behavior that defines the lineage, will operate as a channeling boundary for the course followed by the recursive variations of the total genotype of the organisms members of the lineage conserved around the conservation of the genetic and medium conditions that make possible the ontogenic phenotype/ontogenic niche relations that make possible and realize that configuration of ontogenic behavior. Or, in other words, the phylogenic genetic drift in the new lineage will follow a course lead by the behavioral conservation of the realization of the ontogenic phenotype/ontogenic niche relation that defines the lineage. Moreover, this will occur as a process that results in the recursive association of the conservation of that relation in the shifting of the total genetic constitution of the members of the lineage and the shifting of the configuration of the medium that entails the conservation of this relation, through the shifting of the epigenetic field of the members of the lineage. In general terms, behavior as a relational process as well as the systemic reproductive conservation of a configuration of ontogenic behavior, constitute a dynamic of operational coupling of the ontogenic and phylogenic structural drifts of the organism with the ontogenic and phylogenic structural drifts of the niche in a lineage.

Let us summarize this point in three statements:

1. The course followed by the shifting of the total genetic constitution of the members of a lineage will occur not as the result of a selective dynamics constituted in terms of actual competitive advantages or optimization of relations of adaptation, but as the result of a phylogenic genetic drift that arises delimited operationally by the natural phylogenic drift of the lineage through a dynamics of systemic reproductive conservation of an ontogenic phenotype or manner of living (Fig. 7). If one looks at the phylogenic result of this process, it is as if the conservation of the ontogenic phenotype/ontogenic niche relation operated as a selecting force on the genetic variability of the members of the lineage, but we claim that it is not so because what is involved is the actual process of living and conservation of living in living, not a comparative survival. In these circumstances, then, the differential survival that an observer can see along the history of living systems and which he or she calls natural selection, is a consequence of evolution, and not its generative mechanism. The consequences of what we just said in this and in the preceding

paragraph will be expanded in some of the following sections (see VI., Consequences).

2. The ontogenic phenotype of systemically reproducing living systems can undergo a progressive shift or transformation in a saltatory mode without giving rise to a lineage immediately, or giving rise only to very short successive lineages until a long standing one is established, as a feature of the uninterrupted process of the phylogenic drift. In this process, what is conserved at every reproductive step is the lineage of living systems, and what changes is the particular form of living, or ontogenic phenotype/ontogenic niche relation, of the living systems in systemic reproduction. In these circumstances, the lineage of living systems operates as the carrier of all the other lineages that intersect with it until it or they disappear. In general terms, given the dynamics of phylogenic drift, any ontogenic phenotype/ontogenic niche relation that is conserved in a reproductive sequence can operate as a carrier of one or more ontogenic phenotypes that intersect with it, and reproduce through it. When there is structural intersection of several ontogenic phenotypes in the manner indicated above, the phylogenic drift of the carried ontogenic phenotypes as well as their corresponding domains of possible epigenesis, follow a path defined generation after generation by the phylogenic drift of the carrier lineage. The general result of the operation of the process of structural intersection of ontogenic phenotypes is the spontaneous generation of new lineages, intralinear variations, lineage changes, and ramifications of lineages that follow the phylogenic drift of the carrying ontogenic phenotype.

3. The shift of the ontogenic phenotype/ontogenic niche relation through a series of systemic reproductions happens either in the realization of some of the different possibilities of a single domain of possible ontogenies, or as some partial changes in a given epigenetic field. Furthermore, this process is always the result of the systemic reproductive conservation of a particular basic kind of living system in a medium that appears and changes along the behavioral realization of the newly arising organisms in a phylogenic dynamics that follows moment after moment the path of structural change in which the living systems involved conserve their organization and adaptation. At the same time, and given the systemic behavioral conservation of the ontogenic phenotype/ontogenic niche relation that defines a lineage, two things happen: a) that the lineage is conserved as long as the changes that take place in the total genotype of the members of a lineage do not interfere with the conservation of the ontogenic phenotype/ontogenic niche relation that

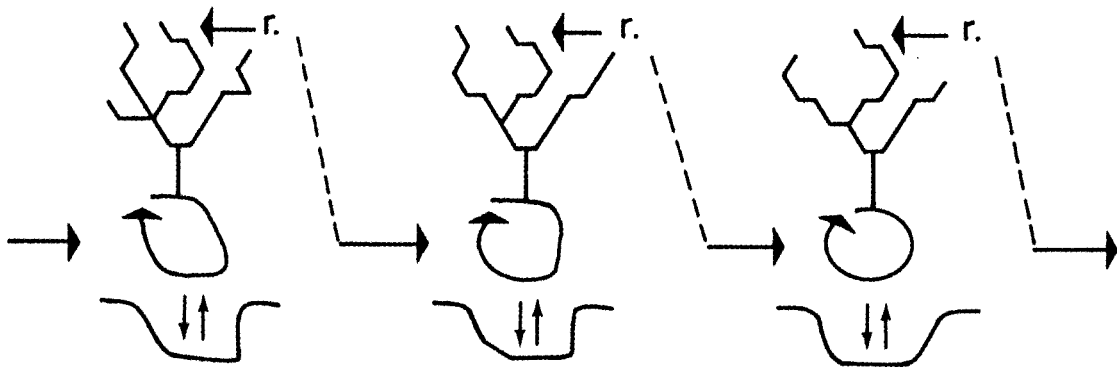


Fig. 7. This figure attempts to illustrate the change or shift of the epigenetic field as well as the change of the genetic constitution that takes place in the course of the generations while the particular ontogenic phenotype/ontogenic niche relation that defines a lineage (and that is epigenetically realized as the arrow and the *r* indicate), is conserved from generation to generation through systemic reproduction.

Esta figura ilustra el corrimiento del campo epigenético, y también de la constitución genética inicial, que ocurren transgeneracionalmente en un linaje, mientras la relación fenotipo ontogénico/nicho ontogénico que define a ese linaje (y que es epigenéticamente realizada, como lo indican la flecha y la *r*), es conservada generación tras generación a través de la reproducción sistémica.

defines the lineage; and b) that as any change in the total genotype of the members of the lineage entails a change in the field of their possible epigenesis, it also entails the possibility for the appearance of some new lineages through the behavioral conservation of a change in the ontogenic phenotype/ontogenic niche relation that the organism involved realize in their living if the circumstances of the medium allow it.

IV.4. The participation of the medium

The medium, as all that the observer sees or imagines as containing a living system or a group of living systems in their realization as such, appears in his or her distinction of it as a structurally determined system with a dynamics of structural change independent from the organism or organisms that it contains. Under conditions of codrift, the organisms involved are part of each other's medium, and operate with the non-organic features of the medium as a background of variable interactions in which all the different organisms flow in their respective ontogenic and phylogenetic structural drifts in conservation of organization and adaptation. In these circumstances, the observer explaining the ontogenic and phylogenetic drift of the living systems that he or she distinguishes, treats the medium as an independent source of opportunities for the shifting of the ontogenic phenotypes, and for the realization of variations in epigenesis along the history of conservation and diversification of lineages.

The medium, therefore, participates not only as a general container, but it operates fundamentally as the domain of the realization of the ontogenic niche of the living systems that it contains. Accordingly, it is not possible to consider the living systems independently of the medium. But at the same time we must not forget that the medium does not specify what happens to the living systems that it contains and with which it interacts because these are structure determined systems, nor that the medium is operationally independent of the living systems that it contains even as it undergoes structural changes contingent to its interactions with them, nor must we forget that the living systems are operationally independent of the medium because they have operational boundaries defined by the conservation of their autopoiesis that separate from it. Finally, we must not forget that a living system and the medium (which ever its composition) in which it realizes its ontogenic niche change together congruently spontaneously as long as the living system conserves organization and adaptation in it.

V. ANSWERS

Let us now see our answers to the questions presented at the beginning of this essay without repeating them here, but inviting the reader to reconsider them again:

V.1. The origin of biological diversity

The current diversity of the living systems on earth is the result of a history of formation, transformation, and extinction of lineages in an ongoing phylogenetic codrift in which the living systems and the non-living aspects of the medium are for each other part of the medium in which they realize their respective niches in the conservation of their respective organizations. The mechanism that gives rise to the codrifting of lineages of living systems is systemic reproduction. In systemic reproduction the conservation of autopoiesis from one generation to the next entails the conservation of the ontogenic phenotype/ontogenic niche relation that realized the living system that reproduced. Although the total genetic constitution of a living system determines what may happen in its epigenesis, the reproductive conservation of the ontogenic phenotype is not a phenomenon determined by the total genetic constitution of the reproducing living system. The reproductive conservation of the ontogenic phenotype of any particular kind of living systems and the consequent constitution of lineages, is a systemic phenomenon that entails the realization and conservation of the ongoing existence of the living systems involved as they live in a continuous flow of interactions in a changing medium in a process that lasts as long as the medium changes congruently with them. If the medium, in which the natural phylogenetic drift of a lineage occurs includes the lineages of other living beings that are also in phylogenetic drift, either the phylogenetic drifts of the lineages braid and form a system of lineages in co-structural phylogenetic drift in which the different lineages change in their respective structural drifts in congruence with each other, or they separate, or some, or all become extinct.

The ongoing phylogenetic co-drifting of living systems that form the biosphere, occurs spontaneously, and begun also spontaneously with systemic reproduction as a complication in the ontogenic codrifts of the original living systems. Systemic reproduction did not change the nature of the phenomenon of structural drift, but changed its scope giving rise to the history of living systems in the process of phylogenetic structural drift, and the diversification of lineages.

The constitution of a lineage is a conservative process, that is, it takes place in the systemic reproductive conservation of an ontogenic phenotype/ontogenic niche relation. At the same time, the diversification of lineages entails the systemic reproductive conservation of changes around a basic ontogenic phenotype/ontogenic niche relation that is conserved as the carrying lineage. This conservative character of the proc-

ess of lineage formation results in the recursive production of systems of lineages that entail similarities as well as differences between the members of the different lineages of the system of lineages. This conservative character of lineage formation is the result of the conservative character of the shift of the ontogenic phenotypes in a background of systemic conservation of epigenetic process.

The fundamentals for the answer the question i) presented at the beginning in the introduction to this essay, are as follows:

1. As long as living systems are autopoietic systems (of first or second-order) existing in structural ontogenic co-drifting; and

2. As long as living systems undergo systemic reproduction in the conservation from one generation to the next of an ontogenic phenotype/ontogenic niche relation; then

3. The consequences are: a) the production of lineages and of systems of lineages that exist in co-structural phylogenetic drifts through the shifting of the ontogenic phenotype/ontogenic niche relation conserved through systemic reproduction, b) the systemic reproductive conservation of variations of the ontogenic phenotypes/ontogenic niche relations that they realize, with the consequent constitution of new lineages, c) the systemic conservation of epigenetic similarities across lineages, and d) the conservation of lineages as long as conditions 1. and 2. are conserved, and the extinction of lineages if they are not.

Then, our answer to the question i) presented in the introduction is: similarities and differences between presently existing living systems are the result of the manner of constitution of lineages through the systemic reproductive conservation of ontogenic phenotype/ontogenic niche relations, under circumstances in which new lineages arise from shifts of the ontogenic phenotype/ontogenic niche relations that are conserved through systemic reproduction.

V.2. *Adaptation*

The conservation of adaptation, that is, the conservation of the relation of dynamic operational concordance between the living system and the medium at the niche, is a condition of existence of the living system. The same is the case for the conservation of the autopoietic organization of the living system as a molecular discrete entity. Living systems exist only as long as their autopoiesis and adaptation is conserved. These two constitutive conditions for the existence of living systems allow us to answer question ii)

in the following terms: The operational congruence and harmony between living systems and their circumstances connoted with the expression adaptation, is a constitutive condition of their existence and does not require explanation. That is, either the living system conserves its adaptation and lives, or it does not conserve adaptation and it dies. Adaptation is a relation of operational congruence with the medium in which a living system conserves living, not a form of living. That is, a living system can exist and, accordingly, be distinguished as such by an observer, only under the condition of interactions in which its autopoiesis and adaptation are conserved in the realization of its niche. Therefore, the condition of existing in adaptation in the medium of a living system is necessarily an invariant as long as it is living. Consequently, given that living systems necessarily exist in adaptation in their niche in their realization as such, there can not be, and there are not comparatively better or worse adapted living beings. The claim that there are or that a living system is more or less adapted to the medium, reveals the opinion of the observer about what he or she considers would be an adequate living for the living system that he or she observes.

It follows from all that we have just said, that the distinction of a living system by an observer always necessarily brings forth a living entity in operational congruence with its circumstance as a living being. And this is so even if in the way of looking of the observer who imagines it in other circumstances, or who imagines a possible future (becoming) for it, it does not always seem to be so. It also follows that the loss of adaptation necessarily brings with it the death of the living system, and that insofar as a living system is alive, it conserves the relation of adaptation with the medium through the realization of its niche, even if for the observer the living system looks as if it were about to die. Since the conservation of the adaptation is a constitutive condition for the existence of living systems, adaptation does not result or emerge from the operation of a mechanism like the one that we biologists connote or indicate when using the notion of natural selection as if this were the mechanism that generates adaptation.

But there is a fundamental consequence to all that we have said so far, and it is that to the extent that the conservation of adaptation is a constitutive condition in the realization of the living, the conservation of adaptation operates as the dynamic reference around which all structural changes must occur in the conjoint structural drift of the living systems and the medium as they

necessarily change together in their recursive interactions. If that were not to happen, the living system would die, and if it dies before reproduction, and there are no other living systems carriers of the same ontogenic phenotype/ontogenic niche relation, its lineage would come to end.

This is our answer to question ii) presented at the beginning in the introduction to this essay.

V.3. Diversity and similarity

What we have said about the conditions of constitution of living beings as autopoietic systems, and about reproduction as the process that generates the phenomenon of heredity through the conservation of a total genotype that either opens or denies the possibility of conservation of a lineage, shows that the similarities and differences that we see among living beings result from the systemic dynamics of constitution and conservation of lineages, and are not determined by the presence of certain particular types of molecules such as the nucleic acids (DNA) or proteins, even if this are necessary for them to occur. The different types of molecules and their different forms of production in the cell, as well as their different ways of transmission in the reproductive process, participate in the conservation of the characteristics of the organisms, or in their disappearance, but do not determine them because these arise in an epigenic process. Indeed, the different kinds of molecules that compose the living systems as well their different manners of production, determine different classes of genetics insofar as they constitute different ways of generating genealogies through their distribution in the offspring in the moment of reproduction, but they do not generate or determine the phenomenon of heredity which is a systemic phenomenon that involves both the organism and the medium (see VI. 4.) This is why no particular class or type of molecules determines, nor can any one by itself determine the ontogenic phenotype/ontogenic niche relation or manner of living that define the identity of the different classes of living systems that they make possible. The total genetic constitution of an organism, as we have said along this essay, determines a domain of possible epigenesis, but which of those possible epigenesis occurs along the life of any particular living system, is the result of the actual interplay of the living of the living system and the medium in the realization of its niche.

But there is more. We have previously state, as a general systemic condition, that whenever in a collection of elements of any kind and in any

domain, some particular configuration of relations begins to be conserved, a space is open for all other relations in that collection of elements to change around the configuration of relations conserved. A consequence of this systemic condition in relation to living systems, is that as a lineage arises through the systemic reproduction of an ontogenic phenotype/ontogenic niche relation, the whole molecular constitution of the living systems members of the lineage becomes open to change around the dynamic molecular configurations conserved in the conservation of the ontogenic phenotype/ontogenic niche relation that defines the lineage. As a result, the total genetic constitution of the members of a lineage drifts along a path defined by the systemic reproductive conservation of the ontogenic phenotype/ontogenic niche relation that defines the lineage. In the history of living systems the genotype follows the ontogenic phenotype in a process that spontaneously moves towards the genetic facilitation of the realization of the ontogenic phenotype/ontogenic niche relation conserved through systemic reproduction in the constitution of a lineage. In a way this is what Julian Huxley (in his book "Evolution: the New Synthesis", 1963) implies when he speaks of the accommodation of the genome in the course of the generations. A more detailed reflection on this latter point is presented in section VI. 6.

All this allows us to amplify our answers to the questions (i) and (ii) above, as follows: The dynamics of the constitution of lineages that we have described above is spontaneous, and leads both to the stabilization of the lineages as well as to the production of new ones, depending on the ontogenic phenotype/ontogenic niche relation realized through the interactions of the living system and the medium in its epigenic realization that is conserved along successive generations through systemic reproduction. The living systems and the medium that contains them are systems that operate historically braided in an ongoing flow of congruent structural changes in a process involving both in a single structural codrift or history of structural coupling. Yet, as a living system and the medium that contains it are operationally independent in their respective structural dynamics as structure determined systems, different types of organisms will give rise to different classes of phylogenetic drifts, with or without formation of lineages, depending on the temporal relation of their different structural dynamics and the structural dynamics of the medium in their codrift. When, in the flow of the natural phylogenetic drift there is a shift in the ontogenic phenotypes, each new ontogenic phenotype arises as changes

in the epigenic path previously conserved in a lineage, and it arises as the systemic realization of one of the possible epigenic path permitted by the total genotype with which the corresponding living system begins its life. Because of this manner of origin of the new ontogenic phenotypes, every new ontogenic phenotype which appears in the natural phylogenetic drift of a lineage, necessarily includes a bigger or smaller part of the initial part of the ontogenic phenotype of the previous generation. In these circumstances, the new ontogenic phenotype will frequently be only a modification of the temporal dynamics of the realization of the ontogenic phenotype of the parental generation, or an expansion or suppression of one or another aspect of its realization (see VI.11). In any case, however, every new lineage will arise as a historically stabilized systemic reproductive conservation of a new ontogenic phenotype/ontogenic niche relation as a result of successive shifts of the ontogenic phenotype along some unspecified number of generations. In this manner, phylogenetic natural drift is the source both of the conservation of similarities and generation of diversity. This is also our answer to question (iii) presented above in the introduction.

V.4. Biological fundament of systematics

As a consequence of the mechanism of lineage formation that we have already discussed, and starting from any point in the reproductive history of living systems, the natural phylogenetic drift will necessarily produce a system of lineages that will emerge in a linear or branched sequential process as a series of successive modifications of a primary ontogenic phenotype. The phylogenetic drift flows as a historical process in which every reproductive shift of the ontogenic phenotype/ontogenic niche relation conserved until then can result in an ontogenic phenotype/ontogenic niche relation that may become conserved giving rise to a new lineage that will last until it is extinguished, or until a new shifting of the ontogenic phenotype/ontogenic niche relation conserved gives rise to another new lineage. In this process, a system of lineages is spontaneously formed in which the earlier ontogenic phenotypes appear more or less included as part of the epigenesis of the later ones. The conservation of more or less extended epigenetic configurations of the ontogenic phenotypes of the ancestors in the realization of the later ontogenic phenotypes of the members of a system of lineages, results in that different epigenic configurations constitute lineages of

ontogenic phenotypes that are carried by lineages of ontogenic phenotypes that include them in their realization as the branching systems of a tree. The natural phylogenetic drift occurs as a system of ramifications of lineages in which the smaller branches retain features of the larger stems from which they arose. A transversal section of a system of ramification of this kind seen from above, allows us to group the sectioned branches according to similarities that depend on the history of origin of each one of them as modifications of a previous configuration. In these circumstances we answer the question (iv) presented in the introduction of this essay as follows: To the extent that we living beings are the present of an uninterrupted branching history of lineage formation in a natural phylogenetic drift, a taxonomist that classifies the living systems that he or she distinguishes in different categories defined by their different degrees of similarity, can do nothing but to group them either by constellations of similarities that have their origin in a history of phylogenetic conservation of some epigenetic configuration, or by similarities that do not have such a character. In these circumstances, a taxonomist, who in doing a classification of any category cannot but put together organisms that resemble in constellations of features that appear to him or her in a non historical context, will spontaneously prefer those similarities that resulted from the conservation of epigenetic coherences in different lineages because they will unavoidably include or reveal additional unexpected phenotypic correlations that would have not been possible if his or her classification had been based on accidental similarities only. The result is and has been in many occasions, that experienced taxonomists have made taxonomic groupings that have had biological historical relevance even when they did not considered possible evolutionary relations. Moreover, the classificatory vision of taxonomists has been a basic source for evolutionary insights in the history of biology.

V.5. Biological significance of the taxonomic categories

If the taxonomist creates taxonomic categories following in his or her classification distinctions of ontogenic phenotypes common to the different forms of organisms that he or she distinguishes, he or she will make biologically significant taxonomic categories by revealing the present moment of the historic becoming of the living beings thereby classified. Moreover, if in classifying living beings

the taxonomist organizes different classes of ontogenic phenotypes that he or she distinguishes according to how they contain one another, in their similarities and differences, he or she will propose a classification in which the taxonomic categories that can be called "higher" will necessarily be based on the distinction of ontogenic phenotypes / ontogenic niche relations that correspond to the conservation of the oldest epigenetic configurations. So, we claim that given the nature of the classificatory act realized by the taxonomist, notions such as kingdom, type, class, family, genus, and species, indeed correspond to taxonomic categories that represent the distinction of ontogenic phenotypes / ontogenic niche relations that define lineages or systems of lineages, and have, because of this, biological meaning. In these circumstances, it also follows that major taxonomic categories correspond to the distinction of ontogenic phenotypes that are realized as aspects of the epigenesis of ontogenic phenotypes that define minor taxa. Thus, when a living system that is distinguished as a member of a particular species realizes its ontogenic phenotype as a member of that species, it realizes simultaneously the epigenesis of the ontogenic phenotypes proper to the genus, family, class, type, and kingdom to which it belongs as a result of being the present form of the phylogenetic drift that gave origin to it. It follows, then, that the taxonomic categories constructed by a taxonomist are not arbitrary to the extent that they are based on the distinction of the ontogenic phenotype/ontogenic niche relations that define the different lineages that he or she connotes in his or her classification. And it also follows that a good taxonomy is precisely one that has been constructed by a biologist who has become a taxonomist by learning the operational looking that allows him or her to make distinctions that grasp the similarities that reveal historical relations. This also means that the generative mechanism of the higher taxonomic categories is not different from the generative mechanism of lower ones (Fig. 8).

Taken together, sections 4 and 5 above express what constitute our answer to the question (iv) presented in the introduction of this essay.

VI. CONSEQUENCES

In what follows we will make some final reflections in which we will examine several consequences of what we have already said for the understanding of the history of living systems and the constitution of the biosphere, and we shall sketch some answers to a few of the open questions in such a domain.

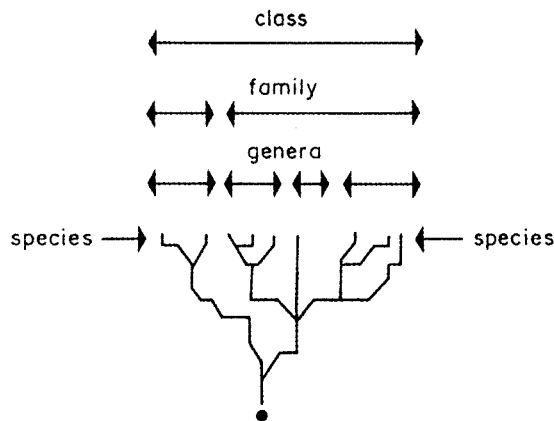


Fig. 8. In this figure we attempt to illustrate a phyletic tree in which the different branching systems represent different ontogenic phenotype/ontogenic niche relations conserved as different lineages. The magnitude of the lateral displacement of the vertical course of the branches at each nodal point represent more or less extensive shifts of the ancestral ontogenic phenotype/ontogenic niche relations. The tips of the phyletic tree correspond to the present species. The horizontal arrows above the phyletic tree represents the different ontogenic phenotypes/ontogenic niche relations connoted by the taxonomist as he or she distinguishes different taxonomic categories while grouping the actual species.

Esta figura ilustra un árbol filogenético, en el cual los diferentes grupos de ramas representan diferentes relaciones fenotipo ontogénico/nicho ontogénico conservadas como diferentes linajes. La magnitud del desplazamiento lateral del curso vertical de las ramas en cada punto nodal representa un desplazamiento más o menos extensivo de la relación fenotipo ontogénico/nicho ontogénico ancestral. Las puntas del árbol filético representan las especies actuales. Las flechas horizontales indicadas sobre el árbol filogenético representan las diferentes relaciones fenotipo ontogénico/nicho ontogénico connotadas por un taxonomo cuando este distingue diferentes categorías taxonomicas al clasificar las especies actuales.

VI.1. Sexuality

In our previous discussion we did not refer to sexuality, because we think that such a reference does not introduce a substantial modification to the phenomenon of phylogenetic drift. Certainly, sexuality modifies the phenomenon of genetic drift by establishing closed networks of gene flow, and through that adds a new dimension to the dynamics of conservation of ontogenic phenotypes and manners of living. Yes, sexuality by adding cell fusion or molecular interchange

into the dynamics of systemic reproduction, expands the genetic variability of the organisms through molecular recombination, but heredity remains the result of the systemic reproductive conservation of an epigenesis that remains capable of realizing a particular ontogenic phenotype/ontogenic niche relation. With the expansion of the genetic variability that sexuality entails through genetic recombination and gene occultation, the fields or domains of epigenic variability are amplified at the same time that they are phylogenically conserved as bonded or closed networks of genetic configurations that constitute lineages of polytypic ontogenic phenotypes, one of which is, of course, sexual dimorphism. With the amplification of the epigenic variability that sexuality brings, the possibility for the shifting of the ontogenic phenotypes conserved through systemic reproduction, is expanded in every reproductive occasion. At the same time, the restrictions on genetic recombinations entailed in any mechanisms that interferes with the gene flow between different communities of interbreeding organisms, result in that the genetic variability within a sexual lineage becomes systemically constrained along its phylogenetic drift within bounds defined by the stability of such restrictions. Yet, none of these phenomena that modulate the course of the phylogenetic drift of the sexual organisms, alters the systemic nature of reproduction and heredity, or the nature of the phylogenetic drift in the terms that we have presented.

VI.2. Natural selection

In modern biology adaptation is seen as a relation of more or less efficiency in the use of the medium by the living systems. As a result, modern biologists see adaptation as a variable, and think that the diversity of living systems is the result of a historical process of continuous improvement of the adaptation of the living systems to the medium in which they live. In these circumstances modern biologists consider natural selection as the mechanism that gives rise to evolutionary change and diversification in a dynamics of continuously improving adaptation. That is, the notion of natural selection is used in biological discourse as if it constituted the generative mechanism of the evolutionary change. Under this view a force or external agent is needed to produce the adaptive change, and this force or external agent is referred to as selective pressure or selective strategy. As we said above, we think differently.

Living systems as molecular autopoietic systems exist in recursive continuous structural change. We do not have to justify structural change in living systems, structural change is in them a condition of existence. Living systems stay alive only as long as they operate conserving their dynamic structural congruence with the medium in which they realize their living in the realization of their niche. This operational structural congruence between the living system and the medium as the living system realizes its niche, is what we connote with the word adaptation, and what we say when we say that the conjoined conservation of adaptation and autopoiesis is a condition of existence in living systems. It is in agreement with this condition of existence of living systems, that we claim: a) that it is not the origin of change or the origin of adaptation what has to be explained in the history of living systems on earth, but the course that their change follows in the constitution of their lineages; and b) that the mechanism that guides the course of change and that gave rise to the present diversity of living systems as well as to their many different manners of living in adaptation and co-adaptation in the network of living systems that is the biosphere, is phylogenetic drift in the generation, conservation, and diversification of lineages through the systemic reproductive conservation of different ontogenic phenotype/ontogenic niche relations. Or, in other words, we claim that the process that gave rise to the diversity of living systems that we find today in the biosphere is not some operation of some mechanism of selection, but the differential survival in the realization of living and constitution of lineages in the conservation of adaptation through systemic reproduction, that we have called natural phylogenetic drift.

In these circumstances, natural selection is not the mechanism that generates differential survival in the evolutionary history of living systems. Evolution is the history of diversification of living systems that takes place through natural phylogenetic drift. And natural phylogenetic drift occurs in course of the systemic reproductive conservation of autopoiesis and adaptation in the recursive encounter of the living systems and the medium as structure determined systems that exist under independent dynamics of structural change. Furthermore, the diversification of lineages in living systems does not course in a competitive dynamics through the survival of the fittest, but it follows the course of the survival of the fit in the conservation of autopoiesis (living) and adaptation.

We think that when Darwin (1872) said that the process of historical change of living systems

occurs "as if there were selection", he used the active form of the notion of selection to refer to the result of a generative mechanism or process that had to be operating in the present of each organism so as to generate differential survival. But Darwin used the notion of competition under the expression of "survival of the fittest", which is in fact an explanatory metaphor that the observer uses to account for the differential survival that he or she observes in the reproductive history of populations. The use of this metaphor has resulted misleading because it has obscured the view of the actual mechanism of the differential survival that results in the course of the generations in natural selection, which is the survival of the fit through the conservation of adaptation. According to us, then, the generative mechanism that applies to each organism in the present of its living and generates differential survival in the course of generations, is the "survival of the fit". And we connote this with the general expression that the history of living systems has followed the path of phylogenetic natural drift. Kimura and Weiss (1964) when speaking of the survival of the lucky, and Cavalli-Sforza (1996) when speaking of genetic drift under the confines of natural selection see this to some extent, but do not fully realize that it is the conservation of adaptation what guides the path of evolution with the result of natural selection.

Indeed we think, and we repeat, that the biological phenomenon that a biologist connotes when speaking of natural selection, is the result of a differential survival that he or she sees when comparing different classes of phenotypes or genotypes in two different historic moments in a population or group of organisms in ontogenic and phylogenetic structural drift and co-drift. Moreover we claim that when there is sexuality, the ontogenic and phylogenetic drift and co-drift occur for every system of sexual lineages within the limits of the gene flow and gene recombinations established by the different mechanisms that restrict the gene flow between non-interbreeding populations. The phylogenetic drift of sexually reproducing organisms is not an exception, and occurs under the same fundamental mechanism of the ontogenic and phylogenetic structural drift and co-drift of asexual individuals and lineages, that is, through the conservation and shift of ontogenic phenotype/ontogenic niche relations in the terms that we have already described.

Moreover, we think that what has happened since Darwin is that the use of the notion of natural selection as connoting a force in order to explain adaptation, and the attention on populations as an opportunity to quantify and predict the

course of evolution, has obscured our view of evolution as a process that occurs in the present of the living individual organisms through systemic reproduction along the path of conservation of autopoiesis and adaptation as the mechanism that generates differential survival. In these circumstances, the difficulty of seeing natural phylogenetic drift as the generative mechanism of evolution, even when there is awareness of the permanent presence of genetic drift, is that natural selection is treated as if it were the mechanism that gives direction to differential survival notwithstanding that one knows that natural selection is a consequence of the course followed by the differential survival that it is supposed to direct (Cavalli-Sforza 1996, pp 75 - 84). We also think that this attitude is the result of not seeing reproduction as a systemic process, as well as of not seeing that what gives direction to the evolutionary process in the constitution of a biosphere as a network of interrelated lineages, is that lineages arise in the systemic reproductive conservation of an ontogenic phenotype/ontogenic niche relation through the conservation of both adaptation and a manner of living, and not through the conservation of a genetic constitution.

Evolution according to us takes place in the dynamics of generation and diversification of lineages, and not in the change of the genetic constitution of populations which is only a result. Living occurs in the present of the operation of the living system in the realization of its living, and nothing occurs in the living system determined by the future. So the differential survival connoted by the expression natural selection must be the result of a process obscured by such a notion, and that process must take place in the continuously changing present that the flow of living is. It is in these circumstances that we claim that the process that gives rise to the conservation and differentiation of manners of living that we biologists connote with the notion of evolution, is the dynamics of generation and differentiation of lineages through the systemic reproductive conservation of ontogenic phenotype/ontogenic niche relations. Indeed, we claim that since systemic reproduction conserves dynamic relational configurations between organism and medium (in the conservation of ontogenic phenotypes / ontogenic niche relations), and not genetic configurations per se, that natural phylogenetic drift channels the genetic drift in a way that does not result in genetic homogenization. Therefore, it is in these circumstances that we claim that it is natural phylogenetic drift what gives rise to the directionality of the evolutionary process that we biologists have attempted to explain since Darwin with the notion of natural selection.

VI.3. Species and speciation

The extensive controversy concerning the notion of species arises somehow from the effectiveness of the taxonomist's way of looking and his or her effectiveness in making organic categories that have biological significance in a background of doubts about the fundamentals of the biological legitimacy of such effectiveness. The question has been: are the taxonomic categories biological entities, or are they only artifacts of classification? Does the species as a taxonomic category represent a biological entity while the other taxonomic categories represent mere classification artifacts? With the notion of the biological species as a genetically closed system of interbreeding populations developed by Ernst Mayr (1963), the matter of giving fundament to the notion of species as representing a biological entity seemed come to an end. And it seemed so because the view of the biological species as a genetically closed system of interbreeding populations revealed a biological mechanisms that restrict the gene flow between its members and the members of other different interbreeding populations, clearly pointing both: a) to a biological entity with a historical existence, and, b) to the biological mechanism that would generate such an entity by enclosing a group of organisms in a common evolutionary destiny of change and conservation of dynamic configurations of gene relations. Moreover, this view of the species as a system of interbreeding organisms was in total concordance with the notion that evolution had to be understood in terms of the changing genetic constitution of populations. According to us, however, the old conceptual difficulties do not disappear totally. And this is so because the biological species notion arises as a notion associated with the view of natural selection as the generative mechanism of the evolutionary process in terms of populations, which, according to us, is something that cannot be accepted because the mechanism that generates natural selection as the consequence of its operation is natural phylogenetic drift. Additionally, the biological species notion as it is usually understood, is associated to a view that treats adaptation as a variable, and sees natural selection as operating on adaptive advantages and disadvantages in face of a continuous competition for survival, while considering that the history of diversification of living systems or evolution, is the history of genetic change of populations. Finally, the notion of biological species arises in a way of thinking that invites accepting the idea that all the characteristics or traits of an organism that an observer can identify

as being conserved through evolution, are genetically determined, and have emerge and are conserved as the result of a selective process that retains them according to their adaptive advantages in a domain or field of competition for survival. Accordingly, we think that the approach that sees species and speciation in terms of populations faces several difficulties under the form of phenomena that it cannot explain. The following are three that we consider the most salient ones:

a) the conservation of asexual lineages of organic forms that are maintained either permanently or transitorily by means that do not entail the constitution of a closed genetic domain as claimed to be required for speciation under the biological species concept;

b) the presence of features of the organism that the observer can clearly distinguish as being conserved in a lineage, but to which he or she cannot attribute some acceptable adaptive origin; and

c) the biological relevance of the taxonomic distinctions that an experienced taxonomist makes, no matter what may be the taxonomic category distinguished.

Our way of dealing with these and other questions in the matter of speciation and taxonomy, follows a path different from that of Ernst Mayr. We think that what a taxonomist does as he or she claims to distinguish a species, and his or her distinction makes biological organic sense in the context of a system of taxonomic distinctions, are two things: one, to distinguish an ontogenic phenotype that defines a lineage of organisms; and two, to claim that the ontogenic phenotype/ontogenic niche relation distinguished as a species has a nodal position in the ramification of lineages in the phylogenetic drift, because the new lineages that may arise from, are also species. If another taxonomist were to claim that the classification made is not adequate, he or she would be claiming either that the classification that the first taxonomist made did not correspond to an ontogenic phenotype/ontogenic niche relation that defines an organic lineage, or that the lineage defined by the first taxonomist does not have such nodal position in the phylogenetic drift because it is only a variation of one, namely, a subspecies. Therefore, we consider that an appropriate characterization of the species as a taxonomic category is: A species is a taxonomic category that corresponds to the distinction of a lineage defined by the conservation of an ontogenic phenotype/ontogenic niche relation that may or may not include sexuality, and which a taxonomist considers that has a nodal character in the dynamics of diversification of lineages because the new

lineages that may arise from it will have the same nodal character in the course of the natural phylogenetic drift. We can also say that a species is a nodal lineage in the terms implied above. We also think that the biological species of Ernst Mayr as an interbreeding population of organisms that is constituted as a genetically closed unity through the biological restriction of the genetic interchange with other such populations by means of various isolating mechanisms, is a special case of the systemic reproductive conservation of an ontogenic phenotype/ontogenic niche relation that includes sexuality. Nothing can happen in the life history of an organism that is not permitted or made possible at the beginning of its existence by its total genetic constitution. Yet, whatever actually happens along the life history of a living system arises in it as a systemic epigenic process, and whatever is conserved generation after generation as a manner of living, is conserved through systemic reproduction with the participation of the genetic system but not determined by this. So, although genetics and gene flow, or lack of gene flow, participate as features of the constitution of the biological species, it is not genetics what determines in any case its particular identity, but the systemic reproductive conservation of the ontogenic phenotype/ontogenic niche relation that defines it. Therefore, it is because of the systemic character of the conservation of the ontogenic phenotype that defines a lineage, that sexual and asexual lineages (species) are constituted and conserved in the same way in the phylogenetic drift. In these circumstances, the difference between sexual and asexual lineages, is that in the asexual lineages the genetic variability of the members of the lineage that opens the possibility for genetic variations in the ontogenic phenotypes conserved, emerges only from internal recombinations and / or mutations, while in the sexual lineages such variability is expanded through sexual gene recombination.

Let us summarize in the next 11 statements:

1. The taxonomist claims to recognize the members of a species through traits that he or she considers to make part of the ontogenic phenotype/ontogenic niche relation that defines the lineage, and is successful to the extent that the course of the natural phylogenetic drift shows that he or she indeed distinguished a nodal lineage.

2. The ontogenic phenotype that characterizes a species, is not genetically determined although its realization in the members of the species depends on the total genetic constitution that makes it possible at the beginning of their existence. What defines a lineage, is the conservation through systemic reproduction of an organism/medium

dynamics under the form of the systemic reproductive conservation of an ontogenic phenotype/ontogenic niche relation.

3. Sexuality and genetic isolation modulate the becoming and conservation of the sexual species, but do not determine what is conserved along its history because that arises in the systemic reproductive conservation of an epigenic process regardless of the presence or absence of sexuality. The isolating mechanisms that restrict the gene flow between populations, operate as features of the systemic dynamics that conserves the ontogenic phenotype/ontogenic niche relation that defines a species, regardless of any reference to genetic determination.

4. Phylogenetic drift is a process of continuous transformation and diversification of lineages through the systemic reproductive conservation along the history of a lineage of variations in the ontogenic phenotype/ontogenic niche relations that defines it. When in this process a particular variation of the ontogenic phenotype/ontogenic niche relation in a lineage begins to be conserved through systemic reproduction in a way that it becomes a nodal lineage, a new species arises. As such speciation occurs in the systemic reproductive dynamics that conserves the structural coupling between organism and medium, and if there are different kinds of organism living in a way in which they form part of each other's medium, speciation will necessarily occur as a systemic process of co-speciation in the constitution of a biosphere.

5. Speciation is not a population phenomenon because a species as a nodal lineage may or may not include sexuality. Asexual species form populations as systems of coexistence that do not entail gene interchange. Sexual species, form systems of coexistence that constitute populations of actually or potentially interbreeding organisms. So the word population is either used to refer to collections of organisms that live in some relation of coexistence, or to refer to organisms that form networks of actual or possible gene interchange through sexuality. Whatever the case, populations are incidental to the process of speciation, and do not constitute it.

6. Even though speciation is not a population phenomenon, the manner of conservation of the ontogenic phenotype/ontogenic niche relation that defines a species will result in the constitution of different kinds of populations that will participate differently in the realization of the manner of living that defines the species. Sexual and asexual organisms will constitute different kinds of populations, and hence, different domains of coexistence. Thus, in the case of sexual organisms,

the interbreeding populations will be closed domains of gene interchange and they will be more or less uniform genetically according to the degree of panmixing of their interbreeding. In the case of nonsexual organisms, the populations that they form will be more or less uniform genetically depending on how much the organism / medium relation restricts the epigenic variability in their ontogenic realization.

7. To the extent that the phylogenetic drift and the speciation that it entails occurs in a domain of interacting and interrelating living systems in the spontaneous dynamics of the flow of living in conservation of organization and adaptation, co-speciation is a necessary outcome under the form of local and distant ecological coherences in the constitution of a biosphere. That is, what an observer sees as ecological congruencies between species, or what he or she sees as ecological coadaptations, are an unavoidable result of spontaneous co-drifting and co-speciation.

8. Speciation will necessarily occur as a spontaneous process in small populations where local habits of living can be conserved as ontogenic phenotypes through systemic reproduction. Furthermore, in large populations of sexually reproducing organisms, the systemic reproduction of habits and behavioral preferences will disrupt the possibilities of panmixing, creating domains of inbreeding which add the dimension of mating preferences to the behavioral channeling of the genetic drift (see appendix, "Habits")

9. In the process of speciation, the shifting of the ontogenic phenotype will appear as saltatory or as gradual to an observer according to the temporal perspective from which he or she makes his or her observations. Yet, in a strict operational sense, the process of speciation will always be saltatory, with big or small saltations depending on the number of generations involved from the beginning of the shifting of the ontogenic phenotype until the final establishment of the new lineage.

10. An observer who compares populations of organisms in different moments of their history while attending to the relative frequency of the different genotypes observable in them without considering that speciation takes place as a phylogenetic drift of ontogenic phenotypes, will see any change in the relative frequency of the different genotypes observed as a result of a change in gene frequencies produced by a process of positive selection of certain genes and of negative selection of others. Such an observer will fail to see that the change in gene frequencies observed is a result of a differential survival of ontogenic phenotypes in a process in which all

genetic changes are coopted in the realization of the ontogenic phenotypes conserved in the conservation of living. Change in the genetic constitution of the organisms members of a population along the latter's evolutionary history, is a result of the differential survival of the members of the population along a history of phylogenetic drift, so it occurs in a dynamics of drift too .

11. As a closed population with respect to genetic interchange with other similarly genetically closed populations, the so called biological species is a special case only because of the participation of sexuality in the ontogenic phenotype/ontogenic niche relation conserved in it, and not because of the form in which this is conserved that is the same as with asexual lineages.

According to us, therefore, speciation occurs in the systemic reproductive conservation and change of lineages of ontogenic phenotype/ontogenic niche relations in a systemic dynamics that involves the living systems and their niches as operational totalities in continuous change while the organization and the adaptation of the participating organisms are conserved. That is, speciation is not a feature of the history of living systems only, but it is a feature of the history of the biosphere. Speciation is a biological process in which living systems and medium change together congruently in a way in which each living system and what it does operates as part of the medium of the others. At the same time, we think that it should be apparent that species, as they appear in the act of classification, have a categorical neatness that does not reflect the fluidity of the evolutionary process, and that the taxonomist in the act of classification makes a magnificent feat of historical abstraction. As abstractions of historical dynamics all taxonomic categories are historical biological entities, not mere taxonomic constructs. Taxonomic categories appear in the distinction of the observer, but they make biological sense only if the taxonomist has enough biological understanding and insight to see through analogical abstractions the past in the present, and to make from the present a future that future biologists will accept.

VI.4. Heredity

The phenomenon of heredity as it appears with systemic reproduction, operates as the fundament of the history of living systems as a factor in the constitution and conservation of lineages. In this essay we have shown that due to its manner of constitution the phenomenon of heredity does not depend on any particular molecular structure even

though the molecular structure conserved in the act of systemic reproduction makes it possible. And we have done so by showing: a) that heredity occurs or takes place in the conservation of organization and adaptation through systemic reproduction; and, b) that systemic reproduction occurs as a process of division that involves organism and medium through the conservation in the systems that result from that division of the structures that make possible the realization of the particular organization of the dividing system, as well the conservation of the structural features of the medium in which the new resulting systems may remain realizing that particular organization. So, in the biological domain, what the word heredity connotes is a systemic process in a structural dynamics that associates living systems and medium in the conservation of the structures and relations of the living systems and the medium under which living is conserved. As such, the process connoted with the word heredity operates guiding the transgenerational conservation and change of all classes of living systems in their historic becoming by setting boundaries, through what is conserved, to the variability of the molecular process that make possible the conservation or extinction of the different ontogenic phenotypes that arise through the systemic reproduction of the living. Finally, it is because heredity is a systemic phenomenon and not a molecular one, that behavior as a participant in the systemic dynamics of living and reproduction, plays a central role in the course followed by the phylogenetic drift of living systems by defining what is conserved and what is not conserved in the ongoing existence of every class of living system along the constitution and conservation of lineages through systemic reproduction.

VI.5. Evolution and the origin of living systems

As we have stated before, whenever in a collection of elements a configuration of relations begins to be conserved, a system arises defined as a unity by the configuration of relations conserved which henceforth becomes its organization. At the same time that a system begins to be conserved, either the conditions of the medium that make its conservation possible also begin to be conserved in the system / medium relation, or the system disintegrates. So, as a system arises the conditions of its existence arise as well, and, therefore, a system begins and exists in the conservation of its organization and adaptation to the medium in which it exists. As a system begins its existence

in the conservation of its organization and adaptation, its ontogenic structural drift begins. This must have happened in the origin of living systems with the spontaneous arising of discrete molecular autopoietic unities that lasted as long as the system medium relation that made them possible were conserved. Furthermore, when these original living systems underwent reproduction through a simple division that resulted in the systemic reproductive conservation of their molecular autopoietic organization, evolution begun as a phylogenetic structural drift in which all could change around the conservation of the autopoiesis and adaptation of the living systems thus generated. In other words, we claim that as living systems appeared on earth with the spontaneous occurrence of molecular autopoietic unities, these first living systems existed in ontogenic structural drift in a non-reproductive dynamics of epigenetic structural variations in the realization of living and dying. We also claim that when reproductive fracture and fusion begun to occur in the dynamics of ontogenic structural variations of the living systems, phylogenetic drift begun in the systemic reproductive conservation of different ontogenic phenotype/ontogenic niche relations with the consequent constitution and ramification of lineages which lasted as long as autopoiesis and adaptation were conserved through systemic reproduction. With what we have just said, and with all that we have presented along this essay as features of the operational domain of living systems, we have shown the spontaneous dynamic conditions that must have given origin to the constitution and history of structural changes of the terrestrial biosphere in a dynamics of change and conservation that has resulted in the present diversity in the manners of existing of the living systems of today. That is to say, we claim that the historical process that we connote with the word evolution as the generative mechanism of the present diversity of terrestrial living systems, is the process of natural phylogenetic drift.

In other words, what we propose with all we have said before is: that the lineages of cells as well as the lineages of groups of cells that are the organisms (be they homogenetic symbionts, as all those whose different tissues come from the same founder cell, or heterogenetic symbionts, as those that come from heterogeneous cellular groups that aggregate themselves in the constitution of a unity) that exist and have existed in the biosphere, were formed under the same mechanism, namely, natural phylogenetic drift. At the same time, we claim that what we have said before is valid for all composite biological entities in their domain of constitution as particular ontogenic

phenotype/ontogenic niche relations. And we also claim that this is why there are different independent and intersecting kinds, types, and classes of lineages, each existing in the operational domain in which the ontogenic phenotype that defines it occurs, and each according to the way of generation of the components of the composite entities that realize or carry such ontogenic phenotypes / ontogenic niche relations in the moment of their systemic reproduction. Finally, we wish to emphasize that the natural phylogenetic drift occurs in the recursive interactions between living systems and medium as a process that necessarily flows in a continuous co-drifting that involves for each living system at every moment all the dimensions of its domain of existence while at the same time each living systems operates as part of the medium of others. Or, in other words, since the natural phylogenetic drift occurs as a spontaneous dynamics in the continuous conservation of the structural coupling between medium and living systems through the conservation of their reciprocal co-adaptation, natural phylogenetic drift constitutes a process in which the biosphere emerges as a multidimensional network of ontogenic phenotype/ontogenic niche relations that form a system of complementary phylogenetic co-drifts as a gigantic entangled systems of ecological coherences.

VI.6. The ontogenic phenotype pulls along the total genotype

The establishment of a lineage in the conservation of an ontogenic phenotype/ontogenic niche relation, frees the genetic variability of the living systems members of the lineage within boundaries operationally set by the epigenetic field that permits the realization of such ontogenic phenotype, and creates a domain of genetic cooption of all those variations for its conservation. In other words, the constitution and conservation of a lineage in the systemic reproductive conservation of an ontogenic phenotype/ontogenic niche relation, permits that in every reproductive saltation the total genotype may change in an open drifting, as long as those changes still conserve the initial conditions that permit the epigenetic realization of the ontogenic phenotype that defines the lineage. If that were not to occur, the lineage comes to an end, or there is a shift in the ontogenic phenotype/ontogenic niche relations generated or conserved through the systemic reproduction of the living. A basic consequence of this is that the longer a lineage lasts, the more the total genotype may shift towards a condition that facilitates more and more the

relational dynamics between living system and medium in which occurs the epigenesis that realizes the ontogenic phenotype that defines the lineage. Furthermore, in this process the medium participates with its own dynamics of structural change, and the systemic conservation of an ontogenic phenotype allows the medium to change in all dimensions as long as the realization of the niche of the reproductively conserved ontogenic phenotype is also conserved.

As evolution begun, the total genotypes of the members of the different lineages became open to drift along their phylogenic conservation within boundaries defined generation after generation by the ontogenic phenotype/ontogenic niche relations conserved in each systemic reproductive step. In other words, when a lineage begins, the total genotype of the members of the lineage follows a path of drift defined by the conservation of the lineage, in a process of genetic drift contained within bounds defined by the conservation of the epigenic realization of the ontogenic phenotype/ontogenic niche relation that is conserved. In evolution it is the phylogenic drift of the ontogenic phenotype/ontogenic niche relations what guides what is conserved or lost in the genome along the history of genetic change in a lineage or system of lineages, and not the reverse: the genetic change of the genome follows the ontogenic phenotype in natural phylogenic drift under the form of a genetic drift bounded by the systemic reproductive conservation of the ontogenic phenotype/ontogenic niche relations. In these circumstances, through the systemic conservation and shift of the ontogenic phenotypes that occurs in phylogenic drift, all genetic variations that do not interfere with the epigenic realization of the ontogenic phenotype realized in each generation, become co-opted in the realization of the ontogenic phenotypes conserved. This co-option of the genetic variability, is part of the operational and structural background that modulates the field of possible epigenic courses that makes possible the shifting of the ontogenic phenotype / ontogenic niche relations in the phylogenic drift. And this can happen, of course, because the ontogeny of a living system occurs as an epigenic process, and there is no genetic determination of what happens in the life history of a living system. Finally, it is worth noting that:

1. Due to the epigenic realization of the ontogenic phenotype, the notion of selective value of genes is not necessary to explain the process of evolution;

2. As the genetic changes in a lineage follow the path defined by the systemic conservation of the ontogenic phenotype/ontogenic niche relation that

defines it, the phylogenic drift, as a historical process in which each moment along it arises as a modification of the previous one, will necessarily follow a unidirectional path defined by the ontogenic phenotype/ontogenic niche relation conserved (see also section VI.13. below); and

3. When there is intersection of several different ontogenic phenotypes in the realization of a particular carrier lineage, the course of the genetic change in the phylogenic drift of the carrier lineage will entail the co-option of all the genetic changes that conserve the realization of the different ontogenic phenotypes that intersect with it (see VI.8. below).

That the genotype should follow the phenotype in evolution seems obvious after what we have said. What is not obvious is which are all the dimensions of genetic variability involved in that process.

VI.7. Behavior and Evolution

That the ontogenic-phenotype/ontogenic-niche relation in the constitution of a lineage should be conserved through systemic reproduction and not through genetic determination, has made behavior, as the domain of the relational epigenesis, the central agent in the establishment of the course followed by the natural phylogenic drift in evolution. That behavior guides the course of the natural phylogenic drift becomes apparent when we recognize that behavior is an aspect of the epigenesis, and that the epigenesis seen in its relational aspect in the domain of realization of the living system as a totality in the medium is, in effect, behavior. The total genotype determines in each living system at the moment of its inception the domain of all the possible epigenic courses that it may follow along its life history, even though only one will in fact take place in its ontogeny. Furthermore, the total genotype also determines in each living system at the beginning of its life the domain of all the behaviors that it may possible live in its interactions in the medium without specifying any one. And the total genotype does so, because behavior also arises in a systemic manner in the actual relations of the living system and medium as an epigenetic process of realization of an ontogenic phenotype/ontogenic niche relation that begins with it. It is because behavior arises in the encounter of the living system and the medium while both operate as structurally independent systems, that it is not possible to speak of genetically determined behavior, and the idea of the inheritance in the lamarkian sense of behaviorally acquired characters, is not tenable.

However, any particular behavioral realization of an organism that as a habit or preference participates in securing the conditions that make possible through systemic reproduction the reappearance of such preference or habit in the next generation, permitting the conservation of an ontogenic phenotype that includes such preference or habit as one of its features, is an opportunity for the constitution of a lineage in which the total genotype will be carried in its phylogenic drift following the conservation of such ontogenic phenotype. If that were to happen, such habit or preference would constitute the operational condition that makes possible the beginning, and then, eventually, the establishment of a lineage. Moreover, such a systemic dynamics will spontaneously result in that the total genotype of the members of the lineage thus constituted, will drift following a path delimited by the systemic conservation of the realization of a behaviorally defined ontogenic phenotype.

To be sure if there were such a thing as a large panmixing population of sexual organisms, behavior would constitute a guide in the phylogenic and genetic drift only if it constituted a factor of reproductive isolation. That is why we think that in sexual populations the shifting of an ontogenic phenotype will occur more easily in small communities in which habit and learned behavioral preferences determine sexual encounters. And this is so, we insist, precisely because habits and learned preferences set boundaries to the areas of habitation as well as to the reproductive choices of the organisms in a way defined by the actual circumstances of their living in the locality that they inhabit, and they do so in a spontaneous systemic dynamics that maintains such habits and preferences as long as the local circumstances are conserved through those very same preferences and choices. When Darwin (1872) an other contemporary authors (as reviewed in McFarland 1993, pp 113-126), speaks of sexual selection, he is speaking of genetic drift guided in the phylogenic drift of a lineage by the mating habits and preferences of the members of the lineage.

What we say in relation to the participation of behavior and habits in guiding the course of phylogenic drift in general, and of genetic drift in particular, is not a hidden way of speaking of lamarkian inheritance of acquired characters, not a way of diminishing the biological significance of genetics. Nothing happens in the life history of a living system that is not permitted or founded on its initial genetic constitution. But we are pointing to a phenomenon that requires more attention, that is, to the epigenic modulation of inheritance as a result of the systemic character of reproduction.

VI.8. Symbiosis and the spontaneous constitution of composite living beings

Whenever in any given domain of elements a configuration of preferential interactions between some its elements begins to be spontaneously conserved, an operational border arises that separates the elements that participate in the realization of such configuration of relations from other elements of the domain, and a composite unity or system as well as its niche or domain of existence arise. When that happens, the newly arising composite unity and its domain of existence emerge together spontaneously in co-ontogenic structural drift. Moreover, all this happens with independence of the actual manner of composition of the composite unity, of the kind of elements involved in it, and of the domain of existence of the new unity as a totality. When the elements that participate in the composition of a composite entity are living systems that conserve their condition as such while participating in the composition, the composite entity is a symbiont. Symbionts may reproduce as symbionts and give origin to a lineage in the conservation of an ontogenic phenotype. Finally, the type of phylogeny that is generated in the constitution of a symbiotic system depends on the type of reproduction in which it participates as a totality and the manner of reproduction of its components.

Thus, eucariotic cells arose as a lineage of heterogenetic symbionts that became singular totalities through the total inclusion as symbionts of some originally independent cells into an other one that acted as the carrier through its reproductive division. Multicellular organisms arose as homogenetic symbionts composed of cells that did not separate after their reproductive division, and that reproduced as multicellular totalities through single cell separation, body fracture, or gamete fusion. In all cases of multicellular organisms what is inherited in reproduction is an initial cellular structure, the total genotype, from which all the cellular lineages that compose the homogenetic symbiont as a whole organism, originate. In heterogenetic symbionts that arise through cellular association without fusion, such as lichens or termites, the reproductive process involves, in the constitution of the founder unity of the new generation, the coming together of members of several different component lineages. As they do so, the different kinds of cells that come together in the composition of such symbiotic unity enter in a phylogenic co-drifting in which their respective phylogenic drifts find themselves subordinated to the conservation of the heterogenetic symbiotic lineage that they integrate. In other

words, the phylogenetic conservation of the heterogenetic symbiotic system results in that the different phylogenetic drifts of the component lineages necessarily become subordinated to the phylogenetic drift of the symbiotic heterogenetic lineage that they integrate; and they do so in a dynamics of subordination that can lead to the total loss of their reproductive independence. Moreover, as there is no intrinsic limitation for the kinds of biological components that may integrate an heterogenetic symbiotic system, these can be cellular or organic, and in principle there is no limit to the diversity of systems and kinds of phylogenetic drifts that can arise through symbiosis.

Finally, in this dynamics of composition, either through the coming together of independent biological entities, or through the systemic internal differentiation of organs, many different systems or composite unities intersect and are conserved in a carrier lineage as we described in the text above in section III.5. We mention this here to emphasize that what happens in symbiosis is only an aspect of the general dynamics of the composition and structural intersection of entities that exist in different relational domains, as we shall further see in the next section.

All that we have said in relation to the constitution of composite unities, is valid independently of whether the observer is or not able at any moment to show the limits of the unity or unities to which he or she refers when speaking of a composite unity. And this is so because by referring to the conditions of constitution of a system or composite unity, the observer refers both to the dynamics of its composition and to its possible becoming once the conditions for its existence and conservation arise. What happens is that in the moment in which an observer distinguishes a system or composite unity, he or she implies an organization as well as a structure, and in so doing he or she implies an operational dynamics that defines and constitutes its limits. According to our explanation, the history of living systems has taken place as a natural phylogenetic drift, with the spontaneous constitution of many different kinds of organic systems and composite unities in many different domains, through the interplay of many different kinds of ontogenic and phylogenetic co-drifts that have intersected in many different ways.

VI.9. The intersection of lineages

As we have already said in section III. 5. every living system operates in the realization of its ontogeny as the carrier of many different organizations that exist in structural intersection

with it, and that are conserved from one generation to the next through its systemic reproduction. The result of this is that every lineage of living systems operates as the carrier lineage of a system of lineages of structurally intercrossing ontogenic phenotypes that otherwise exist in different relational domains than the carrier one. We have also said that such embedded lineages can have, and indeed frequently have, different historical dynamics of phylogenetic drift than the carrier lineage precisely because their members exist in different operational domains than the members of the carrier lineage. This is the case with the different ontogenic phenotypes that the taxonomist distinguishes as the different higher categories, such as genus, family, class, or types, to which each member of a species belongs, and which are conserved through these in the realization of their respective ontogenies and lineages through systemic reproduction. Other cases are lineages constituted by the phyletic conservation of kinds or systems of organs, cellular types, metabolic systems, or supracellular systems such as communities constituted in a behavioral operation that is part of the way of living that defines the whole lineage of its members (social insects). What makes possible these intersections of lineages, is the conservation through the systemic reproduction of the carrier ontogenic phenotype/ontogenic niche relation of a particular total genotype that is capable of the epigenetic realization of all the different ontogenic phenotypes of the intersecting lineages as long as the relational domains in which they exist do not interfere with its realization as a carrier ontogenic phenotype. From all we have said, we can conclude that the more basic is the ontogenic phenotype that defines the carrier lineage, and, therefore, the more numerous the different forms in which this can be realized, the larger is the number of lineages that can intersect in it.

VI.10. The rate of the evolutionary change

Since a living system and the medium that contains it have operationally independent structural dynamics, different lineages can have different rates or rhythms of phyletic change depending on the particular dynamic relations between the living systems and the medium that prevail for the conservation or shifting of the ontogenic phenotype/ontogenic niche relations in each lineage in the succession of their generations. But, at the same time, since all living systems exist in the present, the different temporal dynamics of all the biological processes entailed

in the co-ontogenic and co-phylogenetic drift of living systems that integrate an ecosystem or a biosphere, will either harmonize through the conservation of their reciprocal co-adaptation in the continuous present of their living in co-drifting, or the ecosystem, or the biosphere, or themselves, will disintegrate. Let us say this in a few systemic statements: a) the temporal dynamics at which the different processes involved in the realization of living systems take place, are a feature of their structural dynamics; b) the temporal dynamics of the processes realized through independent structural dynamics are intrinsically independent; c) as the structure of a system changes, its structural dynamics changes too, so that the temporal dynamics of the processes realized in it, or through it, will change as well, unless the particular configuration of that structural dynamics is a feature of what is conserved in the living of the living system in which that process takes place; and, d) as a consequence of the above, if two living systems through their recursive interactions enter in structural coupling, the otherwise independent temporal dynamics of the processes realize through them will undergo a dynamic harmonization defined by what is conserved in each of them through their structural coupling. In general terms, it is in fact the constitutive condition of operational independence between the temporal dynamics of structure determined systems what makes every particular history of structural coupling between them, a history that drifts through the conservation of that structural coupling in a course of temporal harmonization of processes that otherwise take place with operationally independent rates. The result in the biological domain is the generation of the synchronic and diachronic harmonization of all the biological process that integrate a biological entity regardless of their different particular temporalities.

So, the diversity of evolutionary rates in the history of the biosphere, is a consequence of the independence of the dynamics of structural change that exists between living systems and medium in a gross systemic dynamics that has conserved the biosphere. Furthermore, there is no fundament to expect that different lineages should have similarly evolutionary rates, and all that can be expected is what we have already said, namely, that the processes realized through systems that enter in structural coupling should spontaneously enter in a temporal harmony that lasts as long as their structural coupling lasts.

But this is not all. The configuration of all organic relations in any particular biological sys-

tem emerges continuously through systemic reproduction in phylogenetic drift, as a unique changing present in the interplay of the different temporal dynamics of all the biological and non-biological processes involved around the conservation of some configuration of living while everything else is open to change. The result is that an ontogenic phenotype can be conserved in the evolutionary history of a system of lineages only as long as the temporal coherence of all the intra-organic and extra-organic processes involved in the realization of the organisms members of that lineage, as well as of those members of the other lineages participating with them in a history of co-phylogenetic drift, is conserved in the actual realization of those living systems in the present. In general terms then, we think that the temporal harmony of all the cyclic and non-cyclic processes within the organisms and in their relations in the medium observable in the presently living systems, has become established along the history of the biosphere as the spontaneous and necessary result of the structural coupling of the organisms that compose it in co-phylogenetic drift.

VI.11. Recapitulation: relation between ontogeny and phylogeny

We have said that every new lineage arises in the course of the phylogenetic drift of an ongoing one as a new ontogenic phenotype/ontogenic niche relation begins to be conserved from generation to generation through systemic reproduction. Moreover, we have also said that as the new ontogenic phenotype/ontogenic niche relation necessarily arises in the conservation of the basic carrying one, the new ontogenic phenotype must be realized in its epigenesis as a variation in the epigenesis of the preceding one. One of the consequences of this manner of origin of a new lineage, is that the members of every new lineage must repeat in their epigenesis all or some aspects of the initial epigenesis of the members of the lineage from which they arose. Another consequence, is that in a succession of lineages, the epigenesis of the members of a later lineage must repeat successively those aspects of the epigenesis of the ancestral lineages that have been historically conserved in the later lineage as a result of the manner of origin of a new lineage. What an observer sees as a result of the process of phylogenetic drift as he or she compares different classes of living beings are two things: one, that is usually referred to as the "recapitulation in ontogeny of aspects of phylogeny", is the similarity between early features of the epigenesis

of the organisms that belong to recent lineages, and features of the adults organisms of phylogenically ancestral lineages; an other, which is certainly related to the first one, is the conservation in the epigenesis and the adult structural configuration of the organisms of inferior taxa, of intersecting ontogenic phenotypes that define the superior taxa. Yet, there is an additional thing that must be mentioned. As phylogenetic drift flows as a process of change and conservation of the epigenetic possibilities of the members of a changing lineage through the shift of their epigenetic fields, most of the epigenetic possibilities that are conserved in such a process remain hidden under what is actually realized in the ontogenic phenotype/ontogenic niche relations conserved through systemic reproduction. Under these circumstances, it must necessarily happen that there should be cases in which it is possible to modulate through molecular or relational manipulation the epigenesis of an organism, and thus obtain the realization in it of some epigenetic configuration that had been hidden or displaced in the phylogenetic drift, and do so without having to change its genetic constitution. The studies of Kollar and Fisher (1980), on epigenetic induction in the development of birds constitutes a good example of this latter situation.

VI.12. Non-adaptive characters

The notion of nonadaptive traits in modern biology refers to those traits of an organisms that appear as features of its ontogenic phenotype, to which an observer cannot assign a functional reason that justifies their presence according to a selective history. Such nonadaptive characters are called like that in the context of an evolutionary theory that considers that anything an observer can distinguish as a trait or characteristic in a living being is there because it has some function in its survival, and has been selected because it has given to the ancestors of the organisms that exhibit it, or these themselves, some competitive advantages over some of their contemporaries. As must be now apparent, we do not think that this way of looking at the history of living systems connotes the actual mechanism of the history of diversification of living systems that we modern biologists call evolution. The conservation of an ontogenic phenotype/ontogenic niche relation through systemic reproduction, results in that everything that participates in the epigenetic realization of a living system can be conserved in a lineage. At the same time, as the conservation of an ontogenic phenotype/ontogenic niche relation

through systemic reproduction allows for free variation of all epigenetic processes that do not interfere with the realization of the ontogenic phenotype/ontogenic niche relation under phylogenetic conservation, there is always space in the phylogenetic drift of a lineage for the systemic conservation of processes and structures that participate in the realization of the epigenesis of a living system but are not directly connected with the realization and conservation of the ontogenic phenotype/ontogenic niche relation conserved in the lineage. Such structures and processes can vary or remain invariant as long as their variations or stability does not interfere with the double conservation of the organization and adaptation of the living systems that carry them. If at any moment these structures or processes begin to participate directly in the conservation of the ontogenic phenotype/ontogenic niche relation that defines the lineage, they stop being free to change and their phylogenetic drift becomes associated with the phylogenetic drift of the ontogenic phenotype/ontogenic niche relation that defines the lineage. Moreover, if we consider that the realization and the reproductive conservation of an ontogenic phenotype/ontogenic niche relation in the members of a lineage are systemic processes that occur in the present of the living of the members of a lineage, and are not the result of a comparison between these and other living systems, it will become apparent that the notions of adaptive advantage or adaptive value do not connote the mechanism of historical change of living systems in the biosphere, and are only of a metaphorical significance which is often misleading.

VI.13. The directionality of evolutionary change

The word evolution connotes a manner of explaining the present diversity of living as a result of a history of descent with modification. As we have shown along this essay, we consider that the mechanism that generates change through descent with modification is natural phylogenetic drift. And we claim that it is because the history of living systems takes place as a process of natural phylogenetic drift, that evolution takes place as a process that courses without aim or purpose, without following any preestablished direction. Yet, historical processes in their being historical, that is, in their being processes that occur as a becoming in which every moment is originated as a transformation of a preceding one, appear to the observer that looks back from the present as having followed a course of change

from their ancestral form that directed them to attain the form that they have now. But historical processes do not follow a preestablished or intended course or direction, and the direction that an observer sees in them is only the result of the way that they take place. The directional character of historical processes results from the fact that every new situation in them restricts the domain of the changes that can possibly follow to it. So, the present in the history of living systems is a result, not an attainment. Or in other words, we can say that in the case of living systems: since in natural phylogenetic drift living system and medium change together congruently, any shift of the ontogenic phenotype/ontogenic niche relation that is conserved through systemic reproduction in any particular lineage of living systems, will constitute an operational constraint for future shifts of the ontogenic phenotype/ontogenic niche relation as well as for the genetic drift in the phylogenetic drift of that lineage. The result will be that all lineages will indeed follow directional courses of change in which the different directions that they follow are not preestablished but arises *de novo* moment after moment in their phylogenetic drift. Thus, for example, the systemic reproductive conservation of the habit of running and jumping with movements of the anterior extremities that result in a change of direction in the jump while the animal is in the air, either during escape from predators or during the capture of a prey, can have established the direction of the phyletic change that originated birds as a manner of moving whose conservation delimited the path of the structural drift in a lineage of runner dinosaurs. Similarly, the conservation in terrestrial animals of the habit of feeding while swimming in the sea, either as herbivores or as carnivores, could have established the direction of the path of natural phylogenetic drift that led to current marine mammals. Accordingly, and in general terms, we think that in order to visualize the possible origin of the different forms of current organisms, we have to imagine what basic ontogenic habits have to have been conserved generation after generation through systemic reproduction so that these current forms could have appeared as lineages defined by the reproductive conservation of epigenetic variations in the realization of those ontogenic habits.

The shift of understanding implied in our proposal entails the recognition that the directionality seen in the path followed by the natural phylogenetic drift in a lineage or system of lineages, results from the systemic reproductive conservation of

an ontogenic phenotype/ontogenic niche relation under conditions of conservation of adaptation, and not from a process of genetic selection in a domain of variable adaptation.

VI.14. Asynchrony in molecular and organic evolutionary change

That the conservation of an ontogenic phenotype in the phylogenetic drift of a lineage should be a systemic consequence of the conservation of a particular dynamic relation between living system and medium, results also in that if there is intersection of ontogenic phenotypes in the epigenic realization of a living system, the intersecting ontogenic phenotypes will undergo interlaced but independent phylogenetic drifts. The phylogenetic drifts of such intersecting ontogenic phenotypes run independently because each of them exists in a different relational domain, but, at the same time, these same phylogenetic drifts form a co-drifting system with each other and with the living systems that carry them. When this occurs, the phylogenetic drift of such ontogenic phenotypes run independently because each one of them exists in a different relational domain but, at the same time, these same phylogenetic drifts flow in structural intersection because they are all constituted and realized through the systemic reproductive conservation of the autopoiesis of the carrying living system that is realized through them. This is valid for all ontogenic phenotypes, independently of their existence in the organ domain (organs like the liver), in the cellular domain (like the immune system), or in the domain of the molecular productions (as the system of protein synthesis or the cycle of Krebs). In these circumstances, the basic consequence to the independence of the phylogenetic drift of intersecting ontogenic phenotypes that concerns us here, is the following: the temporal courses of the phylogenetic drifts of the ontogenic phenotypes that intersect in the realization of a living system are independent, and they can differ greatly in rhythms if their synchrony is not necessary for the phylogenetic conservation of the carrying system. That this is what happens, is apparent in the asynchronies that can be observed if one compares the rhythms of evolutionary change of molecular and organic intersecting ontogenic phenotypes.

VI.15. The conservative character of evolution

Natural phylogenetic drift is a process of systemic reproductive conservation of ontogenic pheno-

type/ontogenic niche relations in a network of co-drifting organisms that constitutes a biosphere. We claim that what we biologists connote with the expression biological evolution is this process. The ontogenic phenotype/ontogenic niche relation whose conservation constitutes the fundament of the natural phylogenetic drift, and which in its conservation is the carrier of many others that intersect with it, is autopoiesis. So, in a strict biological sense, the evolution of living systems is the history of conservation of autopoiesis in the systemic reproduction of operationally independent systems that exist in co-drift in the constitution of a biosphere. Or, in other words, evolution is the history of the production, ramification, and intercrossing of lineages of living systems in which the different ontogenic phenotype/ontogenic niche relations conserved are variations of the manner of epigenic realization and co-realization of autopoiesis. Moreover, evolution, as a process of phylogenetic conservation of co-drifting lineages of variations in the manner of realization of autopoiesis, is the actual history of the systemic reproductive conservation of ontogenic phenotype/ontogenic niche relations in phylogenetic co-drift that constitute, in many cases, aggregates of living beings. The latter can have many different forms, either as heterogenetic symbionts that form reproductive autonomous unities with a phylogenetic drift in which the systemic reproduction of the living systems that compose them is subordinated to the systemic reproduction of the symbionts as totalities, or as homogenetic symbionts that reproduce as totalities through single cells, or as systems that as totalities are not symbionts but constitute ecological unities composed of living systems with interdependent ontogenic phenotypes as a result of their codrift. The evolution of living systems, therefore, is a process of constitution and diversification of lineages through natural phylogenetic drift that conserves through systemic reproduction any ontogenic phenotype in co-drift with others if the systemic circumstances that make possible such a conservation occur, and takes place in a dynamics of non-genetic systemic determination that is modulated by the regularities of the molecular productions that genetics reveals. As such, evolution occurs without any limitation to its continuation other than the persistence of the relational conditions that make possible the systemic reproductive conservation of autopoiesis, and occurs in a systemic way in which all the living systems that participate in it are involved in the creation of those conditions in the constitution of a biosphere.

VII. FINAL WORDS

The history of living systems on earth and the arising of the biosphere to which we human beings belong, is the results of the spontaneous constitution and conservation of a network of ontogenic phenotype/ontogenic niche relations through the systemic reproduction of living systems. In this history, at least with the appearance of us human beings as languaging animals, reflection about living and self consciousness as awareness of self awareness have become part of what happens in the biosphere and, hence, of the flow of the natural phylogenetic drift that makes it, the biosphere, moment after moment a continuously changing present. That is, now what we human beings think about ourselves and about the world we live, has become part of the medium in which the systemic history of the biosphere occurs. Both our vision and our blindness counts now in the flow of biological evolution. This is why explanations and understanding are not trivial, they define the domains of knowledge in which we human beings exist, and, therefore, what we do as living systems components of the earth's biosphere. And this is why it is not trivial that we think that natural selection is the generative mechanism of evolution and adaptation, or that we think that the conservation of adaptation is a constitutive condition for the existence of living systems and that the mechanism that generates evolution is natural phylogenetic drift. We act differently in each case.

No doubt what seems most impressive as one looks at the biosphere at large and contemplates living systems in their natural existence, is the diversity of manners of living that they exhibit, and the normal dynamic structural coherence or adaptation between the different forms of living systems and the particular circumstances in which each of them lives. As a result, when we want to explain that diversity as a result of the history of change of the biosphere we become so concerned with change and the attainment of the different forms of adaptation in which the different kinds of living systems live, that we do not see properly what is conserved, even though we know that the history of living systems has necessarily taken place as a history of change around the conservation of living. Furthermore, the belief in genetic determinism and in the slowness of the process of selective adaptive change, have blinded us so that we have not been able to easily see the constitutive systemic dynamism of the history of the biosphere, and the actual participation of the dynamics of conservation and change in that his-

tory. Accordingly we have not been able to see that the conservation of the living through the reproduction of living systems and the constitution of lineages is a systemic process, nor have we been able to see that the course followed by the epigenetic change in the life history of a living system or the evolutionary change in a lineage or system of lineages, takes place through the systemic conservation of living and adaptation. Change is taking place continuously in dynamic systems, but the course that change follows in any domain of change at any instant, is defined systemically by what is conserved. And what is conserved in systems in general, and in living systems in particular, is both organization and adaptation.

In this essay we claim that change and adaptation are not what we have to explain because living constitutively takes place under continuous structural change in the conservation of autopoiesis and adaptation. That is, we claim in this essay that the history of living systems has occurred as a conservative process in which what has to be explained is not structural change but the course that it has followed from its origin to the present. It is in this understanding that we emphasize that the history of living systems has occurred in the interplay of conservation and change. But what we wish to emphasize now, is the systemic and not causal nature of the interplay of conservation and change.

Nucleic acids genetics participate in the specification of the organism through the molecular reproductive conservation of the basic features of the initial structure of each new organism, and through that it participates as a basic determinant of what is and what is not possible in the epigenesis of any organism. Nucleic acids genetics is no doubt a fundamental aspect of the constitution and conservation of lineages; as such, genetic change is in the long run the background on which all phyletic change stands, but we claim that it is not and cannot be the guide of phyletic change due to the epigenetic nature of all aspects of the realization of a living system as a particular organism, and the systemic character of reproduction and heredity. Therefore, in this essay we maintain that what is conserved when a lineage is conserved, is the dynamic interplay between living system and medium that give rise to the systemic reproductive conservation of an ontogenic phenotype/ontogenic niche relation under the form of an epigenetic process in which there is no genetic determination.

Our claim that heredity is a systemic phenomenon in which nucleic acids play a fundamental part but do not determine it, is not a claim of inheritance of acquired characters in the

“Lamarckian” sense. But it is the claim that the particular life lived by an organism plays a central part in what happens in its descendants by participating in the creation of the conditions in which they will live and in what is conserved from one generation to the next. Under the claim that all the features of an organism arise through genetic determination those features that cannot be said to be genetically determined are dismissed as irrelevant phenotypic variations, mere habits, or only learned behaviors, with no direct evolutionary consequences unless genetic inheritance appears. But not even in the passion of blind genetic reductionism is it possible to claim that all the features of an organism can be genetically determined without denying that we know that the relation organism/medium necessarily courses as an epigenetic process. In these circumstances, as we the authors claim that heredity is a systemic phenomenon associated to systemic reproduction, we also claim that the course of evolution is guided by behavior, and that habits and learning as phenotypic realizations by expanding ontogenic variability must have expanded and conserved lineage diversification by modulating the shift and conservation of manners of living.

Nothing can happen in the epigenesis of a living system that is not made possible by the total initial structure of the cell or group of cells with which it begins its individual existence. But, at the same time, whatever happens in the actual life history of a living system is a result of the epigenetic realization of the particular ontogenic phenotype/ontogenic niche relation that this happens to live, and is not in any way predetermined by its total initial structure. Genetic recombinations, mutations, and the modulation of genetic activity in epigenesis, are sources of the variability of the initial total structure with which a living system begins its life history in the midst of the genetic and systemic conservation of that total initial structure. At the same time, the medium in which a living system lives also has dimensions of systemic stability and dimensions of non-systemic change that introduce variability in the conditions under which systemic reproduction takes place, opening possibilities for the shifting of the ontogenic phenotype/ontogenic niche relation that is realized in each generation. Yet, none of these two operationally independent domains of stability and change determines by itself what happens in biological evolution; it is in their interplay where the dynamics of evolution takes place, and it is in the operational independence of these domains where the systemic reproductive conservation of autopoiesis and adaptation occurs as the source of both stability and diversification of lineages.

The belief in genetic determinism also has blinded us to the structural fluidity of living systems, and has led us to evolutionary considerations that interfere with our vision of what is conserved in the domain of permanent change in which living takes place, so that we do not properly see the interplay of change and conservation which we know must be there. There is no doubt that genetic conservation is a central part of the conservation of the ontogenic phenotype from one generation to the next, but since genetics does not determine the ontogenic phenotype, the genetic system is open to change in manners that we do not see because we do not expect them. The ontogenic phenotype as the actual realization of a living system hides all genetic variations that do not interfere with its realization or systemic reproduction. The same can be said about the realization of the ontogenic niche which hides all the variations of the medium that do not interfere with its realization along the ontogeny of any particular living system. And it is precisely the occultation of the genetic variability and the variability of the medium by the realization of an ontogenic phenotype/ontogenic niche relation what permitted evolution to occur as a process of natural phylogenetic drift through systemic reproduction. The epigenetic realization in each organism of a particular ontogenic phenotype as a particular case in the domain of possibilities offered by the epigenetic field of the initial cell or system of cells in its encounter with a dynamic medium, is what has permitted the diversification of lineages through the shifting of the ontogenic phenotypes realized and conserved through the successive systemic reproductions of living systems in the conservation of autopoiesis and adaptation. It is due to this condition of occultation of genetic variability and medium variability in the realization and conservation through systemic reproduction of an ontogenic phenotype/ontogenic niche relation that there is no restriction to the temporality or to the diversity of the processes that give rise to new lineages other than those of the particular constraints of the historical circumstances under which a particular ontogenic phenotype/ontogenic niche relation is conserved in natural phylogenetic drift.

A source of difficulty for the understanding of the systemic relation between conservation and change, is the frequent belief in that scientific explanations consist in expressing what occurs in one phenomenal domain in terms of the processes of a more fundamental one. This belief is at the basis of the reductionist attitude that pretends that all biological phenomena are genetically determined. Such attitude blinds us about the differ-

ent domains in which different biological processes or phenomena take place. Moreover, through that attitude we do not see that a living system exists in two phenomenal domains that do not intersect, namely, the domain in which the living system exists as an interacting totality (as some kind of organism), and the domain in which it exists as a molecular system (as an autopoietic molecular network). The living system lives, that is, exists as an organism, in the realization of its niche in the medium which is the domain where it operates as a totality with a changing structure. At the same time, the living system is possible as an organism as it also exists as a dynamic molecular system in continuous structural change, that is, as an autopoietic system open to the flow of matter through it. As these two phenomenal domains do not intersect, what occurs in one cannot be expressed in terms of the phenomena of the other, but the organism is conserved through the structural changes of its molecular realization, and its intrinsic structure as a molecular autopoietic system follow a path of change contingent to its interactions as an organism in the realization of an ontogenic phenotype/ontogenic niche relation. In these circumstances what is conserved and what can change along the living of a living system is different in these two phenomenal domains. Thus, as a living system conserves its relational identity as a particular kind of organism, its molecular structure is open to change within bounds defined by the relational identity conserved. At the same time, as a living system conserves its organization as a closed molecular autopoietic network through its continuous molecular changes, its relational identity as a totality is open to change within the bounds defined by the conservation of its autopoietic realization. The relation between these two domains of existence in living systems is systemic, not causal, and what happens in one only sets boundaries for what can happen in the other while the living system is alive, while both aspects of the living modulate each other through dynamic structural relations. It is this double existence what makes possible the evolution of living systems through natural phylogenetic drift. And it is due to this double existence that behaviors and habits guide the course of phylogenetic drift by defining what is conserved in the relational domain in which the organism operates, as well as what can change in its internal molecular structural dynamics.

The biosphere as a system of living systems that form part of a network of intercrossing lineages in phylogenetic co-drifting, flows as a wave front in a continuously changing present. Nothing hap-

pens in the biosphere as preparation for the future, or taking the future in consideration, even though at every instant the outcome of all and each one of the processes in the biosphere determines what arises in it in its continuous flow of change. We think that it is the flow of change of the biosphere as a continuously changing present, that which we biologists want connote when speaking of evolution to explain the diversity and ecological coherences of the many kinds of living systems that we find in our living. But if it is so, then we biologists must accept that that which we want to connote when speaking of natural selection, is the result of the natural co-phylogenetic drift that occurs in the biosphere as biological diversity arises through the diversification of lineages as a consequence of systemic reproduction under the conservation of autopoiesis and adaptation.

Perhaps it is adequate to give to the notion of natural selection its proper significance by saying that natural selection is the historical outcome of natural drift. Natural selection is not and cannot be a mechanism that generates the process of adaptation of the organisms to conditions that are not there. The history of diversification of living systems is the conservation of what lives through the conservation of adaptation as a condition of living. Yes, evolution is a tautological phenomenon, as all natural phenomena are.

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APPENDIX: TERMS AND CONCEPTS

Adaptation: Relation of operational congruence between a living system and the domain of existence in which it conserves its organization because its interactions in such a domain trigger in it only perturbations (changes of structure without loss of organization). As such, the relation of adaptation in living systems is necessarily an invariant; that is, either adaptation is conserved in the flow of existence of the living system as it only meets perturbations in its interactions with the medium, and the living system continues to live, or the living system disintegrates as it enters in an interaction that triggers its disintegration. In other words, the conservation of adaptation is a condition of existence of living systems. Furthermore, since a living system exists in continuous structural change, either the living system slides in the medium following the path of interactions in which it conserves adaptation in a structural dynamics in which living system and medium change together congruently, or the living system undergoes a destructive interaction and dies (Maturana, 1988).

Autopoiesis: A system that is constituted as a unity as a closed network of productions of components which through their interactions produce the same kind of components that produced them, is an autopoietic system. A molecular autopoietic system as an autopoietic system whose components are molecules, is a living system. A living system as a molecular system is open to the flow of matter (molecules), yet, at the same time, a living system as an autopoietic system is a system closed in its dynamics of states. It is in the interplay of this openness and closure, that a living system exists in a flow of continuous structural change while it conserves autopoiesis and adaptation. It is necessary to remark at this moment, that as a molecular autopoietic system a living system is an autonomous entity in a domain of components (the molecular domain) whose existence does not require any accessory support. Molecular thermal agitation is part of the molecular condition, molecular interactivity is part of their structural condition, and molecular interactions give rise to molecules. All other systems that are claimed to be autopoietic are made of components that exist under the support of other entities that make them do what they are required to do for the realization of the claimed autopoiesis. In this sense, as molecular system, living systems exist as the kind of entities that are perhaps the only ones that are autopoietic.

Epigenesis: Epigenesis is the process of structural transformation undergone by an organism moment

after moment in the course of its ontogeny (in the realization of its living) starting from its initial total structure (total genotype). The epigenesis take place as two interlaced processes of structural transformation of the organism as a whole: one takes place as the organism interacts as a totality in the medium, and the other takes place in the cellular and organic differentiation as that internal process that is usually connoted as morphogenesis. The first one, that we shall call organismic epigenesis, occurs as a transformation that takes place in the interplay of the organism's own structural dynamics and the structural changes triggered in it along the course of its interactions in the medium, and follows a course contingent to the course followed by its interactions. In the organismic epigenesis the autopoietic organization of the living system and its relation of operational congruence with its domain of existence (niche), that is, its adaptation, are conserved. In organismic epigenesis, then, the living system and the niche change together congruently in the realization of the ontogenic phenotype/ontogenic niche relation proper to it. The second process of epigenetic transformation, and which we shall call morphogenic epigenesis, occurs as an epigenetic process in which all the components, molecules, cells, and organs of the organism, undergo structural transformations modulated moment after moment by their indirect and direct interactions with each other in the conservation of the systemic constitution of the organism in the realization of its living. Strictly speaking, then, the epigenesis of a living system is the total ontogenic structural drift that it undergoes in the realization of its living, starting from its inception. As such the epigenesis occurs as a continuously changing present without reference to the past or the future. It is for this condition that there is no predeterminism in the structural becoming of the epigenesis of an organism, and there is not and can not be a genetic determinism. At the same time, it is because the epigenesis occurs as a changing present that the two epigenetic processes that it involves, flow as an ontogenic structural drift in which each follows a path of structural change that arises at every instant as an ongoing emergence without alternatives (Fig. 9).

Epigenetic field or domain of possible epigenetic paths: An observer can say that the total genotype (total initial structure) that constitutes the beginning of a living system, specifies for it an epigenetic field as the domain of all the epigenetic paths possible to it in its life history, and from which only one will be realized. In other words, the epigenetic field

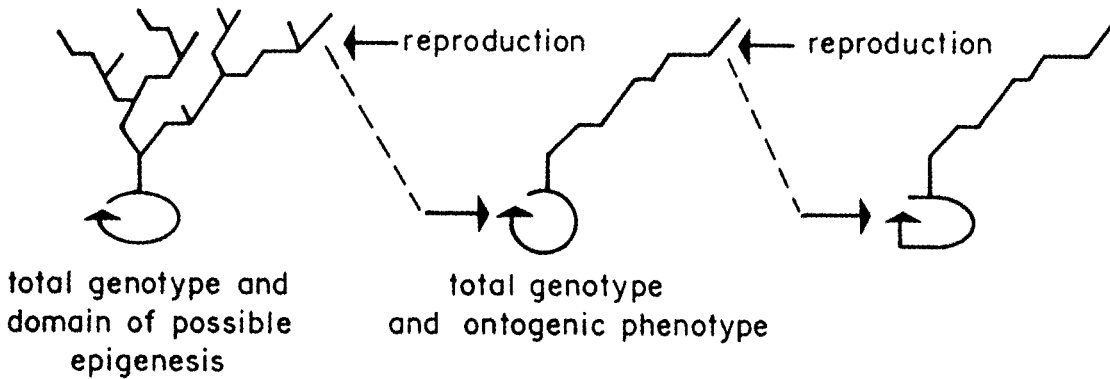


Fig. 9. This figure shows the continuous shifting of the genetic constitution of the members of a lineage that takes place along the systemic reproductive conservation of an ontogenic phenotype/ontogenic niche relation that through its epigenetic realization hides genetic variations.

Esta figura ilustra el corrimiento continuo de la constitución genética inicial de los miembros de un linaje que ocurre juntamente con la conservación, por reproducción sistémica, de una relación fenotipo ontogénico/nicho ontogénico. Puede verse que la realización epigenética de esa relación oculta las variaciones genéticas.

is the domain of all the possible ontogenic drifts that a living system may undergo depending on which history of interactions it happens to live, and is determined in the initial structure of a living being by its total genotype as a domain of its possible ontogenic drifts. Nevertheless, in a strict sense, such a field of possible epigenesis exists only as a domain of possibilities for an observer. And this is so because the epigenetic path followed by every organism starting from its initial structure (total genotype) is the only one that it can actually follow

in a course that arises moment after moment anew according to the structural interactions that it has at that moment with the medium in the realization of its niche, in a process that lasts until it dies. So, the epigenesis is a process of structural drift that arises in the encounter organism medium as operationally independent systems in their structural dynamics (Fig. 10).

Genetic drift: The expression genetic drift is used to refer to the genetic changes conserved in a

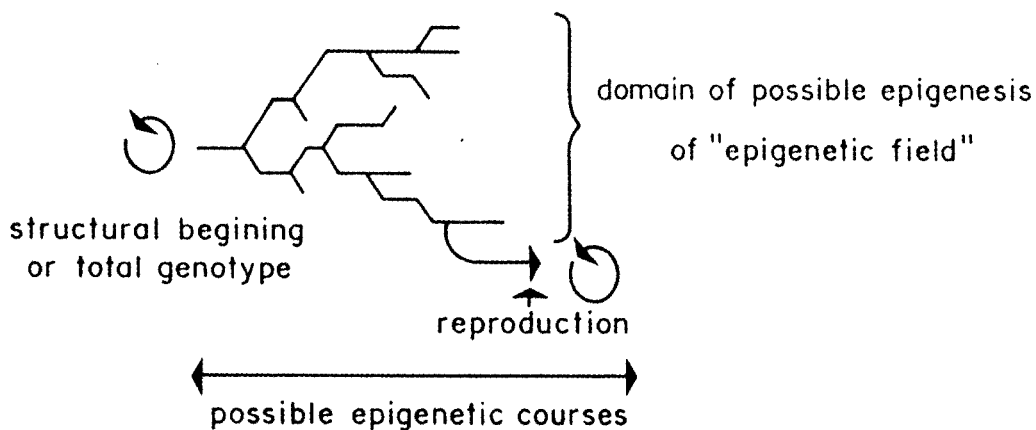


Fig. 10. This figure depicts the many epigenetic courses that an observer may conceive as possible for the ontogeny of any living system at its conception. Only one of all these conceivably possible epigenetic courses will actually occur in any individual life history. That course is indicated in this figure as the path that leads to the arrow that points to an initial new living system through systemic reproduction.

Esta figura ilustra los muchos cursos epigenéticos que un observador concibe como posibles de realizarse en la ontogenia de un ser vivo dado. Solo uno de estos cursos posibles ocurrirá en la historia individual de ese ser vivo. Ese curso es indicado en la figura como el camino que lleva hacia la flecha que apunta a un nuevo ser vivo inicial, resultante de un proceso de reproducción sistémica.

population thought to occur without association to natural selection, due to its neutral character, or as a consequence of accidental isolation, and random population sampling (Beatty, 1992; Kimura, 1992). We shall talk of genetic drift in a wider sense to refer to the genetic changes conserved from one generation to the next in systemic reproduction. Genetic drift is not a special process, but it is the result of the liberation of the genome to change in any possible way while the ontogenic phenotype/ontogenic niche relation is conserved in a lineage. In other words, insofar as a living system is realized in an ontogenic phenotype, genetic drift is a consequence of the liberation of the genotype to vary in a phylogenetic drift that coopts all genetic variations within a domain defined by the systemic reproductive conservation of an ontogenic phenotype. Genetic drift, then, operates as a systemic dynamics that takes place generation after generation in the history of a lineage as a process of cooption of all genetic variations in the conservation or shifting of the ontogenic phenotype/ontogenic niche relation that is conserved through systemic reproduction.

Genetics: Study of the configuration of genealogies in relation to the way the phenotypic characteristics and molecular classes that constitute the different types of living systems are produced and distributed through systemic reproduction. We think that there are different forms in which genealogies are produced according to the different ways or manners of distribution of phenotypic features in a cellular phylogeny. Thus, we think that the form associated with the manner of production and replication of nucleic acids, that is the one generally connoted in speaking of genetics, is the most fundamental one given their participation in the synthesis and structural specification of many classes of molecules as well as in their regular distribution in cell division. But, at the same time, we think that there are other genealogical systems such as those that give rise to different cellular lineages in embryonic development and in cellular differentiation, and which depend only indirectly on nucleic acids because they occur as features of the epigenesis. Moreover, the actual cellular activity and cellular differentiation occurs as an epigenetic process in which what takes place in a cell in the operation of its genetic system (DNA) is moment after moment modulated by its own systemic dynamics and its direct and indirect interactions with the structures of the medium and other cells in the systemic realization of the multicellular system that they may integrate.

Genotype: The ensemble of genes proper to the germinal cells of an organism, constituted by the totality of their nucleic acids.

Habits: Habits are behaviors that are recognized as arising as relational features of the epigenesis of an organism and that become conserved in it along its ontogeny as manners of living acquired out of preference. Habits guide the daily living of an organism and participate in the specification of the relational conditions in which it lives as aspects of its ontogenic phenotype, and contribute in this way to the systemic dynamics under which systemic reproduction occurs conserving epigenetic features of the parental manner of living in the ontogenic phenotype/ontogenic niche relation of the next generation. So, habits if they are conserved through systemic reproduction, guide the course of the phylogenetic structural drift of a lineage.

Lineage: A phylogeny defined by the conservation of a particular ontogenic phenotype/ontogenic niche relation through systemic reproduction. The ontogenic phenotype/ontogenic niche relation conserved through systemic reproduction defines the lineage, and a lineage arises in the moment in which in a particular ontogenic phenotype/ontogenic niche relation begins to be conserved in successive systemic reproductions. A lineage lasts as long as the ontogenic phenotype/ontogenic niche relation that defines it is conserved generation after generation through systemic reproduction, and ends when this process ends. A lineage, then, is in fact the result of the systemic reproductive conservation of a phenotype, a manner of living, and not of the conservation of a genotype.

Ontogeny: The particular history of structural transformation of an organism in the epigenetic realization of its ontogenic phenotype. Ontogeny flows as an epigenetic structural drift under conservation of organization and adaptation. The ontogeny of an organism is its epigenetic realization.

Ontogenic drift or ontogenic structural drift: The flow of epigenetic structural changes of a system in its domain of existence along its ontogeny is what we call ontogenic structural drift. The ontogenic structural drift of a living system follows a course that arises moment after moment following the path in which the organism simultaneously conserves organization and adaptation through its interactions. The structural drift of a system is an "all or nothing process", that is, the system under structural drift either conserves simultaneously organization and adaptation, and thus remains in structural drift, or it disintegrates. Furthermore,

in the ontogenic structural drift of a living system, the living system and the circumstance in which it exists change together congruently, so that a living system will never find itself out of place or in lack of congruence with its domain of existence while it is alive. When the operational congruence (adaptation) between a living system and the medium is lost along its structural drift, the living system disintegrates and no longer exists.

Ontogenic phenotype: Phenotypic transformation of a living system during its epigenesis, that extends from its conception or beginning as a singular entity, until it dies. As such the ontogenic phenotype is the configuration of structural transformation that a living system undergoes in its epigenesis in the realization of its particular life history. The ontogenic phenotype is not the same as the particular life history that a particular living system lives, even though it may coincide with it during shifts of the ontogenic phenotype, but corresponds to a form of life history. When a particular ontogenic phenotype begins to be conserved generation after generation through systemic reproduction, a lineage arises defined by the ontogenic phenotype/ontogenic niche relation that is conserved through it. In more general terms, it is the ontogenic phenotype/ontogenic niche relation conserved through systemic reproduction in the organisms of a lineage or system of lineages, what defines that lineage or system of lineages as some particular species, kind, or class of organisms in the flow of the natural phylogenetic drift. So, that which an observer distinguishes when he or she distinguishes the "vital cycle" of a certain kind of organisms, is the ontogenic phenotype/ontogenic niche relation that defines or characterizes that kind of organisms.

Ontogenic phenotype/ontogenic niche relation: Both living system and medium change together congruently along the ontogenic and phylogenetic drifts in which they participate under conditions of systemic conservation of autopoiesis and adaptation. In these circumstances, what is in fact realized along the history of a lineage of living systems, is the systemic condition in which the living of a living system entails the simultaneous realization of its ontogenic phenotype and of its ontogenic niche. Furthermore, it is this systemic dynamics what we connote when we claim that what is conserved in a lineage or system of lineages is an ontogenic phenotype/ontogenic niche relation, and it is this systemic dynamics what we connote as we claim that the biosphere is a net-

work of interdependent lineages held together through structural coupling in the conservation of interrelated co-ontogenic phenotype/ontogenic niche relations.

Organization: The organization of a system is the configuration of relations between components that defines and constitute the class identity of that system. That is, it is the organization what defines and constitutes a system as a system of a particular kind, and not its components. The organization that defines a system as a system of a certain class remains invariant while the system conserves its class identity. Or, in other words, as long as the organization that defines the class identity of a system is conserved, the system conserves its class identity. To say that a system remains a system of the same kind after some structural changes, means that the structure of the system has changed, but not its organization.

Phenotype: The moment after moment structural and relational present of an organism that determines at every moment its way of relation and interaction in a medium during its realization as such in the flow of its ontogeny, is the phenotype. The phenotype of an organism is continuously arising moment after moment in the encounter of the organism with the medium. An organism operates as a totality in its domain of interactions according to how it is arising in its phenotype. Furthermore, the phenotype of an organism changes in the course of its ontogeny in the continuous interplay of its internal structural dynamics and the changes triggered in it during the flow of its interactions. The phenotype of an organism is at every moment the present of its epigenesis at that moment. The phenotype, therefore, is not an expression of the genotype of the organism, but it is a moment in its epigenetic living. As an observer distinguishes an organism, he or she does so interacting with it according to dimensions defined by it in its phenotypic present, and the phenotype of an organism emerges in the distinction of an observer as the interactional realization of the organism at that moment of its epigenesis. Therefore, according to how the observer orients his or her attention in the distinction of an organism, he or she can distinguish structural, behavioral, or relational aspects in its phenotypic present. In summary, the phenotype is the operational realization of a living system in its domain of existence, and the different phenotypic features that an observer distinguishes in it correspond to different dimensions of the realization of the living system that appear in the distinction of the observer through his or her interactions with it.

Phylogeny: reproductive succession of ontogenies with conservation of a fundamental ontogenic phenotype and conservation or shifting of other secondary ontogenic phenotypes that intersect with the fundamental one in its realization. In other words, since the ontogeny of an organism implies the simultaneous realization of many other entities or different systems that intersect with it in its structural realization, there is intersection of phylogenies in such a way that the realization of one implies the realization of others.

Structure determined system: A structure determined system is a system such that all that happens to it or in it, arises in it in a manner determined by the operational coherences of its structure. Or, in other words, a structure determined system operates at every instant according to its structure at that instant in the interplay of the properties of its components. The structure of a structure determined system determines all that occurs in its internal dynamics as well as what it admits as an interaction. Therefore, it is possible to say that the structure of a structure determined system determines: a) the structural changes that it can undergo with conservation of organization, i.e. changes of state; b) the structural changes that it can undergo in which it does not conserve its organization, i.e. disintegrative changes; c) the structures of the medium that can trigger in it structural changes with conservation of organization (changes of state), i.e. perturbations; and finally, d) the structures of the medium that can trigger in it structural changes with loss of organization (disintegrative changes), i.e. destructive interactions. Points (c) and (d) indicate that it is not the structure of the environment that the observer sees as acting upon a structure determined system what triggers in it a structural change, but that it is the structure of the system what determines what structures of the medium it may encounter as its niche, and what they may trigger in it. The notion of structural determinism is not an ontological assumption, but it arises as an abstraction that the observer makes of the dynamic and relational coherences of his or her operation as such.

Structure: The components and the relations between them that realize a particular system as a particular case of a particular class, is the structure of that system. Since the structure of a system includes its components and the relations that hold between them, the structure of a system involves more dimensions than those involved in its organization which includes only relations. In fact, the organization of a system includes at any

instant only a subset of all the relations realized in the structure of the system at that instant, and it exists as such only as a configuration of relations conserved in the structural dynamics of the system that define its class identity. This means that the organization of a system is not independent of the structures that realizes it. Therefore, the structure of a system can vary in two ways: a) in a way such that the system conserves its organization, and, therefore, conserves its class identity; and b) in a way such that the system loses its organization, and as it does not conserve its class identity, it disintegrates.

Structural coupling: When two or more structure determined systems enter in recursive interactions and undergo structural changes without losing their respective class identities, their structures change together congruently, and there is structural coupling. We call structural coupling both the dynamics of coherent structural changes that occur in such a case, and the condition of structural coherence that takes place as a result of that dynamics. Structural coupling lasts as long as it lasts.

Systemic dynamics: A system is any collection of elements interconnected by a configuration of relations that constitutes the organization that defines and specifies its class identity as a discrete whole. As long as the organization of a system remains invariant, the system conserves its class identity. And vice versa, to say that a system conserves its class identity is to say that its organization has remained invariant. The dynamic conditions that permit a system to conserve its class identity liberate its structure to change within the limits of the conservation of the organization that defines its class identity. When we talk about systemic dynamics, we are talking about what happens in a system as a result of a dynamics that arises as a result of the structural coherences of all the components of the system as they participate in the conservation of the relations that define it, independently of the type of system that it may be. For example: the freeing of the structure of a system to change within the limits defined by the conservation of the organization of the system when the conditions in which this conserves its class identity occur through its inclusion in a larger system (the medium), is a systemic phenomenon. Ontogenic drift and phylogenetic drift are systemic phenomena in the sense that they occur in the dynamics of conservation of an ontogenic phenotype/ontogenic niche relation in the living of living systems without and with the involvement of systemic

reproduction respectively. In both cases, living systems and medium form a system in coherent transformation that lasts as long as autopoiesis and adaptations are conserved through their recursive interactions.

Total genotype: The total genotype is the total initial structure of an organism, and as such it includes all its components, and not only its genome. The total genotype of an organism may have been a cell that arose through a mitotic

division, or through the fusion of two gametes, or through the union in symbiosis of heterogenetic cells, or it may also have been a group of cells as in the case of organisms that form lineages by gemation or by fractures that separate multicellular unities. The total genotype as the total initial structure of an organism determines the domain of all the possible epigenetic paths that such organism may follow in its ontogeny, even though it will follow only one that will arise moment after moment in its epigenesis.