Does Evolution evolve?


Introduction

Probably, evolution has been the scientific topic most hotly debated, both by scholars and non-scholars, 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 utmost 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 easy to achieve (Table 1). The simplest definitions are variations of Darwin's "descent with modification" (Darwin, 1868) 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" (May, 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.

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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. Three readers interested in a deep analysis will find very profitable lectures in Tempelau (1974), Harris (1985), and Gould (2002).

The origin of human beings and 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 modern meaning until the 19th century, the fact of evolution was proposed by Aristoxenus long before the birth of Christ. The study of Natural History was reorganized 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 political-economic system with the appearance of a new class, the bourgeoisie, and with the development of strong national monarchies. It was in this period, the Renaissance, when science began its development as the way to explain the world, besides Religion, with Copernicus, Kepler and Galilei among others. As an example, Leonardo da Vinci (1452-1519) defended, against the current opinion, that the fossils were remnants of ancient organisms, he established a whole new theory of the classification of strata, later independently developed by Steno in 1669, and he estimated that it would take the Amon to deposit the surrounding country (Richter, 1958; Vassil, 1944). This last topic was generalized later, and the development of the ideas of evolution, since the current opinion about the age of the Earth was based on the Bible, and it implied an extremely short chronology. Blasing his calculations on data gathered from the Bible, Archbishop Usher established in the 17th century that the Earth was created in 4004 B.C. October 22nd, although J. Lightfoot was able to solve his calculations and established October 20th, at 9 AM, as the precise time (Dixon White, 1954).

Despite these advances, the absolutely dominant position during the 15th and 16th centuries was the creation. Although the influence of these ideas on the scientific community of his epoch was negligible, the case of José de Acosta (1559-1600) is worth to be mentioned (Aguiar, 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 hypotheses to explain the observed pattern: 1) the American species were created independently; 2) after the Deluge the species spread around the world, but every particular species were locally extinct in some places and survived in other regions and 3) the American species developed from the European species. 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 a simple example of a superficial view; 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 reason for the absence of the Renaissance to evolution was to modify the "scientific environment" and to prepare both the influential 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 centuries as a widespread hypothesis in the scientific community. Boscá and Dussaillant developed the inductive and deductive method respectively (Boscá, 1865). Lennart; and Leibniz invented the microscope (Ford, 1991), Steno established the basic principles of stratigraphy, and Leibniz developed the concepts of the "virtual universe" and the concept of "nature summed in this statement "All advances by degrees in Nature, and nothing by leaps..." (Leibniz, 1996).
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 still discussed and, mainly because everybody 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", published in 1859, which proposed the theory of evolution by natural selection. This theory was based on the idea that individuals that were better adapted to their environment would tend to survive and reproduce, while those that were not would tend to die out. Over time, the population would evolve and adapt to its environment.

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 being descended from a few if not one primitive form). As mentioned in the introduction, these two theories are now considered fact given the amount of accumulated evidence that support them. The rest of the theories concern how and why evolution takes place and are based on what May (2001) calls the "population thinking", a point of view in which any individual is different from every other and thus 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 kind of 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 can be summarized 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 these individuals with the highest probability of survival and reproduction will be 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 synthesis was established in the USA, in the Soviet Union, Lysenko developed his Neo-Lamarckian theory (Templeau, 1974; Tort, 1998). Unfortunately, the Neodarwinian synthesis is an unscrupulous trickster rather than a scientific theory. In individuals is due in part to the competition among the new recombinant genotypes with the population, and in part to chance processes affecting the frequency of genes. The 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 (May, 2001). Though not included in the previous definition, Neodarwinism explicitly invokes selective speciation as the process that generates new species. According to this model a population of the species A is split into 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 May (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 redefining 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 means that only changes in the genotype are considered relevant for evolution. According to this theory, how and why the process of evolution can be summarized 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 these individuals with the highest probability of survival and reproduction will be 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 synthesis was established in the USA, in the Soviet Union, Lysenko developed his Neo-Lamarckian theory (Templeau, 1974; Tort, 1998). Unfortunately, the Neodarwinian synthesis is an unscrupulous trickster rather than a scientific theory. In individuals is due in part to the competition among the new recombinant genotypes with the population, and in part to chance processes affecting the frequency of genes. The 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 (May, 2001). Though not included in the previous definition, Neodarwinism explicitly invokes selective speciation as the process that generates new species. According to this model a population of the species A is split into 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 May (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 redefining 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.

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includes large-scale changes such as polyplody or changes of the gene arrangement (i.e. chromosomal inversions) called chromosomal maladaptation. Further changes can come from transposition of DNA sequences or from changes in the pathway of the DNA of a gene to the eukaryotic cell 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's environment and genetic fitness, some non-link to DNA base sequence may be transmitted to the next generation. Jablonska and Lamb (1995) define an epigenetic inheritance system as the mechanisms that enable a non-functional or structural element to be passed on to the next 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 chromatin, for examples: the pattern of heterochromatinized regions or the bound of regulatory proteins, implying that the next generation inherits the functional state of its ancestor (Jablonska 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. In any case, this restriction only applies to sessile, non-reproducing organisms (Foster, 1998). However, differences between groups that appear to be derived in the same way have been demonstrated in sexually reproducing organisms as shown by the study of Cubas et al (1999) with Linaria (Linaria ouo) and Linaria vulgaris is a flower with a well-known polymorphism in its flower symmetry. The wild phenotype presents a bilaterally symmetric in both petals and stamens while the mutant phenotype is characterised by a radially symmetric (see figure in Cubas et al, 1999). The differences in pattern are caused by a change in the timing of development. The floral primordia are defined by differences in the expression of Lyc groups regulating genes. Comparisons of the base sequence of Lyc 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 Lyc gene (what has been termed expression) that is inherited in the following generations. Cubas et al (1999) propose that this process can be important in plant evolution, although it should be rare among animals due to the separation of the germline 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 organization. Tertiary and quaternary structures of DNA provide other molecules that form a scaffold where chromatin is repressed in a high degree, to build histones. A great part of this 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 biogenesis of the ribosome (the final part of the DNA sequence). As a result of the genome structure, the location of the genes in the chromosome sequence determines their activity, as they present spatial localization (Reich et al, 2002). This means that the degree of variability of two given genomes 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 statures that can act as "landmarks" for different retrovirus and transposable elements. These elements are able to change DNA sequence, often changing their "mark" that corresponds to the sequence they are inserted in or change in the genome. This "molecular mapping" may be very important in horizontal transmission and genome reorganization, two processes that may have been very common across evolutionary history (Sebili, 2002).

Cell structure

The structure 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 (Jablonska and Lamb, 1995). This phenomenon is well known in ciliates. It has been found that the position of a pattern in the surface of the nematodes 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. Ever 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 retrovirus and retrotransposons are significantly involved in the evolution of both genome and life. Retrotransposons (such as the AIDS virus) are made of RNA (ribonucleic acid) and the enzyme that阡by attaching their own genes to those of the 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 episodic of high activity in Eucaryta, even in humans (see Serlisi, 2002 for a review), pointing to an important role not previously recognized. During the process of transcription, retrovirus sometimes transfer genes of other organisms, passing off a part of a gene from one organism and pairing it to another.

Once in the genome, retrovirus may have several fates, which can be highly important for evolution. They can retain their transcription capability and thus 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 are a host DNA functions (viral DNA are a host DNA functions complement at least 4% coding DNA in humans; Nikolis and Lai (2001) or it can decay and form of the non-coding "junk" DNA (Bromham et al, 2002). This importance of retrovirus can be illustrated by their function in the placitation in humans (Collini, 1998), where the retrovirus HERV-W plays a key role in the expression of the syncytiotrophoblast, a protein which mediates placentation in humans. This may be important in human placental morphogenesis and may be critically involved in the development of the placenta (Ferna et al, 2000). Viral contribution to organism functioning has been more closely shown in bacteria, where pathogenic capabilities in Escherichia coli are due to particular genes acquired through horizontal genetic transfer (Ferna et al, 2001; Glaser et al, 2001). Other sources come from the Drosophila species of the mosquito family. Another source of nucleotide sequences is the acquisition of viral 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 at least 300 million 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 archaebacterium 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 eukaryotic symbionts. All these facts give symbiosis an overwhelming role that has 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 eukaryotic way of evolution, opposite to the classic competitive one (Margulis and Sagan, 2000). An organismic or higher complexity levels, symbiosis and cooperation 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 reduced or modified morphological variation.
The analysis of morphological variation in an evolutionary context is comprised in the so-called "representation problem" (Vagner and Altenberg, 1990), addressing the concept of genotypetype phenotype. This correspondance is brought about through the developmental process that links genetic and phenotypic components directly. The importance of organismal, internal mechanisms for evolutionary change was suggested early in the literature (for reviews: Redd, 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 characterized by morphological integration, canalization, dissociation and related processes (Miller and Wagner, 1991, 1996; Wagner, 1996; Wagner and Altenberg, 1996). By modifications of temporal and spatial order during development -heterochrony and heterotopic processes (Caflisch and Fox, 1994)-, these internal mechanisms may have non-genetic influence on variation. Such internal epigenetic conditions have been termed developmental or functional constraints (Mayr and Smith, 1983). They are directly involved in the developmental processes 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 regulatory mechanisms.

Punctuated equilibrium Gradual and continuous change of species along time has been challenged by most prominent paleontologists 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 a paper in which they challenged the fossil record in which it was neither so biased nor so gradual. As a consequence, Punctuated Equilibrium holds that the great majority of species originated in geological moments (punctuations) and they persist in stasis throughout their long duration (Gould 2002: 276). 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 recognized (Gould and Eldredge, 1985). As a result, this theory is not so much about abrupt change, but only that the rate of change is not constant. Specialization occurs during geologically short time periods, although "geologically short" means thousands of generations and this is gradual along these periods. However, Punctuated Equilibrium has several consequences 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 "Coordinated Stasis", coined by Brett and Rickard (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). These periods were punctuated by sudden and drastic changes that affected all lineages simultaneously. The key difference between coordinated stasis and punctuated equilibrium is that the former implies the periodic replacement of whole communities by new lineages (diversity, richness, etc.), not just in the morphology of the individual species, even though environmental disturbance occurs during the period of stasis. Brett et al. (1996) defined block-coordinated stasis as intervals, generally exceeding the million years in duration, during which 60% or more of species-level lineages persist from older to younger samples of appropriate biotas, with only minor and typically non-directional evolutionary changes. Although initially described for Palaeozoic marine assemblages, this pattern has been recognized in terrestrial ecosystems too (Proctor and Hasen, 1998; Moritz, 1999; DiMichele and Phillips, 1998).

Role of complex processes and self-organisation in the genetic of variability The leading role of genetics in heritable variation 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 codes. This means an "informative holistic view of genetics (rooted in" 

Gould's Naturphilosophie), represented by the concept of self-organisation (Mayr and Smith, 1983). Self-organisation is a process in which the pattern at the global level of a system emerges entirely from numerous interactions among lower-level components of the system. Moreover, the rules governing the interactions among the system's components are executed using only local information, without reference to the global pattern (Stott and Camazine, 1993). In its least extreme and reductive form, this means a source of heritable phenotypes that can be added to the genetic variation and both of them integrate by development. Processes of self-organisation have been shown in many systems and morphogenetic processes, as the processes of reaction-diffusion that generate the conical and spiral waves that characterize systems from cardiac muscle or neural tissue to population dynamics of insects (Von Ee and Epstein, 2001). A recent impressive example of these sort of processes comes from an unicellular algae, Acetobacter. This species has a complex morphology with differentiated structures such as the stalked, tubes, tails, and umbrellas. Experimental studies plus mathematical modeling of the morphogenesis have proven that all this complex morphology and the processes of change that occurs during the development of this algae 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. Related with the theory of gradual change in species was the theory of a gradual change in the characters of organisms, although this topic is not developed in one of the worst problems. Neodarwinian Synthesis considered gradual change of characters as one of the bases of evolution while selectionist changes were assumed to be almost irrelevant (Mayr, 2001). However, a certain degree of polyphyleticism, 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 selectionist change? Given that the very basis of gradualism is that there cannot be selectionist changes leading to an abrupt formation of a new species, the upper limit for the changes should be set in a degree of polyphyleticism, if possible the level of individuals of the population, thus keeping the concept of gradual evolution in the temporal change of the populations.

Evolutionary land and rhythms In morphological sciences gradualism and saltationism have been recognized as typogeny, orthogenesis, typostasis, and Cartesian Transformation, which the Synthetic Theory explains by adaptive radiation and ortho-selection concepts. But the directionalism 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, within the synthetic geneticistic perspective has been offered considering the evolutionary change as an "Redis" (Ried, 1975, 1977), which includes internal mechanisms of growth and development in order to complete the externally given potential of the species.

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 (Mayr and Smith, 1983), which would include a certain morphological directionality in evolutionary situations in which external conditions might have changed. The basic body-plans of aquatic mammals (whales 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 rates, they exist for high velocity of change. The biological background of these examples is related to the complex of developmental integration (Olsen and Miller, 1958; Ried, 1975, 1977; Zelditch et al., 1993; Cheviron, 1999). It is the elements that form in ontogeny, at the end of causal sequences, are hypothesized to be less integrated, less constrained and more free to vary. Characters like horns in boids, digits (examples like Elephants, Man, and modern horses), or caprils are less constrained and allow higher velocities of evolutionary change (e.g. Bussolari et al, 1997).

Mechanisms driving evolution

In Darwin's proposal, Natural Selection was the main motor of change; it was the force that shaped the species. Neo-Darwinian 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 equilibrium, each population of randomly reproducing individuals will 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 accumulation of new ones. These processes are responsible for the evolution (Mayr, 2001) and are divided in those stochastic and deterministic ones. The first ones would include all mechanisms 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:

Mutations have 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 phenotype it is the only mechanism of adaptive evolution. Natural Selection allows organisms to adapt to its environment by selection of adapted traits (Blankslee, 2001). A further mechanism (also applicable to sexual selection) is that only individuals and more precisely phenotypes are selected; although Natural Selection has been equalized 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 migration and introgression of individuals (and their genes) to and from other populations of the species. This is a pervasive factor that prevents the divergence of parasitically isolated populations and it is a major reason for the stability of widespread species and for the stability of species (Mayr, 2001).

Genetic drift is a process of random loss of variability through errors of sampling mainly in small populations (see Szyzko et al., 1989; for a detailed description of this mechanism and its evolutionary importance). This process is usually compartmented by gene flow and becomes of capital importance in small founder populations.

Based variation has been cited as a rather uncommon process (May, 2001) that implies genes that affect the segregation of alleles during meiosis in a heterozygote, such that the alleles of one parental chromosome go to the gametes in more than fifty percent. Although such processes do not seem to be very extended it can produce the retention of loss 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 mechanisms driving evolution

Microevolutionary events occur continuously due to the relationships among species and environment. Thus ecological problems, such as density dependence and competition, should be taken into account explicitly, or at least not ignored, in any Evolutionary Theory (Kozlowski, 1990). Although sparse and still preliminary, recent studies on diverse taxa suggest that Natural Selection caused by ecological abilities 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 environmental factors, 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 spreading offspring, which migrate in a density-dependent regulatory mechanism, so the world is flooded with migrants of different species (Kozlowski, 1989). Successful colonizers follow microevolutionary changes, which spread again as new migrants, slightly different from the first ones, are produced after the new population is well established. The nature of dispersal and local microevolutionary processes is one of the causes of biotic identity, 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, the dispersal process is an important source of genetic variation (Orr and Smith, 1998; Dioskhour and Dossbell, 1999; Ferriere et al, 2000), modifying the pattern produced by Natural Selection and other processes (see above) in two ways:

1. It produces relative, or even complete, isolation among populations; Alophey and sympathy are points along a gene flow continuum, which might or might not have an easily identifiable geographic component (Markert et al., 2001).

2. Although viability may be the dominant mode of evolution through space at broad scales, dispersal also plays a significant role in differentiation processes (Zink et al., 2000), producing different rates of gene flow and, thus, differentiation, among the populations over all the species range (e.g. laranian salmonids, Garcés-París et al, 2003). Migrants arriving at new habitats are pressed to get adapted quickly to the new ecological conditions, or fall in colonizing those sites. Diverse studies suggest that the invasion success of many species might depend more heavily on their ability to respond to Natural Selection then on being euryotic (Lu, 2002).

As we have seen, many different processes are affecting 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 mode. 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 Soal et al (1988). They found spatial structure is aubique frequencies of Yorunama 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 aubique frequencies to be higher, and the occurrence within this tribe of some aubique frequency clines most likely due to the operation of chance historical processes, which necessarily preserve a geographic structure.

The impact of most macroprocesses of natural selection in evolutionary trends and rates may appear unimportant to the development of macroevolutionary patterns. However, in a complex world, driven by deterministic chaos, external events, when great amount of time is considered, small-scale stochastic results in regular and clearly distinguishable patterns in many evolutionary processes (e.g. extinction, Higgs et al, 2000). Patterns of well as responding to ups and downs from external causes (Hoekzla et al, 1999). In other words, Evolutionary Theory only from the small-scale processes above.

The concept of evolution Synthesis seems efficient and the present, as the self-organization of these processes by the effect of complexity is also important.

Internalism, complexity, and strength of Natural Selection

The importance of Natural Selection in the system-theoretic approach is that it forms (the external) part of an self-organizing system, which is driven through a developmental process. By probabilistic argumentation it was suggested that Natural Selection, in presence of internal hierarchically genetic, epigenetic and developmental architecture, leads to an internal organizational process (see a copy of Lee and Liao, 1977; Wagner, 1983b; Laidlub, 2001). According feedback loops, Natural Selection and the developmental architecture lead in a common and interrelated— to the correspondences 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 inflammatory epigenetic (Ried, 1977). The importance of the role of Natural Selection as motor of evolution is decreasing as life evolves thereby increasing internal complexity. Not necessarily, but post-stabilized harmony and internal lawfulness (Ried, 1977; 394) are characteristics of the system-theoretic approach to biological evolution leading to the order of living organisms. Is than Natural Selection the motor of evolution? The answer would be yes, but mainly at early stages 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 (Ried, 1977), developmental stages have become "burdened" and have a macro-evolutionary probabilistic notion. A highly-packed structure (i.e. highly constrained) is integrated into biological functions at a very basic organismal level. This may be an early developmental stage, with 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 subsystems participates in internal 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") developmental units which become to a functional causal and developmental chains (Ried, 1975). Developmental or functional constraints of mutant Maynard Smith et al (1985) are modeled as a bias on variation at a microevolutionary scale, which is really outside the developmental burden, and grounded on similar biological reasons. The hierarchical structure of developmental constraints is the hypothetical biological reason why epigenetic copies to some degree or other, it is important that there is a biological substrate of the conceptual nature of "Bionautica" (Ried, 1975).
In development the evolutionary unit is the "biological homeology" (Wagner, 1986a). It characterises large-scale biological organisation and roles light on self-regulatory, epigenetic nature and biology of the developmental process and the evolution of life as a self-organising system.

A new hypothesis: Infiltracoral Natural Selection
An interesting hypothesis has been proposed by Cudato (2002) to describe how a cell may be able to produce rapid changes in its own genome, in order to obtain direct evolutionary implications. It is suggested that a "buffer" 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, Cudato (2002) states many cellular mechanisms able to carry out a similar task within the genome. These mechanisms include the ability of detecting 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.

Species
The population thinking also posits the way in which species are formed. The paradigm considers that already in the main process in forming new species. This model proposes that isolation of previously isolated populations leads to independent evolution of the two subpopulations and eventually become separate 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 Neofundamentalist paradigms, 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 Eukarya, but it is also obvious that they are not discrete units that are only interfere within themselves. There are many examples of valid, full-functioning, individuals born from parents of two different species. The usefulness of hybridization plants from a lot of groups is widely known by gardeners. Tesea from the Salicaceae family, such as willows (Salir 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)斯坦 to disperse by a hybridisation process where cork oaks pollen fertilizes holm oaks' flowers, producing hybrids with the cork oak phenotype (Blasibhi et al., 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, O. testudinaria and O. castanea, morphologically very similar, and with partially overlapping niches and distributions, were studied by Morea and Bota (1999) to determine if their separation as species was correct. The general phylogenetic patterns supported the preliminary morphological hypotheses of the three were correctly distinguished species, but, frequently, single populations of one species were found to be closer to populations of other species than their own populations. Although several morphological diagnostic characters may separate these easily in sites where only one of the species is present, many intermediate individuals are difficult to assign to one or the other. Among individuals of two species, these are present. Many insect species present key-lock systems to avoid fertilization from individuals of other species, that is, the male genitalia are morphologically adapted to the female reproductive system, and make fertilization from other species difficult. However, as it is light in dung beetles (but probably in a lot of groups), most parts of the genitalia are soft, allowing females to be fecundated from closely related species with slightly different edifices (male ejaculate sexual organ). There also examples of viable vorticlate individuals born from parents of different species of the same genus (e.g. luna, Plecotus leu), and those that have hybrids 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 (female-reproductive unit, theoretical approach). They are uncoupled, as gene flow is allowed to exist between different taxonomic species, but not between biological ones. In the light of the "anomalous evidences" discussed, that are not an exception 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 a part of continuum rather than discrete entities.

Infected species: the case of Wobachia
A new mechanism of reproductive isolation and thus to formation of new species is related to bacterial infections. Wobachia is a cytoplasmic-inherited bacterium that causes reproductive alterations in many groups of metazoans including insects, nematodes or apids. A recent estimate ranges from 15 to 20 percent of the living species have at least one form of Wobachia infected by these bacteria (Bordenstein et al., 2001). Another study using butterflies (Giggins et al., 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 Acraea genum, they found two kinds of infections: low- and high-prevalence ones. Whilst the latter is easy to detect, the former have gone understudied. Despite recent attempts, these authors conclude that sex-ratio distorting Wobachia (see next paragraph) may be common in insects that have an ecology and/or genetics that permit the invasion of these microorganisms. This reproductive isolation caused by Wobachia has been recently studied in two species of parasitoid wasps from genus Nasonia (W. gwaltney and C. longicornis) (Bordenstein et al., 2001). These are two closely related species (estimated time of divergence of 0.26 Ma) isolated by the Wobachia infection, as shown by the fact that reproductive isolation disappears when wasps are treated with antibiotics that eliminate Wobachia infection. This is a new kind of barrier that act in a sharp, non-gradualistic, way, that leads to the isolation of subpopulations that could diverge afterwards.

Fast-specialising sympatric cichlids
Cichlids are a highly species 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 have many species of their basic "Bauplan" but present a high diversity of ecological adaptations and reproductive strategies (see Markert et al., 2001). In many East African lakes, hundreds of different endemics species have evolved since Pleistocene, ranging from nearly one to a few tens per lake, and even hundreds, such as in lake Tanganyika and in lake Victoria. The figures for the latter are impressive, as more than 500 species have been listed at present, with a dramatically increased high speciation rate (Weberh, et al., 2003). So, why are there so many cichlid species in a single lake?

In a review article, Galis and Metz (1998) stated that three species may have evolved in sympathy 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 sympathy when a genetic correlation develops between components of the mating recognition systems and competitive adaptive traits (Kondrashov and Kondrashov, 1999; Dickman and Oulafi, 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 appear in only a few decades) to correspond to the giant speciation 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 "wave effect" in the formation of species which can generate 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 resources preserved in the genome (Galas and Metz, 1998; Verheyen et al., 2003). This example points out that more practical and realistic model is to consider allopatry and sympathy as points along a gene flow continuum, with or without a geographic component (Markert et al., 2001; see below). The use of this new phylogenetic methods available nowadays will result in a better comprehension of the evolutionary relationships, so many new evidences on this issues is likely going to be at sight in the next years 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. Garcia-Paris et al., 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 phylogeny, has provided new data that may contradict the view of speciation as a strictly adaptationist process.

There are ecological-level self-organized processes, different from the adaptation to the environment, and spatially-mediated effects, different from total or partial isolation, that influence speciation (end thus evolutionary) rates. For example, in the new Unified Theory of Speciation and Biogeography (Hubbell, 1997, 1999, 2002; see discussion on gene flow), spatialation evolve independent from niche structure (where natural selection and Sexual selection is acting), relying on the structuring of dispersal and population density effects. As seen before, microevolutionary processes occurs when dispersal takes place successfully after superposing 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 range distribution (b-diversity), and thus high numbers of species as act at the edge of their geographic ranges, that constitute the edge for most species. Environmental stress suffered by individuals living at the edge of their previous adaptations may produce high intra-species extinctions (Bertels, 2002), and speciation occurs as a result. Because evolutionary changes through lateral gene transmission and symbiosis may also be higher in range margin and threatened areas; rapid changes, and information sharing, may be at these places, which can be facilitated by the use of laboratory experimentation, with high speciation rates 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 change, since it is a process that allows for the adaptation to disturbances), a living ware in which many different used bricks are stored. The above-described areas may act as architecture studies, where new and innovative buildings are designed, starting from the structures of the former ones, and using old, well-tested, and now-designed bricks.

Global problems of the paradigm and others
In the previous pages we have paid attention to facts and theories that do not seem to fulfill the assumptions of the Neodarwinian paradigm. These ideas and data show the limits of what has been considered the valid view and why of evolutionary processes. 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 definition: change of traits and transmission of these changes, as a consequence of an ancestral-descendant dependence. Different hypotheses have explored the characteristics of evolution from different points of view (individuals, specics), 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” (May, 2001). Therefore, individuals, populations and species have been since then considered the three principal units of evolution. Nevertheless, this consideration could 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. (Selby, 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 (Martin-Plaza, 1997).

Nevertheless, 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 are these functional or structural, intermingling each other and the limits among them are not really disconnected. Although in practice, a categorization 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 to 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 genotypo-phenotype relationship
Darwinian theory is based on variation, actually on a continuous and abundant source of variation. Since the introduction of the Synthesis, the 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, Gould, 1994; Gould, 1997, 2002). In a recent paper, Newman and Müller (2000) propose a new framework for the origin of morphological characters by means of epigenetic mechanisms and their epigenotypes by the genome. According to this theory, the close mapping between genotype and phenotype is a highly desired condition, a product of evolution rather than its precondition. Prior to the genetic canalization of the phenotypes and their subsequent stabilization, 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 conditionally active interactions among the organism’s tissues (Newman and Müller, 2000). According to the authors, this concept leads to understand findings as the Cambrian explosion, the origins of morphological innovations, homology or the rapid change of forms. This framework, although not mentioned by their authors, supposes a complete new vision of evolution since the gradual, population based, genetic neo-Darwinian paradigm is changed and could include satiation 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 Maris, 2001); the assumption arising 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 necessary for this task. However, the ecological theory necessitates that evolutionary studies ecologists have pursued hardly for more than half a century (Ghalior, 2001). As there are too many contingencies and too much factors may be interacting at the same time it may lead to different compositional units and they may enter in different ways into mechanistic explanations (von Dassow and Munro, 1999).

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 specialization rates into the classical MacArthur and Wilson theory (1963, 1997). 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. This constant not only species richness, but also relative species abundance in source communities and the rate and strength of specialization events (Hubbell, 1997, 2001). It seems that the final product of specialization, that is, local species richness, is controlled by a kind of “thermostat” that maintains a certain number of immigrant species that are able to establish in a given site and, where this number is small, promotes specialization events: this is a clear case of ecologically-driven evolution, different from the adaptationist paradigm. Moreover, this hypothesis suggests a deeper level of 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 spatial and temporal environment gives rise to a few general patterns 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 throughout time, it becomes clear that evolution may be 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, adaptation to the environment is a minor component compared with the complex stochastic processes.

Concluding remarks
First of all, we would like to state that the present paper and the different approaches include 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 pertaining to the evolution process, that we feel the necessity to remark that one aspect admits not questioning whatever: 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, ramified, and consistent has the evidence for evolution become that if anyone could now disproves it, I would have my conception of the orderliness of the universe no 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 it is not more a law than that you are hearing or reading these words (Miller, 1995).

As the well-known sentence by Dobzhansky establishes "nothing in Biology makes sense except in the light of evolution" (Dobzhansky, 1973). This makes Evolution the most powerful (genotypes) that can survive (that is, comply with Natural Selection requirements) depend on these variations. From there, the fittest, or better, may or may not be the ones producing the most number of descendants. In a continuously changing world, a high amount of contingent factors (stochastic or not) are effectuating survival rates, self-organizing the outcome of the processes included in the Modern Synthesis Theory.
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 30's and 40's 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 contributions, or they affecting a very small number of forms. And now, at the beginning of the 3rd millennium, all these leftover are reclaiming a place within the Evolutionary theories.

In a conference opening plenary, Doullite (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 transfers 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 (Doullite, 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 Neodarwinian paradigm. Therefore, regarding sources of variation, it is possible to assume by the Neodarwinian paradigm that some sources other apart from changes in the geneotype are possible, as those of cell structure or genome organization. Also, self-organization, canalization 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

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

<table>
<thead>
<tr>
<th>Sources of variation</th>
<th>Example</th>
<th>Amplitude</th>
<th>Relationship to paradigm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-genetic heritable variation</td>
<td>Will known in athletics</td>
<td>Presumably affecting all organisms in short extent</td>
<td>Minor adaptation</td>
</tr>
<tr>
<td>Cell structure</td>
<td>Human organs, etc.</td>
<td>Well known in bacteria</td>
<td>Minor adaptation</td>
</tr>
</tbody>
</table>
| Genes | V. p. Linhais | All groups
| | Well known in bacteria | All groups
| | Alkaloids | All groups
| | Origin of eukaryotes | Presumably affecting | |
| Mechanisms during evolution | Exotic species | All groups
| | Multi-species | All groups |
| | Lateral transfer | All groups |
| Integration | Integration of exogenetic mechanisms | All groups |
| Integration of endogenetic mechanisms | All groups |
| Integration of environmental feedback | All groups |

### Figures

**Fig. 1.** The Evolutionary Mechanism: Evolution as an integrated process. The present figure shows evolution as a temporal flow, in which all different levels are integrated although in different scales. The upper part represents an ecosystem, in which living forms (in contrast to the term biosphere) and environmental conditions interact. Islands of exogenous and endogenous processes. Such interactions result from complex systems leading to self-organization, forming ecosystems which at the same time scale; organisms evolve through time from variations in their heritable information (including non-genetic information) that are self-organized and also regulated and integrated by development (lower right part of the figure). The resulting phenotype is the output of the external processes, including Natural Selection, Genetic Drift, and genetic exchanges in a complex process leading to self-organization. The result of these external processes leads to a flow by modifying the heritable information.

The irregular shape of the cylinder that surrounds the external mechanism represents the differential contribution of these processes through the evolutionary time.
consider without substantial modification the paradigms, such as
inhabitants of accused characters, environmentally driven
mutations or symbiosis. These are presumably affecting any
organisms, so they should not be ignored.
On the other hand, changes in populations or characters may
be gradual, but actually saltatorial-like events. Thus,
phenomena as punctuated equilibrium or those related to
evolutionary processes could also be fitted into the Neodarвинian
paradigm, although with some modifications. However, the
concept of complexly invasive to evolutionary systems and
spatio-temporal patterns implies a entirely new view of nature,
requiring an update to the paradigms.
With reference to the mechanisms driving evolution, the
Neodarвинian paradigm does not support any other except
Natural Selection and stochastic processes, although other
mechanisms have been observed, e.g., 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 Neodarвинian paradigm.
Finally, the processes that conduct to speciation must be
reconsidered, as some events, such as fastspeciation,
are hardly explained through a gradualist point of view. Besides this,
speciation as those induced by mutations, such as the
Wobachia 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 Neodarвинian paradigm, so a new
revision might be necessary for speciation regarding geography.

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
integrated in a progressively broader evolutionary theory. Under any
condition, we were not intention to give a new evolutionary paradigm
considering all the exceptions not provided by the
Neodarвинian paradigm. Nevertheless, evidences mentioned in
this paper are obvious evidence to reconsider that a new
integrated or, at least, a more open-minded concept of
Evolution could currently be adapted. Fig. 1 tries to reflect the
interconnected, 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 base for further development of field dealing with
living matter, from genetics to psychology, from conservation biology to
morphology. While new data appear, improving our knowledge
about the details of evolution, evolutionary biologists that is,
in all biologists, have to bear in mind that our theory is still incomplete.


