Resumen

La Síntesis Neodarwinista (o Moderna) ha permanecido como la Teoría de la Evolución incuestionable desde su desarrollo en los años 30 y 40 del siglo XX. La Síntesis propone que las poblaciones biológicas están formadas por individuos de características diferentes entre sí, que estas diferencias surgen por mutaciones al azar del genoma y que la evolución está dirigida por la Selección Natural, que actúa sobre la variabilidad disponible. Es tal la fuerza del paradigma Neodarwinista, que en el lenguaje no científico se utiliza "Darwinismo" como sinónimo de "evolución", confundiendo el Hecho de la Evolución con la Teoría de la Evolución. La Síntesis Neodarwinista es una explicación de los fenómenos observados a partir del conocimiento disponible cuando dicha Síntesis fue propuesta. No es, por tanto, sorprendente que en las últimas seis décadas se hayan descrito numerosos fenómenos que no estaban incluidos en el paradigma. Muchos de estos mecanismos se refieren a la génesis de la variabilidad en los organismos, como la existencia de información heredable no genética, la transferencia horizontal de genes, la simbiosis o las mutaciones dirigidas por el ambiente. A esto hay que añadir las limitaciones que imponen el desarrollo y el diseño estructural a la propia variabilidad, como han señalado diferentes estudios. La Selección Natural permanece en su papel de directora de la evolución, pero debe compartirlo con procesos internalistas, que pueden también jugar un papel importante en el establecimiento de tendencias evolutivas. La Síntesis Neodarwinista asume que el ritmo de la evolución es gradualista, pero recientes observaciones han demostrado que la especiación se puede producir a velocidades mucho más rápidas de lo admitido tradicionalmente. Una aportación enteramente nueva a la Teoría de la Evolución es la existencia de mecanismos de auto-organización que actuarían a todas las escalas de la organización biológica. Algunas de estas nuevas aportaciones son asumibles perfectamente en el paradigma, otras suponen modificaciones menores al modelo, pero hay un tercer grupo que supone un auténtico desafío. El paradigma Neodarwinista debe enfrentarse a este desafío, bien sea incorporándolas en una nueva Síntesis, o dando paso a una Teoría de la Evolución enteramente nueva.

Palabras clave: Evolución, Neodarwinismo, Teoría Evolutiva.

Abstract

The Neodarwinian (or Modern) Synthesis has remained the unchallenged Theory of Evolution since its development in the 1930-40s. It establishes that every biological population is composed of individuals with different characteristics, that these differences arise by random mutations affecting the genome, and that evolution is driven by Natural Selection acting over the available variability. The strength of the Neodarwinian paradigm is such that in non-scientific language "Darwinism" is used as a synonym of "Evolution", confusing the Fact of Evolution with the Theory of Evolution. The Modern Synthesis is an explanation of the observed phenomena based on the knowledge available when it was proposed. It is not surprising that in the past six decades several phenomena have been described that were not included in the paradigm. Many of these recent discoveries are related to the sources of variation in the living organisms, such as non-genetic heritable information, horizontal transfer of DNA by viruses, symbiosis or environmentally driven mutations. In addition, the role of structural and developmental constraints in modulating this variation has been stressed by several studies. The role of Natural Selection as a driving mechanism remains undeniable, but it is now clear that some internalist processes probably play an important role, side by side with Natural Selection, in directing evolution. Implicit in the Neodarwinian paradigm is the notion of gradual change but some recent observations have shown that evolution (speciation) may proceed at a velocity considerably higher than admitted by the paradigm. A new addition to Evolutionary Theory is the role of self-organisation processes acting at all scales of biological organization. Some of the new discoveries listed above fit well into the paradigm, another implies some minor modifications, but there is a third group that constitutes a true challenge for it. The paradigm should face the challenge and be able to incorporate them in a new synthesis, or be replaced by an entirely new Theory of Evolution.

Key words: Evolution, Neodarwinism, Evolutionary Theory.

Does Evolution evolve?

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Introduction

Probably, evolution has been the scientific topic most hotly debated, both by scholars and non-scientists, since at least the 19th century. Its widespread presence in our world is such that when we introduced the search string "evolution" in the Internet Search engine Google, we found over 9.000.000 links containing this word. Evolution is not only the backbone of Biology, it has crucial implications for Philosophy and Sociology and, even, it has been called in support of certain political ideas. Given the great relevance of the term, it is of the outmost importance to have a precise and universally valid definition of it. This objective seems easy to achieve *a priori*, though a search in several current dictionaries and books on evolution or general Biology will show that such a consensus is not so easy to achieve (Table 1). The simplest definitions are variations of Darwin's "descent with modification" (Darwin, 1988) but other ones even include the origin of life from the inorganic world. In many cases the definition of evolution is strongly linked to a particular theory of evolution, sometimes with an extremely reductionist approach (Table 1).

It should be noted that the term "evolution" refers to three related but independent concepts (Ruse, 1987):

1. The Fact of Evolution. That is, the fact that species are not constant and that they descend from other ones.

2. The History of Evolution. The way evolution did occurred on Earth. The phylogeny of organisms.

3. The Theories of Evolution. The processes and mechanisms that govern evolution, *i. e.* how and why does evolution occur.

The difficulty to find a simple and practical definition may be explained both by the confusion between these three independent concepts and by the fact that its meaning depends on the (historical) context where it is used. Just as an example of this confusion, we may quote the words of a reputed evolutionist: «It is now actually misleading to refer to evolution as a theory, considering the massive evidence that has been discovered over the last 140 years documenting its existence. Evolution *is no longer a theory, it is simply a fact*» (Mayr, 2001; our italic; for a detailed discussion of the factual or theoretical character of evolution, see Gould, 1981).

Despite its title, the aim of this paper is not to evaluate if these concepts are the result of historical development. Of course, they are. The idea of Evolution has evolved through the history of science, its development has been conditioned by the philosophical conception of the world in every historical period, and it has evolved incorporating new observations and discoveries from other scientific disciplines, as we briefly summarise in our first section. Our aim here is to put the term in its historical background and to make evident that the Theory of Evolution should continue its development to incorporate several recent discoveries and observations. We review some of these innovations from several biological sub-disciplines and discuss the way they fit, or not, inside the current paradigm.

TABLE 1. Some current definitions of the term evolution, classified by their most significant traits.

Descent with modification /hereditary change

«Any cumulative change in the characteristics of organisms or population from generation to generation; descent or development with modification.»

(Lincoln, 1982)

«Descent, with modification from one (or at most, a few) original ancestors.»

(Craig, 2001)

«Evolution is a process that results in heritable changes in a population spread over many generations»

(Moran, 1993)

Including the origin of life

«The theory that all the living forms in the world have arisen from a single source which itself came from an inorganic world»

(Kerkut, 1960)

«The gradual process by which the present diversity of plant and animal life arose from the earliest and most primitive organisms, which is believed to have been continuing for the past 3000 million years»

(Isaacs et alii, 1991)

Gradual change

«A process of gradual change by which one form of something slowly changes into a similar, but significantly different form.»

(Gray, 1967)

«Concept that embodies the belief that existing animals and plants developed by a process of gradual, continuous change from previously existing forms.»

(Anonymous, 2002)

«Proceso continuo de transformación de las especies a través de cambios producidos en sucesivas generaciones»

(Anonymous, 2001)

«The gradual process by which the present diversity of plant and animal life arose from the earliest and most primitive organisms, which is believed to have been continuing for the past 3000 million years»

(Isaacs et alii, 1991)

Genetic change

«Biological evolution … is change in the properties of populations of organisms that transcend the lifetime of a single individual. … The changes in populations that are considered evolutionary are those that are inheritable via the genetic material from one generation to the next.»

(Futuyama, 1986)

«…in fact, evolution can be precisely defined as any change in the frequency of alleles within a gene pool from one generation to the next»

(Curtis and Barnes, 1989)

«Evolution is a generation-to-generation change in a population's frequencies of alleles or genotypes. Bacause such a change in a gene pool is evolution on the smallest scale, it is referred to more specifically as microevolution»

(Campbell et alii, 1999)

«Organic evolution is a series of partial or complete and irreversible transformation of the genetic composition of populations, based principally upon altered interactions with the environment»

(Dobzhansky et alii, 1977)

Evolution. The historical background

It is not our intention here to write an exhaustive history of the development of the concepts represented by the word evolution, nor to account for all the historical events and scientific discoveries that influenced such development, but to draw a general picture of the process, in order to provide the historical background for the central discussion. Those readers interested in a deeper analysis will find very profitable lectures in Templado (1974), Harris (1985), and Gould (2002).

The origin of human beings and of life on Earth has been a basic question in every culture. All religions provide mythical explanations to these topics, but the first scientific answers were provided by the ancient Greeks. Although, as we will explain later, the word "evolution" was not used in its present meaning until the 19th century, the fact of evolution was proposed by Anaximander as early as in the 6th century B.C. and later by Empedocles of Acragas (c. 450 B.C.). Anaximander established that the Earth had been covered in water at one stage, with plants and animals arising from mud, and later humans arising from fish. Probably Anaximander was aware of the existence of many rocks incorporating shells and other marine fossils, a knowledge much more widespread in the Classical World than it is usually thought (Mayor, 2000). The philosophers of the Socratic period paid minor attention to Natural History until the arrival of Aristotle (384-322 B. C.), who is cited by Darwin himself as a precursor of the

evolutionary ideas (Darwin, 1988: 3). Nevertheless, the citation was incorrect, since Darwin quoted a paragraph from the *Physics* of Aristotle where in fact he was criticising the evolutionary ideas of Empedocles (Aristotle, in Harris, 1985). The idea that the existing animals and plants were not always as we see them today re-appears in the Classical World with the Epicurean philosophers, as transmitted by Lucretius (c. 95-5 B. C.) (Mayor, 2000). The main contribution of these forerunners is that they gave rise to the idea that the living beings are the result of a historical process of development. On the other hand, the processes or mechanisms proposed to explain this development are extremely naïf or just does not exist at all, although the ideas of Empedocles and the Epicurean philosophers may be interpreted as extremely ingenuous versions of Natural Selection.

With the establishment of Christianism as the dominant religion in Europe, God became the cause of every observed phenomenon, the Bible was established as the supreme authoritative source for the interpretation of the world, and the study of Natural History was relegated to the interpretation and transmission of the texts of some classical philosophers, Aristotle in particular. This situation was only challenged when the feudalism was substituted as the politic-economical system with the appearance of a new class, the bourgeoisie, and with the development of strong national monarchies. It was in this period, the Renascence, when science began its development as the

way to explain the world, besides Religion, with Copernicus, Kepler and Galileus among others. As an example, Leonardo da Vinci (1452-1519) defended, against the current opinion, that fossils were remains of ancient organisms, he established a primitive version of the law of superposition of strata, later independently developed by Steno in 1669, and he estimated the time it would take the Arno to deposit the surrounding outcrops (Richter, 1883; Vasari, 1946). This last topic was extremely important for the development of the idea of evolution, since the current opinion about the age of the Earth was based on the Bible, and it implied an extremely short chronology. Basing his calculations on data gathered from the Bible, Archbishop Ussher established in the 17th century that the Earth was created on 4004 B. C. October 22nd, although J. Lightfoot was able to refine his calculations and established October 23rd, at 9 AM, as the precise time (Dickson White, 1898).

Despite these advances, the absolutely dominant position during the 15th and 16th centuries was fixism, the Genesis was the unquestioned source of explanation for the origin of the World, plants, animals, and man. Although the influence of his ideas on the scientific community of his epoch was negligible, the case of José de Acosta (1539-1600) is worth to be mentioned (Aguirre, 1957). Acosta –a Jesuit missionary in South America– was impressed by the diversity of life in the New World, although simultaneously he was able to perceive striking similarities between many American and Old World species. Acosta proposed three alternative hypothesis to explain the observed pattern: 1) the American species were created independently; 2) after the Deluge the species spread along the world, but every particular species went locally extinct in some places and survived in other regions and 3) the American species developed from pre-existent European ones. Acosta accepted the second hypothesis, while the third one was proposed only as a null hypothesis, probably as a way to avoid the predictable consequences of defending such ideas. The case of Acosta is more than an anecdote; it shows that, although some individuals were able to generate plausible explanations for observed phenomena, the scientific community and the whole society were not prepared to receive them. Indeed, the main contribution of the science of the Renascence to evolution was to modify the "scientific environment" and to prepare both the illustrated people and the whole society to be receptive to such ideas. The 17th century was a period of important contributions to construct the basis for the establishment of the fact of evolution in the next century as a widespread hypothesis in the scientific community. Bacon and Descartes developed the inductive and deductive methods, respectively (Harris, 1985), Leeuwenhoek invented the microscope (Ford, 1991), Steno established the basic principles of stratigraphy, and Leibniz developed the concepts of the "chain of being" and the "continuity of nature" summarised in his statement «All advances by degrees in Nature, and nothing by leaps...» (Leibniz, 1996).

In the 18th century the bourgeoisie became the dominant social class and the ancient economical and political structures were coming to a crisis. It is not surprising that France, the country of the *Encylopédie* and eventually of the bourgeois revolution, illuminated by the spirit of Enlightenment, was the birthplace of the most important contributors to the development of evolutionary thought during that period. All sub-disciplines of Natural History, as well as science in general, experienced remarkable advances. Maupertuis established that the hereditary characters were inherited from both parents and proposed that the living species where the result of a process of historical development (Tort, 1996), controlled by a naïf version of Natural Selection, reminiscent of Empedocles' ideas (Maupertuis, 1745). George-Louis Leclerc, Comte de Buffon also championed the fact of evolution, and suggested that the Earth was much older than Ussher and Lightfoot had estimated, though he failed in providing any coherent mechanism to explain organic change (Tort, 1996). However, the scientific paradigm still supported by the most prominent European naturalists, like Cuvier and Geoffroy de St. Hilaire, was fixism. Nevertheless, and somewhat paradoxically, their scientific research was eventually essential in preparing the scientific community to receive the idea of evolution. In 1735, Linnaeus published his fundamental work *Systema Naturae*, a keystone for the future development of biology, although written from an orthodox fixist viewpoint. Cuvier, advanced pioneer of comparative anatomy, established that fossils were remains of extinct organisms. He thought that organisms were integrated entities, every part in perfect harmony with other parts, so any alteration of the species morphological plan would render chaotic results (Templado, 1974). St. Hilaire was the reverse of the medal, he saw organisms as modifications of a few master forms, the archetypes, modified to make each particular species suitable for a specific environment. In modern words, he identified the existence of homologies but his position in the evolution *versus* fixism debate was rather confusing (Harris, 1985; Darwin, 1988). Undoubtedly, the most famous 18th century evolutionist was Lamarck, although he is often misquoted and frequently attacked and discredited. The ideas of Lamarck are usually reduced to the inheritance of acquired characters, a theory supported by many other naturalists, but his theories were rather more complex. Lamarck's wide and deep knowledge of the animal kingdom, allowed him to arrange the animals along a "scale of life" from the simplest to the most complex (Lamarck, 1986). According to his theory of evolution new very simple organisms are spontaneously generated every minute and, generation after generation, they are "ascending" along the "scale of life" giving rise to more and more complex species. Extinction does not exist in the Lamarckian universe, every species evolves into another more-perfect one according to a teleological view of evolution, and all fossil species are ancestors of recent (more complex) ones.

Thus, at the turn of the century, the idea that living organisms were the result of a process of historical development, the fact of evolution, was widely spread in the scientific community, although it was not universally accepted, mainly because nobody had been able to provide a sound and well-documented mechanism to explain it, a theory of evolution. This was the fundamental contribution of Charles Darwin's "The origin of species", *i. e.* to propose a profusely documented theory of evolution, based on an admissible mechanism, Natural Selection. As is well known, Darwin's theory is strongly influenced by the ideas of Malthus (Templado, 1974). Basically, Natural Selection theory states that in any living population the number of births is much larger than the maximum sustainable by the available resources; that every individual in a particular species is different from any other individual; that the individuals contribute differentially to the next generation; and that the individuals that survive are the best adapted to their particular environment. This process, repeated generation after generation, leads to gradual changes in the population, that give rise to new races and, eventually, to new species (Darwin, 1988). It should be noted that the expression «survival of the fittest» is not due to Darwin, but to Herbert Spencer. Spencer was a pioneer of sociology, strongly influenced by positivism, and the father of "Social Darwinism". He was the author of the expression «nature red in teeth and claws» and even he coined the term "evolution" in its modern meaning. As a matter of fact, it is anachronistic to use the word "evolution" in the way we do above to refer to the ideas of the pre-19th century naturalists; it would be more accurate to use the contemporaneous term "transformism". Neither Darwin nor Lamarck, nor any other previous naturalist would have used the word "evolution" in its modern sense, because it referred to a very different process. The etymological origin of this word is the Latin term *evolutio* that means "unfolding" and it was used in the context of the embryological theory of preformism to designate the process that leads the "primordial being" to the new-born (Bynum *et alii,* 1985). Darwin's theory was not only strongly supported by a large number of observations, in addition it was proposed in a time when both the society and the scientific world were prepared to receipt it. On the one hand, Spencer's version of Darwinism reinforced the ideas of liberalism and capitalism, and on the other hand, evolution gave strong support to the materialism sustained by the left wing philosophers.

At the beginning of the 20ᵗʰ century the fact of evolution, common descent and species change, was widely accepted among educated people, but Darwin's theory of evolution was object of severe criticisms concerning basically two topics: time and tempo. Darwin had estimated that it took the mammals 300 million years to reach its present diversity by means of Natural Selection (Sampedro, 2002). In 1862 Lord Kelvin estimated the age of the earth by calculating the time it would take an earth-size molten sphere to cool to its present temperature, and concluded that the planet was about 100 million years old (Grzimek, 1976; Bynum *et alii*, 1985; Gould, 2002). The second counter-evidence came from the rediscovery of Mendel's Laws in 1900, since Mendelian characters were discrete and the changes were abrupt (smooth *versus* rough peas), no intermediate stages were observed. In 1901, Hugo de Vries showed evidences of the role of mutations and stated that evolution was driven by "large mutations" instead of by small and cumulative changes (Templado, 1974). Furthermore, Bateson found that small changes in genotype may cause large and abrupt modifications in phenotype and called this phenomenon "homeotic change". Thus, during the first decades of the 20th century gradualism was against the evidence, and the favoured evolutionary theories were closer to saltationism or abrupt change. Simultaneously, Teilhard de Chardin developed his teleological and orthogenetic theory of evolution, impregnated of metaphysics, in an attempt to conciliate science and Catholicism (Templado, 1976).

New evidences were accumulated through the 20's and 30's in support of gradualism and new dating methods based on radioactive decay expanded the age of the earth to some thousand million years. In 1930 Fisher reconciled Darwinism and genetics by showing that gradual change may be explained in terms of Mendel's Laws (Gould, 2002). It was mainly the work of three authors, Fisher, Haldane, and Wright, somewhat irreverently nicknamed the Second Holy Trinity by Gould (2002), what set the basis for the new paradigm. In the late 30's Dobzhanski met the American geneticists and evolutionists and their joined efforts gave rise to the so-called Modern Evolutionary Synthesis (or Modern Synthesis), based on the assumption that evolution is driven by Natural Selection. Both geneticists and systematics agreed in the next years that evolution seemed to be gradual, relegating saltationism to the well–known phenomena of polyploidy, although considering it as somehow anecdotal. Population genetics mathematically proved that evolutionary change may be promoted by weak selection pressures actuating on minor genetic differences. Evidences against the inheritance of acquired characters and the theories related to orthogenesis –evolution aimed in a particular direction by causes other than adaptation (Tort, 1996)– were found and these theories were considered as erroneous and erased from the research programs. Finally, the palaeontologists, mainly by means of Simpson, declared that the fossil record was in accordance with the Neodarwinian theory of evolution, as well as it provided the environmental context for Natural Selection. Thus orthogenesis was definitely abandoned (Leigh, 1999). However, Modern Synthesis was not immediately accepted world-wide. At the same time that the Modern Synthesis was established in the USA, in the Soviet Union, Lysenko developed his Neolamarckian theory (Templado, 1974; Tort, 1996). Unfortunately, Lysenko was an unscrupulous trickster rather than a scientist, and used his political influence to get a position that allowed him to control the soviet Biology until his dismiss in the late 50's. Worst of all, the debate between the two theories was established in terms of the Soviet Neolamarckism versus the Capitalist Neodarwinism. Lysenko's theories were unsupported by evidence, and they were eventually given up in the Soviet Union after the end of Stalin's era. Its worst consequence was that any theory of evolution alternative to the Modern Synthesis would be discredited from then onwards. As Leigh (1999) points out, the Modern Synthesis gained general acceptance by refuting other theories, rather than by accumulating evidences in favour of Natural Selection as the main, or single, evolutionary mechanism.

The Neodarwinian paradigm

The General Theory of Evolution, as established by Darwin, is in fact composed of many theories. The first two are the descent with modification (the fact that species change), and the common ancestor (all living beings descent from a few if not one primitive forms). As commented in the introduction, these two theories are now considered facts given the amount of accumulated evidence that support them. The rest of theories concern how and why evolution takes place and are based on what Mayr (2001) calls the "population thinking", a point of view in which any individual is different from every other and thus every species is no more than a cluster of different individuals. Joining this approach with the Malthusian theories of competition for limited resources, natural selection arose as a motor of change in populations and the creative force for evolution. Another theory, also a consequence of the population thinking, is that species' change is merely the elimination of the less competitive or adapted individuals and the multiplication of the more adapted ones and, thus, that species change gradually. This gradual change leads to progressively more adapted forms.

The Modern Synthesis, as was called by their authors, consists on the integration of genetics into the Darwinian theory to form what is known as the Neodarwinian paradigm. According to this theory, how and why the process of evolution occurs can be summarised as follows: «...an enormous amount of genetic variation is produced every generation, but only a few individuals of the vast number of offspring will survive to produce the next generation. The theory postulates that those individuals with the highest probability of surviving and reproducing successfully are the ones best adapted, owing to their possession of a particular combination of attributes. Since these attributes are largely determined by genes, the genotypes of these individuals will be favoured during the process of selection. As a consequence of the continuous survival of individuals (phenotypes) with genotypes best able to cope with the changes of the environment, there will be a continuing change in the genetic composition of every population. This unequal survival of individuals is due in part to competition among the new recombinant genotypes within the population, and in part to chance processes affecting the frequency of genes. The resulting change of a population is called evolution. Since all changes take place in populations of genetically unique individuals, evolution is by necessity a gradual and continuous process» (Mayr, 2001). Though not included in the previous definition, Neodarwinism explicitly invokes allopatric speciation as the process that generates new species. According to this model a population of the species A is separated in two different populations (B and C) by a new barrier. Populations B and C accumulate gradual changes through time that eventually generate two different species.

The Neodarwinian paradigm as defined by Mayr (2001) rests on several premises: i) there is a continuous source of heritable variation that is based on changes in the genotype; ii) change in populations proceeds gradually and, as a consequence, changes in characters should also proceed gradually; iii) Natural Selection and stochastic processes drive the process of evolution; and iv) species and higher clades form by the same processes that trigger the change in populations. Some of these premises have been expanded as new evidences were arising. However, the core of Neodarwinism and thus of the generally accepted Theory of Evolution has remained unchanged despite the amount of new data and new approaches that are reclaiming further consideration.

The following sections review these premises, shed light on some of the new evidences and discuss alternatives that have been proposed and the way they may or may not fit into this Neodarwinian paradigm.

Sources of variation

Evolution is based on heritable variation. According to the Neodarwinian paradigm, only changes in the genotype expressed in the phenotype are relevant for evolution. This leads to assume that the rules of genetics are the rules of variation for the evolutionary processes which several important premises:

1. The genetic material (DNA) is constant and cannot be changed by the environment. This assumption eliminates the inheritance of acquired characters as a valid mechanism of evolution.

2. The DNA contains the information that permits the production of the proteins that make up the phenotype of every organism. Thus, only changes in the genotype are relevant to evolution.

3. Although a gene is normally constant from generation to generation, it has the capacity to mutate occasionally into a different form. Such a newly mutated gene (mutant) will again be constant, unless another new mutation occurs. According to Morgan (1910) a mutation is a spontaneous change of the genotype. Mutation are assumed to be random in their phenotypic expression. Changes in the genotype are due to errors of replication during cell division, including base pair replacement by a different one (called gene mutation). It also

includes large-scale changes such as polyploidy or changes of the gene arrangement (i.e. chromosomal inversions) called chromosomal mutations. Further changes can come from transposition of DNA sequences or from changes in the pathway from the DNA of a gene to the aminoacids of the phenotype.

Non DNA-sequence based genetic variations

Although the Neodarwinian paradigm establishes that the genetic material contains all the inheritable information of an organism, strong evidence exists nowadays that information non-linked to DNA base sequence may be transmitted to the next generation. Jablonka and Lamb (1995) define an epigenetic inheritance system as the mechanisms that enable a functional state or structural element to be passed from one generation to the next, without requiring a persistent stimulus from the environment, and without changes in the DNA base sequence. Some of these mechanisms affect the chromatine, for example the pattern of heterochromatinized regions or the bound of regulatory proteins, implying that the next generation inherits the functional state of its ancestor (Jablonka and Lamb, 1995). The major caveat to consider epigenetic changes as playing a major role in evolution is that the modifications should survive the gametogenesis to be maintained generation after generation although, in any case, this restriction only applies to sexually reproducing organisms (Fox Keller, 1998). However, differences due to changes in the epigenetic inheritance system have been demonstrated in sexually reproducing organisms as shown by the study of Cubas *et alii* (1999) with *Linaria* (Linnaeus 1749). *Linaria vulgaris* is a flower plant with a well known polymorphism in its flower symmetry. The wild phenotype presents a bilateral symmetry in both petals and stamens while the mutant phenotype is characterised by a radial symmetry (see figure in Cubas *et alii*, 1999). The differences in pattern are caused by a change in the tempo of development of the floral primordia caused by differences in the expression of *Lcyc* regulating gene. Comparisons of the base sequence of *Lcyc* in both wild and mutant phenotypes did not yield any positive result (apart from a non-expressed third-position change). Further studies demonstrate that the differences were due to the degree of methylation of the *Lcyc* gene (what has been termed *epimutation*) that is inherited in the following generations. Cubas *et alii* (1999) propose that this process can be important in plant evolution, although it should be rare among animals due to the separation of the germinal and somatic lines. Thus, epigenetic inheritance systems broad their range of action while the strict Neodarwinian view is more or less restricted to Metazoa.

Genome structure has also an important role for evolutionary trends. A genome is not only a group of genes, placed in DNA molecules. In Prokaryotes, these molecules present simple tertiary structures and are fixed most times to the inner part of the cell membrane. Among Eukaryotes, most (but not all) of the

genome is located in the nucleus, and shows a complex organisation. Tertiary and quaternary structures of DNA involve many other molecules that form a scaffold where chromatine is compressed in a high degree, to build the chromosomes. A great part of these DNA is non-coding, that is, it does not host information about valid genes. Most of these sequences play a role in the chromosomal structure, for example, in the telomeres (the final part of the chromosome, where the pack of DNA is 'closed'). As a result of the genome structuring, the location of the genes in the chromosome sequence determines their variability, as they present spatial autocorrelation (Reich *et alii*, 2002). This means that the degree of variability of two given genes becomes more similar as the distance between them decreases. That is, that there are high- and low-variability areas in the chromosome. Moreover, the location of genes in the DNA sequence is 'marked' by several non-coding sequences that can act as 'landmarks' for several retroviruses and transposable elements. These elements are able to change DNA sequence, after recognising the 'landmark' that corresponds to the sequence they are going to insert or change in the genome. This 'molecular mapping' may be very important in horizontal transmission and genome reorganisation, two processes that may have been very common across evolutionary history (Sentís, 2002).

Cell structure

Another source of heritable variation comes from some aspects of the cell structure that are inherited from the pre-existing cell structure, without involvement of the genome (Jablonka and Lamb, 1995). This phenomenon is well known in ciliates. It has been found that the pattern of cilia in the surface of *Tetrahymena* and *Paramecium* differs in different clones. The pattern is maintained from generation to generation, and it is not altered when cells with different patterns go through the sexual process of conjugation. Even more, it has been shown that experimentally altered cilia patterns are inherited, although the genotype is not affected by the treatment.

Horizontal transfer

Horizontal transfer refers to any transfer of genes between organisms without involving reproduction. There are many ways by which horizontal transfer of genes can proceed but only retroviruses seem to be a widespread and important source for new genetic information. Recent studies estimate that over 8% of human genome is from viral origin (Bromham *et alii*, 2002; over 10% according to Sentís, 2002). The main part is restricted to the non-coding DNA but some sequences are highly involved in the evolution of both genome and life. Retroviruses (such as the AIDS virus) are made of RNA (ribonucleic acid) and reproduce by attaching their own genes to those of their host. This process is driven by an enzyme, the reverse transcriptase, which transcribes a DNA sequence from a RNA sequence used as model. Recent data show that the gene of reverse

transcriptase is the most copied one in the human genome, and also that the protein presents episodes of high activity in Eucaryota, even in humans (see Sentís, 2002 for a review), pointing to an important role not previously recognised. During the process of infection, retroviruses occasionally transfer genes of other organisms, peeling off a part of a gene from one organism and passing it to another.

Once in the genome, retroviruses may have several fates, which can be highly important for evolution. They can retain its transposition capability and thus they may cause an increase in the rates of change of the genome, both by replication or transposition of sequences within a genome. Viral DNA can be also co-opted within the host DNA functions (viral DNA comprises at least 4% coding DNA in humans; Nekrutenko and Li 2001) or it can decay and form part of the non-coding "junk" DNA (Bromham *et alii*, 2002). The importance of retroviruses can be illustrated by their function in the placentation in humans (Harris, 1998), where the retrovirus HERV-W causes the expression of the syncytin, a protein which mediates placental cytotrophoblast fusion *in vivo*, and thus may be important in human placental morphogenesis (Mi *et alii*, 2000). Viral contribution to organism functioning has been more clearly shown in bacteria, where pathogenic capabilities in *Escherichia* and *Listeria* are due to particular genes acquired through horizontal genetic transfer (Perna *et alii*, 2001; Glaser *et alii*, 2001). Another example comes from the *Drosophila* species of the *melanogaster* group, where at least a telomere is of viral origin, meaning that nuclear genome structure needs of the acquired viral sequences to maintain its present structure.

Symbiosis

Although not explicitly included or excluded in modern synthesis theory, symbiosis seems to be a key factor in comprehending evolution. In fact, our own cellular architecture is the product of ancient symbiotic interactions. As Lynn Margulis demonstrated years ago (Margulis, 1981), one of the major steps in evolution, the origin of the first eukaryotes, was due to the formation of a chimera through the symbiosis between an archaeobacterium and an eubacterium. The union of their genomes lead to the formation of the eukaryotic nucleus as has been shown by genetic analyses (Gupta and Golding, 1993). Moreover, some of the principal organelles, like mitochondria or chloroplasts, were also originally endosymbionts. All these facts give symbiosis an overwhelming role that have not been acknowledged despite the accumulated evidence. This importance can be extended to many other phenomena beyond the origin of the eukaryotic cell leading to a different view and co-operative view of evolution, opposite to the classic competitive one (Margulis and Sagan, 2000).

At organismic or higher complexity levels, symbiosis and co-operation are still important in nature. Most endosymbionts, and also parasites, may have evolved at the same time as their hosts, producing a high degree of inter-relationship among both

species, in which living without the partner becomes a hard, or even impossible, task. Nature is plenty of this kind of relationships, for example the relationships between the roots systems of most plants and both fungi and nitrogen-fixing bacteria. At least 90% of vascular plants have mycorrhizae, a symbiotic and complex interaction between roots and fungi that improves inorganic nutrient absorption (Gianinazzi-Pearson and Gianinazzi 1986; Smith and Gianinazzi-Pearson 1988). On the other hand, the well-known genetically complex symbiosis between legumes and *Rhizobium* bacteriae, where both symbionts own genes that promote several actions in the other, such as the development of bacterial nodules where nitrogen is fixed (Downie and Johnston 1986; Peters *et alii*, 1986; Rolfe and Gresshoff 1988), is not the exception but the rule in terrestrial plants. Both symbiotic relationships may have had a key role in the success of vascular plants in colonising land, as is evidenced by the strong influence of the arbuscular mycorrhizal fungi of a given site on its plant diversity (see Urcelay and Díaz, 2003). This high degree of interaction has resulted for most species in similar evolutionary patterns between symbionts, or between host and parasite. For example, the phylogeny of the Nearctic cockroach genus *Cryptocercus* is identical to that of its bacterial endosymbionts from the genus *Blattabacterium*, evidencing they have co-evolved during at least 70 Myr (Clark *et alii*, 2001).

Environmentally driven mutations

According to the paradigm, mutations are assumed to be random in their phenotypic expression. Jablonka and Lamb (1995) argue that mechanisms that alter the base sequence of DNA as a response to certain external stimuli have been produced by Natural Selection. A classical example are the strains of *Escherichia coli* with a non-functional copy of the gene necessary to metabolise the sugar salicin that show mutation rates 12 fold higher for this gene in a selective medium with salicin than that expected if mutation were at random, and without increase in the general rate of mutation (Hall, 1988). Directed changes in DNA have been reported for eukaryotes as well, including yeasts, plants, and metazoans, humans inclusive (Jablonka and Lamb, 1995). As mentioned above, the inheritance of environmentally driven epigenetic mutations is made difficult by the gametogenesis, which usually erases all methylation and chromatin modifications. However, Jablonka and Lamb (1995) list up to 29 cases of transgenerational epigenetic inheritance in eukaryotes.

Sources of morphological variation and the developmental process

Morphological variation is the classic component of evolutionary theory, since it was shape of organs what stimulated interpretations in functional and mechanistic terms within theories of adaptation (Alberch, 1990). Evidence exists however, indicating non-genetically coded sources of increased or reduced morphological variation.

The analysis of morphological variation in an evolutionary context is comprised in the so-called "representation problem" (Wagner and Altenberg, 1996), addressing the genotype-phenotype map. This correspondence is brought about by the developmental process that links genetic and phenotypic complexity levels. The importance of organismal, internal mechanisms for evolutionary change was recognised early in biology (for reviews: Riedl, 1975; Gould, 1977). The complex architecture of the developmental process is the reason why a direct mapping of genes to morphology is often not possible, and the units of genetic evolution do not correspond directly to the units of morphological evolution.

Development is characterised by morphological integration, canalisation, dissociation and related processes (Müller and Wagner, 1991, 1996; Wagner, 1996; Wagner and Altenberg, 1996). By modifications of temporal and spatial order during development —heterochronic and heterotopic processes (Zelditch and Fink, 1996)–, these internal mechanisms may have non-genetic influence on variation. Such internal epigenetic conditions have been termed developmental or functional constraints (Maynard Smith et alii, 1985). They are directly involved in morphological evolution because they produce a bias on morphological variation and have been claimed to be involved in character formation, i.e. biologically homologous structures that «share a set of developmental constraints, and are caused by locally acting self-regulatory mechanism of organ differentiation» (Wagner, 1989a:62).

Typical examples for epigenetic morphogenesis of invariant structures are those of transdetermination. The alimentary canal in lampreys and newts develops from floor cells of the archenteron, while the alimentary canal in sharks derives from roof cells of the archenteron. Another example is the source of cells developing the lens of the eye, which in vertebrates are of ectoderm origin, whereas in amphibians derive from endoderm source cells. Many other such examples exist (Wagner, 1989a; Minelli, 1998; Laubichler, 2000).

However, examples exist also for non-genetically increase of morphological variation, when epigenetic mechanisms are involved in the generation of evolutionary novelties, specially in the connective tissue context, mechanical stress and pressure forces as consequences of changes in body proportions. This is also the case for the phylogenetic origin of the fibular crest in theropod dinosaurs and in birds (Müller and Wagner, 1991; 1996).

Role of complex processes and self-organisation in the genesis of variability

The leading role of genetics in heritable variation genesis has been challenged by the sciences of complexity. According to Goodwin (1994), morphology is caused as an emergent property of complex systems during the process known as morphogenesis without needing specific genetic orders. This means an alternative holistic view to genetics (rooted in Goethe's *Naturphilosophie*), represented by the concept of self-organisation (Maynard Smith, 2000). Self-organisation is a process in which the pattern at the global level of a system emerges solely from numerous interactions among lower-level components of the system. Moreover, the rules specifying interactions among the system's components are executed using only local information, without reference to the global pattern (Scott Camazine et alii, 2001). In its least extreme and restrictive form, it means a source of heritable phenotypes that can be added to the genetic variation and both of them integrated by development. Processes of self-organisation have been shown in many systems and morphogenetic processes, as the processes of reaction-diffusion that generate the concentric and spiral waves that characterise systems from cardiac muscle or brain tissue to population dynamics of insects (Vanag and Epstein, 2001). A really impressive example of these sort of processes comes from an unicellular alga, *Acetabularia*. This species has a complex morphology with differentiated structures such as the rhizoid, bractea, tallus, and umbrella. Experimental studies plus mathematical modelling of morphogenesis have proven that all this complex morphology and the processes of change that occurs during the development of this alga are not genetically regulated but are a consequence of self-organisation processes driven by slight differences of calcium concentration in the medium and between it and the cytoplasm (Goodwin, 1997).

The pattern of evolution: Gradualism

Darwin's "population thinking" of nature led him to consider the changes of species as gradual. Individuals having less fitted phenotypes are removed from the population while those with fitter phenotypes multiply themselves increasing thereby the adaptation of the whole population. Thus, change happens in a gradual and continuous way, being faster when selective pressures are high and more slowly whenever they are low. Joined with the theory of gradual change in species was the theory of a gradual change in the characters or organs, although this topic brought Darwin some of his worst problems. Neodarwinian Synthesis considered gradual change of characters as one of the basis of evolution while saltationist changes were assumed to be almost irrelevant (Mayr, 2001). However, a certain degree of polymorphism, with discrete characters, should be assumed as it is generally observed in nature (for example in the blood group) and it is clearly relevant for evolution. Thus, what should be considered an abrupt saltationist change? Given that the very base of gradualism is that there cannot be saltationist changes leading to an abrupt formation of a new species, the upper limit for the changes should be set, in sexually reproducing species, by the capacity of the new phenotype to reproduce with the rest of individuals of the population, thus keeping the concept of gradual evolution in the temporal change of the populations.

Punctuated equilibrium

Gradual and continuous change of species along time has been challenged by most prominent palaeontologists since the very first versions of evolutionary theories in the 18th century. However, after the Modern Synthesis and the works of Simpson (Simpson, 1944, 1949), disagreements between the fossil record and the Neodarwinian gradualism were neglected or attributed to biases of the fossil record. In 1972, Eldredge and Gould, published an alternative way to interpret the fossil record in which it was neither so biased or so gradual. As a central proposition, Punctuated Equilibrium holds that the great majority of species originated in geological moments (punctuation) and they persist in stasis throughout their long duration (Gould 2002: 766). Later analyses demonstrated that Punctuated Equilibrium is fairly common in the fossil record, if not the dominant pattern. Although usually considered an alternative theory, Punctuated Equilibrium (Eldredge and Gould, 1972) is actually only a minor modification of the paradigm, as the authors themselves recognised (Gould and Eldredge, 1993) as it do not imply abrupt change, but only that the rate of change is not constant. Speciation occurs during geologically short time periods, though "geologically short" means thousands of generations and thus, change is gradual along these periods. However, Punctuated Equilibrium has several consequences at taxonomic levels higher than population, that may imply evolutionary processes that differ from the Neodarwinian paradigm, i.e. macroevolutionary processes (Gould, 2002).

One of such processes is included in the term "Co-ordinated Stasis", coined by Brett and Baird (1992) to describe their observation that during the Palaeozoic several species remained virtually invariant morphologically through long time periods (from 3 to 7 million years long). These periods were punctuated by sudden and drastic changes that affected all lineages simultaneously. The key difference between co-ordinated stasis and punctuated equilibrium is that the former implies that the periods of stasis involve invariance in properties of the community (diversity, richness, etc...), not just in the morphology of the individual species, even though environmental disturbance occurs during the period of stasis. Brett et alii (1996) defined blocks of co-ordinated stasis «as intervals, generally exceeding one million years in duration, during which 60% or more of species-level lineages persist from older to younger samples of appropriate biofacies, with only minor and typically non-directional evolutionary changes». Although initially described for Palaeozoic marine assemblages, this pattern has been recognised in terrestrial ecosystems too (Prothero and Heaton, 1996; Morris, 1996; DiMichele and Phillips, 1996).

Complex systems and spatio-temporal patterns

As is discussed here, and will be discussed later (see heading "mechanisms driving evolution" and Concluding Remarks), the joint action of a bunch of small-scale ecological, populational and stochastic processes may be driving evolution at least as intensively as large-scale ones. Hewzulla et alii (1999) studied the general patterns of extinctions and speciation events from the record available for the last 600 Myr. for terrestrial and marine systems. In both cases, they found a general trend, which explained the main patterns of differentiation and extinction through time, but with some apparently stochastic error components (that is, function residuals). When they explored those errors, they found a fractal structure in the deviations from the general trend for marine systems. Fractals are the outcome of complex systems, where a huge amount of stochastic processes gives rise to some kind of ordered general patterns (see below for a discussion of the chaos theory and the role of complexity and self-organization in nature). Thus, their results indicate a strong self-organizing behaviour of the deviations from the general trend. On the contrary, they found self-organizing patterns only in the residuals of a few localised events in terrestrial systems where the general trend was more stationary. This result is logical if we take into account that all oceans are interconnected in contrast to terrestrial areas, where isolation may have produced spatial patchiness in the self-organization which thus do not act as a unique system.

It is clear that some laws of complexity are operating on evolution, and, as we will discuss later, the Earth is an extremely complex system. The typical chaotic behaviour of these systems implies the development of complexity (or stochasticity), both in time and space, leading to restructuring order in some areas. This may be one of the explanations (but not the unique) for the non-continuity of the spatio-temporal patterns in evolutionary rates that produce saltationism in the development of the Tree of Life.

Evo-devo and rhythms

In morphological sciences gradualism and saltationism have been recognised as typogenesis, orthogenesis, typostasis, and Cartesian Transformation, which the Synthetic Theory explains by adaptive radiation and ortho-selection concepts. But the directionality is difficult to explain in probabilistic terms facing the changing nature of the environment and by simple external mechanisms of random genetic change and Natural Selection. Thus, an alternative systems-theoretic perspective has been offered considering the evolutionary developmental perspective (Riedl, 1975, 1977), which includes internal mechanisms of growth and development in order to complete the externally given conditions of evolution.

In such a perspective the notion of developmental and functional constraints becomes again important. They are defined as a bias of variation, related to functional or developmental reasons (Maynard Smith et alii, 1985), which would maintain certain morphological directionality in evolutionary situations in which external conditions might have changed. The basic body-plans of aquatic mammals (lungs in cetaceans) or flying mammals (no feathers in bats) are indications of internal developmental necessities for maintaining the internal structural

organization despite dramatic external environmental modifications. Whereas such examples serve as demonstration for low evolutionary rhythm, others exist for high velocity of change. The biological background of these examples is related to the complex of developmental integration (Olson and Miller, 1958; Riedl, 1975, 1977; Zelditch et alii, 1993; Cheverud, 1996; Zelditch, 1996). Body elements that form late in ontogeny, at the end of causal sequences, are hypothesised to be less integrated, less constrained and more free to vary. Characters like horns (in bovids), digits (examples like *Eohippus*, *Hipparion* and modern horses), or carpals are less constrained and show higher velocities of evolutionary change (e.g. Buscalioni et alii, 1997).

Mechanisms driving evolution

In Darwin's proposal, Natural Selection was the main motor of change; it was the force that shaped the species. Neodarwinian Synthesis has added –with the advance of time and knowledge– several other causes in shaping the genetic change in populations and thus in shaping species evolution. According to the Hardy-Weinberg equation, each population of randomly reproducing individuals would keep its gene pool constant from generation to generation in the absence of a number of processes that may lead to the loss of existing genes or to the acquisition of new ones. These processes are responsible for evolution (Mayr, 2001) and can be divided in stochastic and deterministic ones. The first ones would include all mechanism leading to changes in the population without any *a priori* advantage for the individuals while the second ones suppose changes towards more "adapted" organisms. Natural Selection, as will be commented below, can be considered the only process leading to more adapted organisms. According to Mayr (2001) evolutionary processes include:

Mutation has been previously discussed under the section "Sources of variation". It means a change in the population by adding new heritable variation.

Natural Selection means the differential probability of contribution of the phenotypes (and thus of the genotypes) to the next generation. Natural Selection, of course, acts over the present variation as a process of sorting or elimination. According to the paradigm, it is the only mechanism of adaptive evolution. Natural Selection allows organisms to adapt to its environment by selection of adapted traits (Blakeslee, 2001). A further point to stress (also applicable to sexual selection) is that only individuals and more precisely phenotypes are selected; although Natural Selection has been equalised to genotype selection, it is not the real case.

Gene content and thus the available variability of each local population, except in the most isolated ones, is strongly affected by *gene flow*, i.e. the immigration and emigration of individuals (and their genes) to and from other populations of the species. This is a conservative factor that prevents the

divergence of partially isolated populations and it is a major reason for the stability of widespread species and for the stasis of populous species (Mayr, 2001).

Genetic drift is a process of random lost of variability through errors of sampling mainly in small populations (see Suzuki et alii, 1989 for a detailed description of this mechanism and its evolutionary importance). This process is usually compensated by gene flow but becomes of capital importance in small founder populations.

Biased variation has been cited as a rather uncommon process (Mayr, 2001) that implies genes that affect the segregation of alleles during meiosis in a heterozygote, such that the allele of one parental chromosome goes to the gametes in more than fifty percent. Although such process does not seem to be very extended it can produce the retention of less fitted variations if they are positively biased.

Non-random mating or *Sexual Selection* has been claimed as a very important factor in sexual reproducing species. In such species there may be a preference by one of the sexual partners for a particular phenotype of its mates. This leads to a non-random favouring of certain genotypes.

Integration and self-organization of ecological mechanism driving evolution

Microevolutionary events occur continuously due to the relationships among species and environment. Thus, ecological problems, such as density dependence and metapopulation structure, should be taken into account explicitly, or at least not ignored, in any Evolutionary Theory (Kozlowski, 1999). Although sparse and still preliminary, recent studies on diverse taxa suggest that Natural Selection caused by ecological shifts or invasions of novel habitats plays an important role in adaptive divergence and speciation (Orr and Smith, 1998). The phylogenetic information hosted by a species plays a major role in its ecological responses (relationship with environment, competitive traits, etc.), being determinant in the assembly of communities (Tofts and Silvertown, 2000), both from local species pool, and from migrants from nearby sites. When a given species becomes successful in a given place, it produces exceeding offsprings, which migrate in a density-dependent regulatory mechanism, so the world is flooded with migrants of different species (Kozlowski, 1999). Successful colonisers follow microevolutionary changes, which spread again if new migrants, slightly different from the first ones, are produced after the new population is well established. This mixture of dispersal and local microevolutionary processes is one of the causes of biodiversity, assuring the immense, permanent variability of nature, and regulating genetic and ecological structure of populations via permanent gene flow in heterogeneous landscapes (Kozlowski, 1999).

In this framework, dispersal arises as an important source of genetic variation (Orr and Smith, 1998; Dieckmann and Doebeli, 1999; Ferriere et alii, 2000), modifying the pattern

produced by Natural Selection and other processes (see above) in two ways:

i) It produces relative, or even complete, isolation among populations. Allopatry and sympatry are points along a gene flow continuum, which might or might not have an easily identifiable geographic component (Markert et alii, 2001). Although vicariance may be the dominant mode of evolution through space at broad scales, dispersal also plays a significant role in differentiation processes (Zink et alii, 2000), producing different rates of gene flow and, thus, differentiation, among the populations over all the species range (e.g. Iberian salamanders; García-París et alii, 2003).

ii) Migrants arriving at new habitats are pressed to get adapted quickly to the new ecological conditions, or fail in colonising those sites. Diverse studies suggest that the invasion success of many species might depend more heavily on their ability to respond to Natural Selection than on being eurioic (Lee, 2002).

As we have seen, many different processes are effecting evolution at small spatial and temporal scales. First, environmental variation, responsible for Natural Selection, translates into biological processes in a complex, non linear way. Second, other processes, such as mutation rates, Sexual Selection, genetic drift and biased variation, also effect evolutionary *tempo* and *modo*. Third, effects of dispersal modify the spatial patterns of these trends and rates. All these factors are integrated as a complex system, driven by deterministic chaos (see below). A good example of a complex system, in which a high amount of local, small evolutionary events, produces a noisy structure, from which a general pattern arises in space, is provided in Sokal et alii (1986). They found spatial structure in allele frequencies of Yanomama Indians, with a strong decline in overall genetic similarity with geographic distance. However, they found the effect of stochastic and social factors in determining village allele frequencies to be higher, and the occurrence within this tribe of some allele frequency clines most likely due to the operation of chance historical processes, which necessarily present a geographic structure.

The impact of most local processes of natural selection in evolutionary trends and ratios may appear unimportant to the development of macroevolutionary patterns. However, in a complex world, driven by deterministic chaos' laws, when a great amount of single phenomena are aggregated, small-scale stochasticity results in regular and clearly distinguishable patterns in many evolutionary processes (e.g. extinctions; Higgins et alii, 2000). Patterns of biological evolution are driven by its own internal dynamics as well as responding to upsets from external causes (Hewzulla et alii, 1999). So, inferring Evolutionary Theory only from the small-scale processes admitted by the Neodarwinian Synthesis seems insufficient at the present, as the self-organization of these processes by the effect of complexity is also important.

Internalism, complexity, and strenght of Natural Selection

The importance of Natural Selection in the system-theoretic approach is that it forms (the external) part of an self-organizing evolving system and participates in shaping the developmental process. By probabilistic argumentation it was suggested that Natural Selection, in presence of internal hierarchical genetic, epigenetic and developmental architecture, leads to an internal (organismal) copy of the external environment (Riedl, 1975, 1977; Wagner, 1989b; Laubichler, 2000). Along feedback-loops, Natural Selection and the developmental architecture lead –in common and interrelated– to the correspondence of the organism and its place in Nature.

Natural Selection is therefore a necessary but not sufficient argument in explaining evolutionary change. The probability of reasonable changes in morphology is increased by an imitatory epigenotype (Riedl, 1977). The importance of the role of Natural Selection as motor of evolution is decreasing as life evolves thereby increasing internal complexity. «Not entelechy, but post-stabilised harmony and internal lawfulness» (Riedl, 1977: 354) are characteristics of the system-theoretic approach to biological evolution leading to the order of living organisms. Is then Natural Selection the motor of evolution? The answer would be yes, but mainly at early phases of biological evolution or whenever internal organismal integration is low.

At a higher level, mechanisms of the developmental process have important implications for macro-evolutionary events. According to the Systems Theory of Evolution (Riedl, 1977), developmental constraints are considered "burden" and have a macro-evolutionary probabilistic notion. A highly–burdened structure (i.e. highly constrained) is integrated into biological functions at a very basal organismal level. This may be an early developmental stage of vital inductive importance for subsequent epigenetic developmental stages or a specific role within a chain of vital functions. According to the Systems Theory of Evolution, for an organ to be evolutionarily changed this burden must be low. Highly burdened characters are unlikely to be evolutionarily modified, because of their low (close to zero) probability to survive the mutational change. By this mechanism of subsequent developmental integration, the organism "copies" the functional nature of its environment and "becomes adapted" by Natural Selection. In that reasoning the evolutionary unit consists of morphologically integrated ("burdened") structures, which become most easily modified at the end of functional causal and developmental chains (Riedl, 1975). Developmental or functional constraints *sensu* Maynard Smith et alii (1985) are modelled as a bias on variation at a micro-evolutionary scale, which is a metric perspective of developmental burden, and grounded on similar biological reasons. The hierarchical structure of developmental constraints is the hypothetical biological reason why ontogeny copies to some degree phylogeny. The sum of developmental constraints is the biological substrate of the controversial nature of "Baupläne" (Riedl, 1975).

In development the evolutionary unit is the "biological homology" (Wagner, 1989a). It characterises large-scale biological organization and sheds light on the self-regulatory, epigenetic nature and biology of the developmental process and the evolution of life as a self-organizing system.

A new hypothesis: Intracellular Natural Selection
An interesting hypothesis has been proposed by Cedano (2002) to describe how a cell may be able to produce rapid changes in its own genome, in order to obtain direct evolutionary improvements. In the same way that a 'debugger', a computer program designed to identify and correct bugs (failures) in the source code of other program, is able to repair and create new code lines, Cedano (2002) lists many cellular mechanisms able to carry out a similar task within the genome. These mechanisms include the ability of identifying defects in the produced proteins, develop improvements to adjust their tertiary and quaternary structures to the required substrate or action, translate these improvements into a nucleic acid (either DNA or RNA) sequence, and include it in the nuclear genome. Although promising, there is no evidence to support this hypothesis, except that all the mechanisms necessary for its work are available in the cells.

Speciation
The population thinking also bases the way new species are formed. The paradigm considers that allopatry is the main process in forming new species. This model proposes that isolation of previously joined populations leads to independent evolution of the two subpopulations and eventually become separated species. The same process extended through geological times will be responsible for the formation of upper clades, i.e. genera, families, etc. Other processes as sympatric speciation are also accepted by Neodarwinian paradigm, which according to Mayr (2001) may be mainly caused by Sexual Selection splitting subpopulations of a, in other respect, continuous population.

Validity of the species concept
Nowadays, it is clear for most biologists that the species concept is only a useful simplification of the biodiversity phenomenon. It is obvious that species do exist, at least in Eukaryota, but it is also obvious that they are not discrete units that are only interfertile within themselves. There are many examples of valid, full-functioning, individuals born from parents of two different species. The easiness of hybridise plants from a lot of groups is widely known by gardeners. Trees from the Salicaceae family, such as willows (*Salix spp.*) or poplars (*Populus spp.*) are usually hybrids in natural conditions. The evolutionary and biogeographic importance of this kind of hybridisation is illustrated by the example of Western Mediterranean oaks (*Quercus spp.*): the genome of cork oaks (*Q. suber*) uses holm oak (*Q. rotundifolia*) stems to disperse, by

a hybridisation process where cork oaks pollen fertilises holm oaks flowers, producing hybrids with the cork oak phenotype (Belahbib *et alii*, 2001).

In insects, this kind of reproductive behaviour seems also to be common in many genera. A great amount of particular cases has been reported, for example, in butterflies and coleopterans. For example, three taxonomically accepted species of Mediterranean dung beetles, *Onthophagus similis*, *O. opacicollis* and *O. fracticornis*, morphologically very similar, and with partially overlapping niches and distributions, were studied by Martín-Piera and Boto (1999) to determine if their separation as species was correct. The general phylogeographic patterns supported the preliminary morphological hypothesis of the three were correctly distinguished species, but, frequently, single populations of one of them were found to be closer to populations of other species than populations its own species. Although several morphological diagnostic characters may separate them easily in sites where only one of the species is present, many intermediate individuals, difficult to ascribe to one of them, appear in places where two or the three species are present. Many insect species present key-lock systems to avoid fertilisation from individuals of other species, that is, the male genitalia are morphologically coincident with the female reproductive system, and make fecundation from other species difficult. However, at least in dung beetles (but probably in a lot of groups), most parts of the genitalia are soft, allowing females to be fecundated by males from closely related species with slightly different edeagus (male ejective sexual organ). There are also examples of viable vertebrate individuals born from parents of different species of the same genus (e.g. lions, *Panthera leo*, and tigers, *P. tigrisi* have hybridize in captivity).

There are two main approaches to the species concept; taxonomic (both morphological and genetic-based; an operative simplification of the genetic continuum of nature), and biological (a closed inter-fertile unit; theoretical approach). They are uncoupled, as gene flow is admitted to exist between different taxonomic species, but not between biological ones. In the light of the "anomalous evidences" discussed, that are not a exception in nature but even the rule in several groups, the theoretical model have been considered to be misleading by some authors (in Mayr, 2001), arguing that, like many other phenomena, the species can be view as part of a continuum rather than discrete entities.

Infectious speciation: the case of *Wolbachia*
A new mechanism for reproductive isolation and thus to formation of new species is related to bacterial infections. *Wolbachia* is a cytoplasmatic-inherited bacterium that causes reproductive alterations in many groups of metazoans including insects, nematodes or spiders. A recent estimate ranges from 15 to 20 percent of the living species of insects that are infected by these bacteria (Bordenstein *et alii*, 2001). Another study using butterflies (Jiggins *et alii*, 2001) states that this

figure of around 17% may be an underestimation. After an intensive examination of a large amount of individuals from several species of the *Acraea* genus, they found two kinds of infections: low- and high-prevalence ones. Whilst the latter is easy to detect, the former infections may have gone unnoticed in previous estimations. These authors conclude that sex-ratio-distorting *Wolbachia* (see next paragraph) may be common in insects that have an ecology and/or genetics that permit the invasion of these parasites.

Reproductive isolation caused by *Wolbachia* has been recently studied in two species of parasite wasps from genus *Nasonia* (*N. giraulti* and *N. longicornis*) (Bordenstein *et alii*, 2001). These are two closely related species (estimated time of divergence of 0,25 Ma) isolated by the *Wolbachia* infection, as shown by the fact that reproductive isolation disappears when wasps are treated with antibodies that eliminate *Wolbachia* infection. This is a new kind of barrier that acts in a sharp, non-gradualistic way, that leads to the isolation of subpopulations that could diverge afterwards.

Fast-speciating sympatric cichlids
Cichlids are a highly speciose world-wide-distributed group of fishes, proposed as a good empirical model to test theoretical approaches to speciation due to its rapid evolutionary rate. They share most aspects of their basic "Baupläne" but present a high diversity of ecological adaptations and reproductive strategies (see Markert *et alii*, 2001). In many East African lakes, hundreds of different endemic species have evolved since Pleistocene, ranging from nearly one to a few tens per lake, and even hundreds, such as in lake Tanganika and in lake Victoria. The figures for the latter are impressive, as more than 500 species have been listed at present, with a dramatically high speciation rate (Verheyen *et alii*, 2003). So, why are there so many cichlid species in a single lake?

In a review article, Galis and Metz (1998) stated that those species may have evolved in sympatry due to the joint action of two main factors: a high plasticity of their feeding apparatus, permitting the exploitation of distinct trophic niches, and also rapidly evolving mate recognition systems. New theoretical approaches suggest that this kind of reproductive isolation might evolve in sympatry when a genetic correlation develops between components of the mating recognition systems and competitive adaptive traits (Kondrashov and Kondrashov, 1999; Dieckmann and Doebeli, 1999). Although this view of the speciation system does not contradict classic Modern Synthesis Evolutionary Theory, the timing of these differentiations is much too high (with new species arising in only a few decades) to correspond to the gradualistic view of genetic changes (see above). This rate is modified by the joint effect of different traits. Recent studies claim also for the influence of historic factors, such as the survival of individuals that may have generated different lineages during the last desiccation of the lake (between 15,600 and 14,700 years ago), and of evolutionary

mechanisms such as atavisms and the use of ancestral genetic programs retained in the genome (Galis and Metz, 1998; Verheyen *et alii*, 2003). This example points out that is more practical (and realistic) to consider allopatry and sympatry as points along a gene flow continuum, with or without a geographic component (Markert *et alii*, 2001; see below). The use of the new phylogeographic methods available nowadays will result in a better comprehension of speciation processes, so many new evidences on this issue are likely going to be at sight in the next years due to the investigation in this group.

Spatial and ecological components of speciation
Geographic variation supplies one answer to the problem of speciation, as first claimed by Wagner (1868); most species present populations, placed in different sites, that differ from each other sufficiently to be called races or subspecies, and eventually species (Mayr, 1999). As previously discussed (see section "Integration and self-organization of ecological mechanisms driving evolution"), microevolution, and thus speciation, has a strong spatial component. Even when isolation of populations is not complete, genetic divergences are able to separate new taxa (e.g. García-París *et alii*, 2003). This evidence is not strictly outside the Modern Synthesis paradigm, but nearly half a century of development of ecology and biogeography, including the appearance of molecular ecology and phylogeography, has provided new data that may contradict the view of speciation as a strictly adaptationist process.

There are ecological higher-level self-organised processes, different from the adaptation to the environment, and spatially-mediated effects, different from total or partial isolation, that influence speciation (and thus evolutionary) rates. For example, in the new Unified Theory of Biodiversity and Biogeography (Hubbell, 1997, 1999, 2001; see discussion on gaia below), speciation rates are independent from niche structure (where natural selection and adaptation is effecting), relying on the structuring of dispersal and population-density effects. As seen before, microevolutionary processes occur where invasions takes place successfully after surpassing the filter provided by these effects.

Another interesting process may occur at range margins of a species distribution. These margins are usually located in zones with high species replacement (b-diversity), and thus high numbers of species, such as environmental gradients, that constitute the edge for most species. Environmental stress suffered by individuals living at the edge of their previous adaptations may produce high retro-transposon activity (Sentís, 2002), and favour symbiotic interactions, so evolutionary changes through lateral gene transmission and symbiosis may also be higher in range margin and threatened areas; rapid changes, and information sharing, may occur at those places, which can act as centres of evolutionary experimentation, with high speciation ratios and a significant role in evolutionary radiations. In this context, it is important to include biodiversity,

the final product of evolution, into the Evolutionary Theory. Evolution works with used bricks, and biodiversity may be an evolutionary response to change (or, at least, an important part of nature's resiliency against disturbance), a living ware-house where many different used bricks are stored. The above-described areas may act as architecture studios, where new and innovative buildings are designed, starting from the structures of the former ones, and using old, well-tested, and new-design bricks.

Global problems of the paradigm and others
In the previous pages we have pay attention to facts and theories that do not seem to fulfil the assumptions of the Neodarwinian paradigm. These ideas and data show the limits of what has been considered the valid how and why of evolutionary process. However, there are other theories, ideas that cannot be rooted within the paradigm but that imply new bases and concepts. Some of these theories are commented in the following paragraphs.

Unit of evolution
Since the first scientific theories of evolution (see Table 1), two constants aspects have been always recurrent in its definitions: change of traits and transmission of those changes, as a consequence of an ancestral-descendant dependence. Different theories have tackled those characteristics of evolution from different points of view (individuals, species), but the more suitable suggestion from Darwin and afterwards from Neodarwinism is the linking between individuals and species through the concept of populations, that is to say, the "population thinking" (Mayr, 2001). Therefore, individuals, populations and species have been since then considered the three principal units of evolution. Nevertheless, this consideration must be taken only as a functional one. On the other hand, living matter is structured in interconnected, overlapped hierarchical levels of organization, and evolution is expressed in all them, from molecules to organisms, through genes, cells, tissues, organs, etc. (Solbrig, 1991). Therefore, concerning structure, it could be also possible to speak about several units of evolution in agreement with those hierarchical levels of organization.

So, distinction between functional and structural evolution units should be taken into account, according to the consideration of evolutionary processes or patterns, respectively (Martín-Piera, 1997).

Nevertheless, with the arrival of the new theories of chaos and nature complexity, the concept of units of evolution has started to be dealt with a reductionist one, being the product of the restricted human point of view about nature (Waldrop, 1994). Indeed, the various units, be these functional or structural, intermingle each other and the limits among them are not really disconnected. Although in practice, a categorisation

in units is necessary, the notion of evolution as an integrated continuous whole should be always kept in mind.

As evolution occurs at genetic, developmental and morphological complexity levels it can be resumed that the significance of any observation in nature depends on the scale of investigation. Genetic units have different properties than developmental units, and developmental units of evolution differ from morphological units, and so on. Each of the associated reference processes may lead to different compositional units and they may enter in different ways into mechanistic explanations (von Dassow and Munro, 1999).

Evolutionary aspects of the genotype-phenotype relationship
Darwinian theory is based on variation, actually on a continuous and abundant source of variation. Since the introduction of the Synthesis, this source has been mutation, changes in the genotype that are expressed in the phenotype. However, this assumption has been challenged by many authors, who have looked for the origin of form in other areas, joined under the term epigenetics (see for example, Goodwin, 1994; Gould, 1977, 2002). In a recent paper, Newman and Müller (2000) propose a new framework for the origination of morphological characters by means of epigenetic mechanisms and their co-optation by the genome. According to this theory, the close mapping between genotype and phenotype is a highly derived condition, a product of evolution rather than its precondition. Prior to the genetic canalisation of the phenotypes and their subsequent stabilisation, the environment dictated a many-to-many mapping between genes and forms. Forms were the result of epigenetic mechanisms, first physical processes characteristic of condensed, chemically active materials and later conditional, inductive interactions among the organism's tissues (Newman and Müller, 2000). According to the authors, this concept helps to understand findings as the Cambrian explosion, the origins of morphological innovations, homology or the rapid change of form. In fact, this framework, although not mentioned by their authors, supposes a complete new vision of evolution since the gradual, population based, genetic Neodarwinian paradigm is changed and could include saltationist events, not based on genetic changes and leading to processes not restricted within populations.

Complex ecological systems, self-organization and evolution
Complex systems, and chaotic dynamics, constitute a new paradigm in the study of the entire nature (Gleick, 1988). Briefly, theory of complexity tells us that nature is built from a huge amount of small interactions, occurring and effecting over a multitude of scales. However, many distinguishable patterns and structures arise from this chaotic complexity (see Shinbrot and Muzzio, 2001); that is, order coming from chaos. This self-organization is intrinsic to chaotic dynamics, which probably constitutes the most important property of nature.

Understanding how small ecological processes with evolutionary effect translate into the patterns of evolution present in biodiversity seems crucial for an updated evolutionary theory. However, the ecological theory necessary for this task is difficult to build up from the empirical studies ecologists have carried out for more than half a century (Ghilarov, 2001). As there are too much contingencies and too much factors may be interacting at the same time, only a few patterns, which appear at broad spatial and temporal scales, can be taken as general (Lawton, 1999). It is becoming increasingly accepted that nature is structured as a complex system, a product of a huge number of effects with a fractal-structured outcome (Brown et alii, 2002) where only a few "windows of order" appear in which complexity can be adequately be described.

New theoretical advances support this view of nature. For example, the theories of Island Biogeography and of relative species abundance have been recently joined together in the Unified Theory of Biogeography and Biodiversity (Hubbell, 1997, 1999, 2001), by incorporating speciation rates into the classic MacArthur and Wilson theory (1963, 1967). Surprisingly, this unification has pointed out the existence of a fundamental biodiversity number, q, different for each community or site, but constant within at small time-scales. That controls not only species richness, but also relative species abundance in source communities and the rate and strength of speciation events (Hubbell, 1997, 2001). It seems that the final product of speciation, that is, local species richness, is controlled by a kind of "thermostat" that limits the number of immigrant species that are able to establish in a given site and, where this number is small, promotes speciation events: This is a clear case of ecologically-driven evolution, different from the adaptationist paradigm. Most of the detail about niche structure is lost or becomes ineffective at controlling community structure on large spatial and temporal scales (Hubbell, 1997). In such circumstances the complex structure of the assemblages and their relationship with environment gives rise to a few general patters that can be explained by large-scale studies. This fact diminishes the relative importance of most evolutionary ecology processes, as adaptation to the environment is a minor component compared with the complex stochastic processes.

If we look at the whole living nature, with millions and millions of individuals of several millions of species, which interact all around the Biosphere through time, it becomes clear that evolution may be by far more than just a few characters that are chosen and/or fixed by Natural Selection. The Biosphere is plenty of interacting complex systems, nested in several levels of organization into a enormous integrated chaotic system. Since complex systems are highly dependent of initial conditions, little variations in the starting point lead to highly different results. In this framework, Natural Selection does not act as a active selector, but as a passive filter for evolutionary innovations; ecological conditions vary highly across space and time, so in a given ecosystem and moment, the few pheno-

/genotypes that can survive (that is, comply with Natural Selection requirements) depend on these variations. From these, the fittest, or better, may or may not be the ones producing the highest number of descendants. In a continuously changing world, a high amount of contingent factors (stochastic or not) are effecting survival rates, self-organizing the outcome of the processes included in the Modern Synthesis Theory.

Combined and integrated evolution of Gaia
In the last thirty years, the idea of Earth as a self-functioning superorganism has been formulated and popularised. This theory was proposed by James Lovelock with the name of "Gaia", after the Greek mother-Earth goddess. According to Lovelock (1988), «the evolution of organisms and their material environment proceeds as a single coupled process». Therefore, one of the more important contributions of this hypothesis is the idea that inorganical and organical worlds are inseparable. So, evolution concerns Gaia, not the organisms or the environment taken separately (Lovelock, 1988). Moreover, since the origin of life, Earth has acted as a self regulating living system maintaining the conditions (temperature, oxidation state, etc.) suitable for its biota (Lovelock, 1979). On one hand, this fact has lead to the affirmation that the history of Gaia «has more to do with co-operation than competition, with integration of organisms and environment rather than struggle and competition» (Bunyard, 1996). On the other hand, this fact also supposes that every matter level is sequentially interconnected with other levels, and therefore there is a continuity of matter, each continuous level contributing with new emergent properties.

Concluding remarks
First of all, we would like to state that the present paper and the different aspects included in it do not intend to necessarily contain the views of all researchers in biology. As it has become evident, there are so many views and proposed mechanisms pretending to be exhaustive. But, having established this point, we feel the necessity to remark that one aspect admits not questioning whatever: what we have called the fact of evolution occurs and it explains the plethora of species we see today. All previous pages refer to how and why evolution occurs, no doubt it occurs. «So enormous, ramifying, and consistent has the evidence for evolution become that if anyone could now disprove it, I should have my conception of the orderliness of the universe so shaken as to lead me to doubt even my own existence. If you like, then, I will grant you that in an absolute sense evolution is not a fact, or rather, that is no more a fact than that you are hearing or reading these words» (Muller, 1959).

As the well known sentence by Dobzhanski establishes «nothing in Biology makes sense except in the light of evolution» (Dobzhanski, 1973). This makes Evolution the most powerful

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TABLE 2. Main issues that have to be included in Evolutionary Theory. Several examples from the text are cited, and the extension at which they may be operating is listed under Amplitude. The last column indicates how they fit into the Neodarwinian paradigm.

Theories and Observed Phenomena	Example	Amplitude	Relationship to paradigm
Sources of variation			
Non-genetic heritable variation			
Cell structure	Well known in cilliates.		Major addition
Genome organization		Presumably afecting all organisms at some extent	Minor addition
Horizontal transfer	Human placenta, etc... Well known in bacteria		
Inheritance of acquired characters	V. g. Linaria	At least plants, fungi and Unicellular organisms	Do not fit
Enviromentally driven mutations	Well known in bacteria	All groups?	Do not fit
Selforganization	Acetabularia	All groups to some extent?	Major addition
Canalization and developmental constraints		All organisms	Minor addition
Symbiosis	Origin of eukaryotes	Presumably affecting	Do not fit
Patterns of evolution: gradualism			
Punctuated equilibrium		All groups	Minor modification
Complex systems and spatio-temporal patterns		All organisms	Do not fit
Evodevo and rithms			Major modification
Mechanisms driving evolution			
Integration and self-organization of ecological mechanisms			Do not fit
Internalism, mechanism of development		All organisms	Do not fit
Intracellular Natural Selection	Not tested		Do not fit
Speciation			
Infectious speciation:	Wolbachia Proved in arthropods		Do not fit
Fast-speciation	Sympatric cichlids	Probably all groups	Minor modification
Spatial and ecological components of speciation		All organisms	

and integrative concept of Biology, a concept around which all fields of biology may interact and communicate. But, at the same time, it supposes a great risk for the concept of evolution itself, since the different fields within Biology may view evolution in rather different ways, not always compatible. The large development of all fields of Biology since the Evolutionary Synthesis in the late 30ies and 40ies of the past century has outgrown this last unified and almost fully accepted vision of how and why change in living forms happens. Evolutionary Synthesis was build up to explain the process of evolution as a whole. Since its enunciation, several new mechanism have been discovered and many of them have been incorporated into the Neodarwinian paradigm. However, other discoveries have been left apart, sometimes because they did not fit into the framework of Neodarwinian paradigm or because they were considered only small contribution, or they affecting a very small number of forms. And now, at the beginning of the 3rd millennium, all these leftovers are reclaiming a place within the Evolutionary theories.

In a conference opening plenary, Doolittle (2000) claimed that «the concept of genomic lineages may be inappropriate for understanding cellular evolution, although it is not clear what will replace it». The extensive lateral gene transfer in the basis of the tree of life is leading modern biology to rethink the relationship between lineages of genes, lineages of organisms and prokaryotic taxonomy (Doolittle, 2000).

We have represented in Table 2 the main facts and theoretical advances that must be included in any modern evolutionary theory, and also in what extent they fit into the Modern Synthesis paradigm. Therefore, regarding sources of variation, it is possible to assume by the Neodarwinian paradigm that some sources other apart from changes in the genotype are possible, as those of cell structure or genome organization. Also, self-organization, canalisation and developmental mechanisms could be integrated in the paradigm with little effort. However, there are other proven phenomena able to produce variation that are difficult to
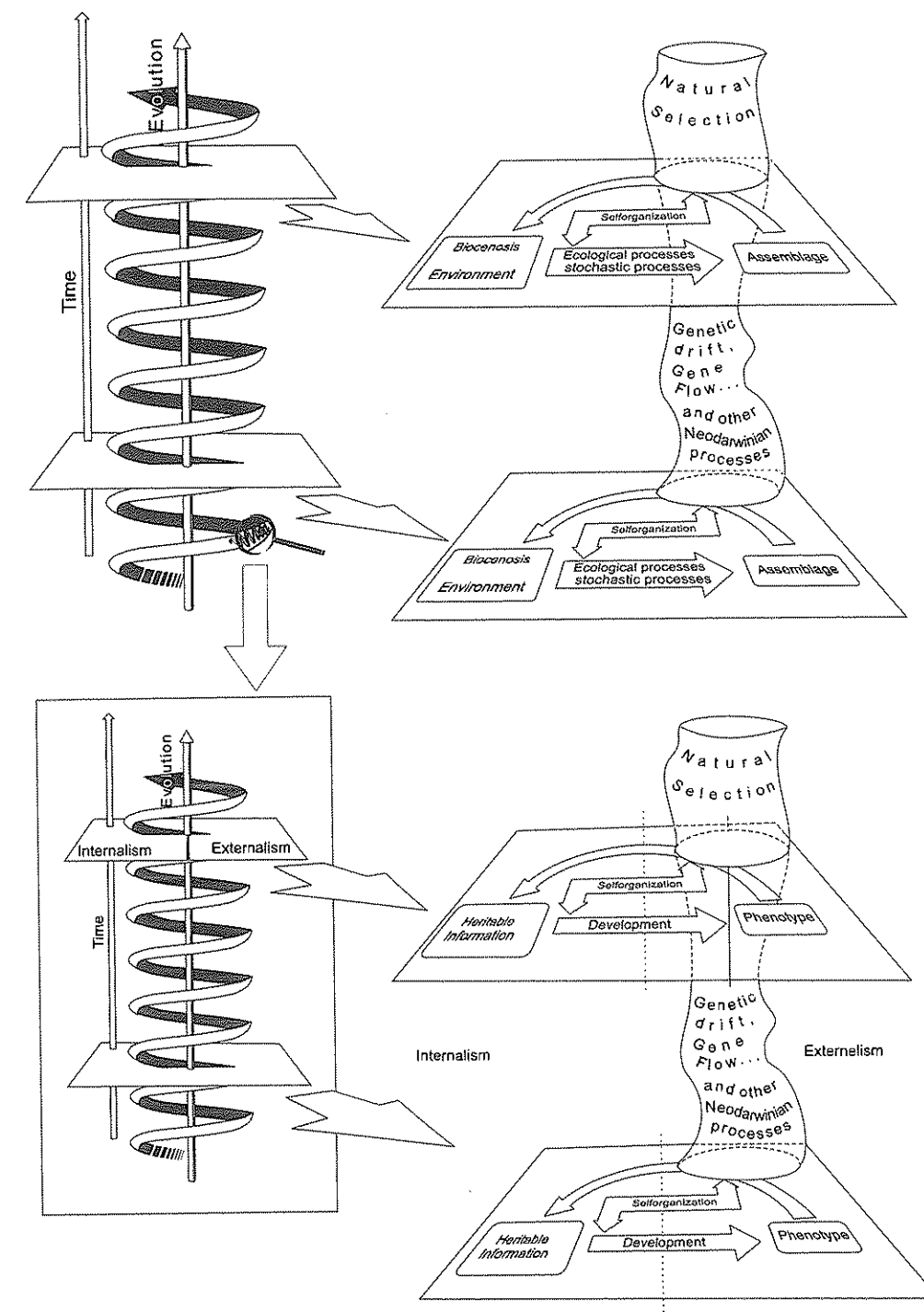

Fig. 1. The Evolutionary Metahelix: Evolution as an integrated process. The present figure shows evolution as a temporal helix, in which all different levels are integrated although at different scales. The upper part represents an ecosystem scale in which living forms (comprised in the term biocenosis) and environmental conditions interact by means of ecological and stochastic processes. Such interactions result in complex systems leading to self-organization, forming assemblages which at the same time are integrated in a complex system of environmental, historical and biogeographical factors. Altogether, these factors lead to changes in the components of the system (biocenosis and environment). The Evolutionary Metahelix is composed of multiples helices that correspond to the evolution of the different living beings. At this lower scale, organisms evolve through time from variations in their heritable information (including non-genetic information) that are self-organised and also regulated and integrated by development (lower right part of the figure). The resulting phenotype is the subject of the externalist processes, including Natural Selection, Genetic Drift, ... participating again in a complex process leading to self-organization. The result of these externalist processes feeds back the helix by modifying the heritable information. The irregular shape of the cylinder that surrounds the externalist mechanism represents the differential contribution of these processes through evolutionary time.

consider without substantial modification of the paradigm, such as inheritance of acquired characters, environmentally driven mutations or symbiosis. These are presumably affecting any organism, so they should not be ignored.

On the other hand, changes in populations or characters may not be gradual, but actually saltationist-like events. Thus, phenomena as punctuated equilibrium or those related to evodevo processes could also be fitted into the Neodarwinian paradigm, although with some modifications. However, the concept of complexity intrinsic to evolutionary systems and spatio-temporal patterns implies a entirely new view of nature, requiring an update to the paradigm.

With reference to the mechanisms driving evolution, the Neodarwinian paradigm does not support any other except Natural Selection and stochastic processes, although other mechanisms have been observed, as ecological integration and self-organization, internalism, or mechanisms of development. These probably exist in all organisms, but have not been taken into account in the Neodarwinian paradigm.

Finally, the processes that conduct to speciation must be reconsidered, as some events, such as fast-speciation, are hardly explained through a gradualist point of view. Beside this, rapid speciations as those induced by infections, such as the *Wolbachia* case, or differences in rates of evolution by the influence of spatial or ecological factors seem to be more common than expected in all groups. These facts are absolutely not contained in the Neodarwinian paradigm, so a new revision might be necessary again regarding speciation.

In the present paper, we wanted to review the historical concept of Evolution in the course of human scientific development and how our knowledge about biological phenomena has been more or less integrated in a progressively broader evolutionary theory. Under any circumstances, it was not our intention to give a new evolutionary paradigm considering all the exceptions not provided by the Neodarwinian approach. Nevertheless, evidences mentioned in this paper are obvious enough to reconsider that a new integrated or, at least, a more open-minded concept of Evolution could currently be adopted. Fig. 1 tries to reflect the interrelated, self-organised and modular nature of evolutionary processes.

From the evidence presented here, as well as from many other cases and questions that have not been mentioned, it is clear that the whole present evolutionary theory (Modern Synthesis) needs to be updated. As an integrative concept, evolution is fully necessary as the very base for further development of every field dealing with living matter, from genomics to psychiatry, from conservation biology to morphology. While new data appear, improving our knowledge about the details of evolution, evolutionary biologists (that is, in fact, all biologists) have to bear in mind that our theory is still incomplete.

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