

**DARWINIAN AND NON-DARWINIAN PRINCIPLES IN EVOLUTION**

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## 1. Universal Evolution

For every real thing, we may sensibly ask how it came into being, how it changed, and how it might end. In fact, every real thing has a history, an origin, a sequence of states and an end. In short: every real thing evolves. Although in some cases it might not find an answer yet (or ever), the "evolutionary question" is always legitimate.

At first sight, we might doubt this. We might still stick to the conviction that there are at least some things which don't undergo any change, have no origin and no possible end.

Let's discuss three examples. To the naked eye, the "fixed" stars seem to be durable, immutable, permanent objects. But astrophysics has taught us that they are evolving, that they are "born", that they exist for some time in a stationary (not static!) state and finally "die" from lack of energy in a violent explosion or by shrinking to a white dwarf, neutron star or black hole. In fact, the astrophysical processes are so powerful that it is perfectly adequate to call our habitat "the violent universe" (Nigel Calder).

Now, how about the "substance" of stars and universe, about matter, about the chemical elements? How about atoms, elementary

particles, quarks? Are not they, at least, stable, permanent, eternal? No, they aren't. We now know that and how chemical elements are built in stars from hydrogen, and that even hydrogen is a product of cosmic processes.

Finally, is not the universe itself eternal, everlasting? No, it is unsteady, unstable, transient. Not only has it emerged from a huge explosion, the notorious big bang, but it is still expanding, still evolving. Its future is uncertain, but it definitely will never settle down to a quiet state but will either collapse and disappear from the scene or expand forever, thereby thinning out indefinitely.<sup>1</sup> There is, then, in the real world no exception to Heraclitus' clear-sighted dictum "πάντα ῥεῖ", all is in flux".

But with Heraclitus this was only a conjecture. He could not prove it. In his time, other thinkers could claim just the opposite. To Parmenides, for instance, all change is mere deception. The world, the Being, the One, is immutable, eternal, everlasting. And only recently, our scientific outlook is definitely subscribing to Heraclitus, not to Parmenides any longer. This is the merit of evolutionary thinking.

## 2. Evolution as a Descriptive Concept

The evolutionary question may be posed on a descriptive level: What are the possible states of the system in question? In which sequence do they follow each other? What are the initial and final conditions? And how do changes in the initial state affect later

stages? On this level, the evolutionary consideration is purely kinematical. The primary question is "how?", not "why?" As we have seen, this question is perfectly legitimate. What is more, it is stimulating, heuristically fruitful and methodologically sound.

Evolution in the kinematic sense is comprehensive, all-embracing, truly universal. As Julian Huxley put it, it is possible, in fact indispensable, to view all of reality "sub specie evolutionis", to regard this whole universe as one single, unique evolutionary process. Evolution combines and unites all real systems and therefore all factual sciences. It is a genuinely synthetic conception.

This is true under several aspects. There is, first, the historical aspect. It was, in fact, the theory of evolution which gave biology structure and profile as an autonomous science. If it is true that Newton founded modern physics in 1666 and that Lavoisier established chemistry as a science in 1789, then it was Darwin who provided biology with its scientific status in 1859. Thus, it was quite adequate when his contemporary and colleague Alfred Russel Wallace called Darwin "the Newton of biology" (although, in a final assessment, we should not forget men like Gregor Mendel, James Watson, Francis Crick and Manfred Eigen). In a speech celebrating the centenary of Darwin's birth, the great zoologist August Weismann claimed that before Darwin biology didn't even exist, because the different biological branches - zoology, botany, anthropology - were as yet mere heaps

of unrelated facts, disconnected disciplines, branches without an inner linkage.<sup>2</sup> Such a linkage was eventually provided by the theory of evolution.

Similar considerations apply to other sciences. Many traits of real-world systems can only be understood as outcomes of an evolution, that is historically. Cases in question are to be found in astronomy, geology, paleontology, etymology and linguistics, archeology, and several other disciplines.<sup>3</sup>

There is, second, a more systematic aspect. Initially, evolutionary ideas had become useful in different disciplines quite independently.<sup>4</sup> When Kant and Laplace successfully tried to use Newton's theory of gravitation in order to explain not only the stability but also the origin of our planetary system, this had, at first sight, little or nothing to do with the ideas of Bopp, Rask or the Grimm Brothers who conjectured that the striking similarities between different Indo-European languages might be due to their genealogical relationship and even a common origin. If the diagram of Hertzsprung and Russell, exhibiting relevant information about different kinds of stars, is kinematically interpreted as showing different stages of astrophysical evolution, then this step might appear to be totally unrelated to the fact that the well-known similarities between different organisms may be explained by their descendance from a common ancestor.

The concept of evolution, however, not only allows to draw analogies (between the genealogies of languages and of organisms, for instance), but it puts all evolutionary accounts in one uni-

fied context, in the perspective of universal evolution. By assigning all evolutionary "segments" their proper place in a long chain of cosmic processes, in a true "history of nature", the concept of evolution shows once again its synthetic effect. Moreover, it not only allows to build up a sequence of evolutionary processes, it also enables us to identify the gaps therein. Although evolution is more or less continuous, there are still many blanks in our knowledge of evolution. Thus, the links between the first steps of molecular evolution (being postulated or even imitated in the laboratory) and the most primitive organism to be found today, are nearly completely missing and hitherto unknown. Likewise, our knowledge about the evolution of man is still quite deficient. Thus, the idea of universal evolution is helpful in ordering both our knowledge and our ignorance. Evolution in the kinematic sense, though not directly observable, may nowadays be regarded as a well-established fact.

### 3. Evolution as an Explanatory Concept

But we want more. We are interested in the dynamics of systems. Our problem is not only how things change, but why. We strive for causes, forces, determinants, factors, motives, reasons. What we look for are not just descriptions, but rather explanations. Karl Popper even claims explanations to be the aim of science.<sup>5</sup> Whether this is in fact the case, will be left open here. That explanations rank among the aims of science, may well be taken for granted.

The distinction between descriptions and explanations is not an absolute, but rather a relative one. What counts as an explanation on one theoretical level, may appear as a "mere" description if seen from a higher level. We describe - or explain - the fall of a body by Galileo's laws of free fall. But they are derived from and explained by Newton's laws of motion and of gravitation. From the latter's perspective, Galileo's laws are purely descriptive. But even Newton's laws may be explained in turn by Einstein's field equations whereby they are "degraded" to mere descriptions. The same could happen with Einstein's theory itself with respect to an even "deeper" level, a unified theory of all physical interactions, for instance.

Similar, there are different levels of evolutionary theory. The (descriptive) similarity between several kinds of animals may be explained by their phylogenetic relationship, that is, by their descent from a common ancestor. But phylogenetic trees are, of course, pure descriptions in the deeper perspective of a causal theory of evolution trying to uncover the forces responsible for evolutionary change. Thus, in the context of evolution, explanations are usually causal explanations, explaining the time-dependent behavior of organic systems.

In looking for such causal explanations for cosmic processes, we have been, in part, successful. We know some of the forces which run our universe. We are quite familiar with the causal laws of stellar evolution, including the origin and evolution of our chemical elements. We know less well the laws of galactic



and planetary evolution. We have some ideas about the evolution of our atmosphere, the surface of our planet, and the "cooking" of the first biologically relevant molecules.

Perhaps the most impressive part of our evolutionary outlook is the theory of organic evolution. And it is certainly Darwin's theory of natural selection which marks the greatest advance in our understanding of life processes. Not only does it unify and integrate all disciplines of biology in a coherent scheme of mutually relevant facts, it finally allows and gives explanations.

#### 4. Darwinian Principles

As everybody knows, organisms reproduce. They make, as it were, copies of themselves. Now, this reproductive or copying process is not always proceeding with perfect accuracy. There occur mistakes, copying errors, called variations by Darwin and identified as genetic mutations by his followers. Through this imperfect copying process, variety and diversity are introduced into organic populations. Different traits, however, offer different chances in the "struggle for life". They lead to varying fitness. This diversity, inevitably introduced by genetic changes, leads to differential reproduction. Although chance events may play a constitutive role, differential reproduction is not a random process. It is essentially deterministic. This process is called natural selection. Selection, then, is not an additional or independent force, but the result of a discriminating interaction between organism and environment.

The theory of evolution has several particular traits, among them the following:<sup>6</sup>

- All organisms, even those within one and the same species, vary from each other. New variations are constantly emerging. (Principle of variation by mutation and recombination)
- These variations are, at least in part, inherited, that is, genetically transmitted to the next generation. (Principle of inheritance whose mechanisms were not known to Darwin)
- All organisms produce more offspring than can possibly survive to grow up and to reproduce in turn. (Darwin's principle of overproduction)
- On average, survivors will exhibit those heritable variations which increase their adaptation to local environments. (Survival of the fittest or principle of natural selection)
- Therefore, species are not immutable. (Principles of evolution or - to use Darwin's own terms - transmutation or descent with modification, as opposed to creationism, for instance)
- Variations occur in relatively small steps as measured by information content or organized complexity.
- Therefore, phylogenetic change is gradual and relatively slow. (Gradualism as opposed to saltationism or to Cuvier's catastrophe theory)
- Inheritance must be of a particulate or atomistic nature. (No blending inheritance as Darwin wrongly believed.)
- Variations are random, not preferentially directed toward favorable adaptations.

- The path of evolution is not pre-programmed, not goal-directed, not determined, not predictable.
- Functional traits are outcomes of natural selection, not of some teleological, goal-setting instance. (This counts against the "argument from design" postulating the existence and activity of an extra-natural creator, an argument put forward by Darwin's theological teacher William Paley.)
- No higher principles operates in nature. Darwin's theory is a completely naturalistic approach to the phenomena of life.
- Organic evolution has led to more and more complexity. However:
- Evolution is not inherently progressive. Whether increase in complexity should be called progress, is a matter of convention.

The principle of natural selection has proved extremely powerful, first of all with respect to the central questions of evolution, but in other areas as well. It was first formulated by Charles Darwin in 1838. In his autobiography, he writes:

In October 1838 ... I happened to read for amusement Malthus on Population, and being well prepared to appreciate the struggle for existence which everywhere goes on from long continued observation of the habits of animals and plants, it at once struck me that under these circumstances favorable variations would tend to be preserved and unfavorable ones to be destroyed. The result of this would be the formation of new species.<sup>7</sup>

Even so, it took Darwin twenty-one more years to publish his

theory.<sup>8</sup> Thus, it is now more than a century that the principle of natural selection is scientifically known and discussed, criticized and tested. And all over this time, it has been applied to more and more systems. It is, in fact, not an overstatement if a volume commemorating the centenary of Darwin's death carries the title "Evolution from molecules to men".<sup>9</sup>

Darwin himself had started out by treating the origin of species. (See the title of his main work: The origin of species by means of natural selection or the preservation of favoured races in the struggle for life.) Species are natural classes of organisms. The organisms Darwin had in mind were plants and animals. But his principles turned out to apply to far more systems. This extension worked in both directions, "backwards" and "forwards", both in time and complexity. This will be shown in the next sections.

#### 5. Backward Applications of Evolutionary Theory

In the backward direction, there is first the world of micro-organisms. Until 1950, that is, for a whole century following Darwin, our paleontological record was dominated by macrofossils. They refer to the last six hundred million years of evolution. Although this is, in a sense, quite a long time, it covers only about 15 percent of the age of the earth, hence, as we now know, of organic evolution in general. The discovery and investigation of microfossils during the last decades has therefore effectively widened our evolutionary perspective. We now have access

to the age of microorganisms which lasted for three thousand million years and was reigned mainly, if not solely, by bacteria. And we have even grasped some idea of bacterial evolution.<sup>10</sup> This information is not derived from bacterial phenotypes, not from classification by shape, biochemical processes or cellular organization. Here, phylogenetic relationships are identified and even measured by analyzing and comparing genotypes. Thanks to modern sequencing methods, macromolecules and even genes can be used as evolutionary chronometers. These methods yielded quite unexpected results, among others the discovery of the archaebacteria, considered to constitute the oldest known family of organisms.<sup>11</sup> In this completely new area, the idea of evolution has proven constitutive and absolutely indispensable.

The next step backwards in time and scale is the idea of a common ancestor. If complexity has been increasing in evolution then it must decrease if we go backwards in time. This contention is borne out by every phylogenetic tree. But phylogenetic trees exhibit still another characteristic: The number of species and other taxonomic divisions is, at least on average, increasing in time, hence decreasing if we follow time backwards again. It is, after all, this fact which gives phylogenetic arrangements their tree-like appearance. This observation quite naturally prompts the question how such a tree might end - or start for that matter. How many species would constitute the beginning of life? Darwin himself was well aware of this question, but also very cautious in answering it.

I cannot doubt that the theory of descent with modification embraces all the members of the same great class or kingdom. I believe that animals are descended from at most only four or five progenitors, and plants from an equal or lesser number.

Analogy would lead me one step farther, namely, to the belief that all animals and plants are descended from some one prototype. But analogy may be a deceitful guide.<sup>12</sup>

Nowadays, we feel quite certain that all organisms must have had one common ancestor. For, we know even more traits common to all organisms than Darwin knew, as for instance the (near) universality of the genetic code. Such common traits are most easily explained by the assumption of a common ancestor.

#### 6. More Steps Backwards: Origin of Life and Molecular Evolution

Even so, the question remains open how this single progenitor looked like. This question coincides with the next step in our way backwards, with the problem of the origin of life. On this, Darwin did not make public any definite opinion. We may, however, make out some development in his pertinent intimations. In a letter to Joseph Hooker, dated 1863, Darwin still claims that it would be mere rubbish thinking to speculate on the origin of life. In 1871, he declares the question how life itself originated hopeless, but sees it, nevertheless, as a problem for the distant future. In the same year, however, he even allows himself to speculate on the origin of life and on the question why

the de novo formation of organisms is not observed in more recent times.

It is often said that all the conditions for the first production of a living organism are now present, which could ever have been present. But if (and oh what a big if) we could conceive in some warm little pond, with all sorts of ammonia and phosphoric salts, light, heat, electricity, etc., present, that a protein compound was chemically formed ready to undergo still more complex changes, at the present day such matter would be instantly devoured, or absorbed, which would not have been the case before living creatures were formed.<sup>13</sup>

This argument is quite correct. For, even if we should find out one day that, under the conditions prevailing on primeval earth, the emergence of living systems was a necessary and inevitable consequence of physico-chemical laws, this insight would not mean that life must or could also arise under present conditions. Life itself has changed conditions on earth so drastically that there is no chance for a new genesis. The most remarkable change organisms have brought about is the fact that they have replaced the reducing atmosphere of the earth by an oxidizing one. Thus, life itself prevents the emergence of radically new forms of life. Therefore, the theory of evolution and even "the origin of species" does not explain the origin of life, but only the descent of living systems from living systems, the transformation of old species into new ones, the processes which build vivum ex

vivo, organisms from organisms. Darwin was, of course, quite clear about this. In 1881, one year before his death, he wrote to Nathaniel Wallich:

You expressed quite correctly my views where you said that I had intentionally left the question of the Origin of Life uncanvassed as being altogether ultra vires in the present state of our knowledge, and that I dealt only with the manner of succession. I have met with no evidence that seems in the least trustworthy, in favour of so-called Spontaneous Generation. I believe that I have somewhere said (but cannot find the passage) that the principle of life will hereafter be shown to be a part, or consequence, of some general law.<sup>14</sup>

When Darwin asserted (in his letter to Hooker) that it would be rubbish thinking to speculate on the origin of life, he added that one could quite as well (or quite as bad) think of the origin of matter. It is curious enough that nowadays we are seriously theorizing about both origins, that of life and that of matter. But true also, that it took us a hundred years to progress scientifically to those deep problems.

From such recent investigations, it has turned out that, whereas the theory of organic evolution in its entirety is a purely biological theory, the principle of natural selection is not. It applies not only to living organisms, but to self-reproducing systems in general. Among those systems are biological macromolecules, first of all RNA molecules. Such molecules can spontaneously build, form stable configurations, duplicate, make



"errors" in duplication. In different environments, they have different stability and different rates and qualities of replication. That is, they may evolve.

Thus, the concepts and principles of evolution have been extended to the pre-biological era of molecular evolution.<sup>15</sup>

This is a further link in the chain of evolutionary processes. It turns out that the principle of selection is not restricted to the living world, it can even be derived from physico-chemical considerations alone. Thus, it bridges the apparent gap between non-living matter and living systems.

This does not mean, however, that the problems of the origin of life were solved. We have good reasons to believe that the gap between non-living and living could be and was in fact bridged from the inorganic side. How exactly this happened we do not know yet. The first representatives of life are objects of still much speculation.<sup>16</sup> It might well take us another hundred years to solve these problems.

## 7. The Lower Limit

How far backwards might the principles of evolution be extended? If molecules can carry information and perform functions, if they can replicate, mutate and be selected, why not, then, atoms, elementary particles, stars, or galaxies as well? Is there a lower limit to the applicability of evolutionary concepts?

Yes, there is. Although all real systems evolve, not all of them evolve according to Darwinian principles. There are systems

where the principle of selection does not apply "yet". The lower limit of applicability is self-replication. It lies below all existing organisms, below unicells, below viruses, below "protobionts" (Folsome, Kaplan) or "eobionts" (Pirie, Bernal), below "progenotes" (Woese), "hypercycles" (Eigen, Schuster) and "microspheres" (Fox), probably even below RNA molecules. It possibly lies with simple crystal defects (Weiss, Cairns-Smith) or just clay inclusions.

But the limit exists. It makes no sense to apply the concepts of mutation and selection to stars because they do not reproduce, because they have no offspring and because there is no inheritance. Where no information is transmitted, no transmission errors can occur. There are no mutations. Nor can there be any selection understood as differential reproduction as long as there is no reproduction at all.

Thus, although the concept of evolution applies to all real systems, the concepts and principles of organic evolution apply only to self-replicating systems. We must therefore carefully distinguish the different ranges of evolutionary concepts. Although the principles of organic evolution apply to areas and systems quite different from those they originally were devised for, they are not universally applicable.

## 8. Forward Applications of Evolutionary Theory

In "The Origin of Species", Darwin did not treat the descent of man. His only hint at this problem is one single sentence: "Much light will be thrown on the origin of man and his history." But it was evident from the very idea of organic evolution that man could not be excluded from the evolutionary outlook. It would be against all scientific standards first to formulate a supposedly universal law of nature and then to exempt man from this universal law. Such inconsistency would not have suited Darwin's intentions. He was quite clear about this delicate problem. While working on the "Origin", he has collected ample evidence on the descent of man. But he wanted to keep the problems (and his critics) apart. To claim that man has somehow descended from an animal ancestor, is one thing, to specify from which animals and how and in what time, another. Darwin's discretion was, however, of no avail. Ever since the "Origin", the discussion on his theory included, or even centered on, the descent of man himself. In fact, when Darwin finally published his pertinent book "The descent of man and selection in relation to sex" in 1871, several other thinkers had already anticipated his thoughts, as, for instance, Charles Lyell and Thomas Henry Huxley in England (1863), Carl Vogt and Ernst Haeckel in Germany. Even so, Darwin didn't even venture to propose a phylogenetic tree for man. The reason is given by Isaac:

In 1871 the Neanderthal and Gibraltar skulls were the only significant human fossils known. In his 1863 essay, Man's

Place in Nature, Huxley had already shown that the Neanderthal form was effectively a variant of the human type rather than an evolutionary link, so that Darwin's concept of human evolution was of necessity 'fossil-free'.<sup>17</sup>

With respect to the fossil situation, we are much better off today though many problems are still waiting for definite solutions. There is no doubt whatsoever that man descended from ape-like creatures. The origin and descent of man is a perfectly sound application of the theory of evolution. What more do we want? Can there be more to evolution than its application "from molecules to men"? [Yes, there can. The theory of evolution is not restricted to biochemical and morphological traits. It is meant to apply to all organismic features. And organismic features include such variegated traits as social behavior, communication, cognitive faculties, moral norms, aesthetic standards. How far do the principles of organic evolution rule such traits? Where lies the "upper" limit of applicability for the principle of selection?

In the last section we have come to the conclusion that the "lower" limit is self-replication. Wherever systems reproduce under some kind of restriction - be it limited supply of food, of space, or of energy -, where resources of any kind are scanty, there will be competition, differential reproduction and, therefore, selection. This means that the principle of selection is applicable wherever there is self-replication with slight variations under limited resources. Self-reproduction, then, is not

TABLE 1: Expansion of the Domain of Evolutionary Theory

physico-chemical evolution	o r g a n i c e v o l u t i o n		scientific and philosophical disciplines
	systems	traits	
universe galaxies stars planets (earth)		aesthetic standards moral norms intelligence cognitive faculties communication social behavior animal behavior	evolutionary aesthetics (as yet nonexistent) evolutionary ethics (fragmentary) } evolutionary psychology and epistemology
atmos- phere conti- nents rocks	biosphere ecosystems higher taxa	macroevolution	sociobiology ethology  "synthetic theory" (J. Huxley 1942)
pebbles	species (Darwin) men animals plants	microevolution	theory of natural selection
	races populations		population genetics
	microorganisms bacteria archaebacteria		
	protobionts eobionts progenotes microspheres hypercycles RNA molecules crystal defects	origin of life	biogenetics
crystals			
macro- molecules molecules atoms elementary particles quarks energy spacetime universe	lower limit: replicating systems		

only necessary but also sufficient to induce selective processes. Thus, even on the "upper" side, that is with respect to increasing complexity, the principle of selection is not restricted to living systems. If machines were to reproduce themselves - which is, in principle, perfectly possible<sup>18</sup> - they would with necessity undergo evolutionary processes. The same is true for any other real system.

There is, then, no "upper" limit for the applicability of the selection principle. It applies wherever the relevant conditions mentioned previously are fulfilled, without any upper limit as to organic level or to complexity. Table 1 exhibits this expansion of the domain of the theory of evolution in both directions.

#### 9. Non-Darwinian Principles

It is precisely due to its generality, that the principle of selection, though fully applicable to all organic (i.e. self-reproducing) systems, does not cover all of science, not even of biology. As was shown in section 4., there is more to Darwin's theory of organic evolution than mere selection. And therefore, a process may be non-Darwinian although it is perfectly selective. Moreover, the deviations from Darwinian principles may point to quite different directions. Table 2 presents some typical characteristics of such non-Darwinian conceptions.<sup>19</sup>

There are, first, the theories contradicting the idea of evolution in general, namely creationism and catastrophism (with in-

TABLE 2: Types and Traits of Non-Darwinian Evolution

Evolutionary trait (vs. Darwinian trait)	claimed to be relevant for biology by	in fact relevant for	remarks (characteris- tic property)
no change at all, species are created and immutable (vs. evolutionism)	creationism		literal inter- pretation of Genesis, refuted
repeated extermination of all (higher) life forms and independent re-creation (vs. "actualism")	Bonnet 1770 (palingenesis) Cuvier 1812 (catastrophism)		catastrophes (e.g. asteroid impacts) are indeed constitu- tive for evolution
macromutations, "hopeful monsters", saltationism (vs. micromutations)	T.H. Huxley (!) de Vries 1901 Goldschmidt 1940	macro- evolution? cladogenesis?	both theoretically and empirically extremely rare
transmission of individually acquired characters (vs. blind genetic variation and subsequent selection)	Lamarck 1809 Darwin (!) 1859 Kammerer 1925 Lysenko 1930 Steele 1979	cultural evolution	learning by imita- tion and instruction, evolution fast
random (genetic) drift, mainly due to fluctuations of population size (vs. pure adaptationism)	Sewall Wright 1931	bottleneck effect, founder prin- ciple	accepted by "synthetic" theory of evolution
neutral mutations (vs. pan-selectionism)	King/Jukes 1969 Kimura/Ohta 1968	parts of evolution	constant rate of mutations
stasis and rapid evolution: "punctuated equilibrium" (supposed to contradict Darwinian gradualism)	Eldredge, Gould 1972	adaptive radiation, parts of evolution	concept of "explosion" depends on timescale
hyperbolic growth (vs. exponential growth)	Eigen 1971 Schuster 1977	hypercyclic phase of molecular evolution	no chance for competi- tors, no coexistence, all-or-none decision
group selection (vs. individual selection and kin selection)	Wynne-Edwards 1962	explanation of altruism?	whole groups as units of selection
internal selection (vs. external selection)	Gutmann 1981		example: hydraulic models

dependent creation). Scientifically, they are not viable any longer. Even so, biologists should be familiar with the theses and arguments of creationists in order to counter them convincingly.

There is, furthermore, the contention that individually (ontogenetically) acquired characters may be genetically inherited. This thesis of Lamarck is, though quite suggestive, empirically unfounded and seems to be definitely refuted by molecular genetics. Modern theories of organic evolution figuring as Darwinian or Neo-Darwinian are positively distinguished by their denial of Lamarck's hypothesis. Curiously enough, Darwin himself accepted the idea that the use and disuse of parts may lead to inheritable effects and may therefore influence the course of evolution. He consistently kept to the conviction, "that Natural Selection has been the most important, but not the exclusive, means of modification".<sup>20</sup> In that sense, Darwin himself was not a pure "Darwinian" in modern understanding.

That natural selection is effective in and essential for intraspecific evolution (microevolution), is readily accepted by all biologists. The point of divergence is the question whether Darwin's theory of natural selection also explains macroevolution, the origin of new genes, new species, new genera and higher taxonomic categories. This discussion has been revived by provoking theses such as punctualism and neutralism. That there occur, indeed, relatively fast evolutionary changes (which seem to contradict traditional gradualism) and selectively



neutral mutations (contradicting conventional pan-selectionism), is generally acknowledged. Their quantitative share in evolutionary processes, however, is still heavily debated.<sup>21</sup> It is quite possible that from this discussion a new evolutionary synthesis will emerge.<sup>22</sup>

There are still more kinds of non-Darwinian evolution. Following Malthus, Darwin had stated that organisms should always multiply in geometric progression, that is exponentially, as long as there are no limiting constraints. However, according to Manfred Eigen's theory of hypercycles, evolution should have run through a pre-biological and pre-Darwinian phase of hyperbolic growth where superior competitors (or mutants) did not have a chance to hold their own against established hypercyclic systems. This intolerance would have led to an all-or-none decision, to the dominance of one single (proto)type of system without the possibility of coexistence. Such a model would explain the (near) universality of the genetic code.<sup>23</sup>

There is also much disagreement about the units of selection. Is it genes, genomes, individuals, populations, species or ecosystems which are favored or selected against? Conventional Darwinism would exhibit individuals as the units of selection. The existence of altruistic behavior, however, has led to new concepts, theses, arguments and controversies. It is still a matter of debate and - hopefully - of empirical and theoretical investigations whether kin selection can account for all selective phenomena or whether group selection must be taken as

existent and as effective in evolution. <sup>24</sup>

A similar problem concerns the mechanisms of selection. What is, after all, the active components in selection? Is it "the environment" which selects? Are there also internal selectors, selective instances inside organisms?<sup>25</sup> This discussion might be cleared up by reconsidering the concept of selection. As has been shown in section 4., selection should not be (mis)interpreted as an outer force or factor. It is not more than different reproduction due to varying fitness. Whether my fitness is low because I cannot escape enemies or because of inner instabilities, does not make much difference with respect to survival. Thus, the concept of internal selection doesn't contradict Darwinian selection at all. It rather specifies one out of several selective mechanisms.

It would, nevertheless, be quite interesting to know whether there are, at least in higher organisms, internal selectors checking genomes or phenotypes in early stages of development for viability and eliminating defect germ cells, fertilized eggs, or even embryos. Such internal selectors would help to save food, energy and time. Their role would be a quasi-teleological one without being anti-selectionist or anti-Darwinian. How they could possibly arise - by mutation and, at some stage, outer selection - must be left open here.

## 10. Conclusion

Our examples show that the central or, in a sense, universal role of the principle of selection does not preclude other types of evolutionary concepts, principles or theories from being relevant and adequate. It is, therefore, absolutely necessary to be quite clear which kind of evolution one is talking about. Do we mean mere change or do we have in mind increasing complexity? Do we talk about inorganic or about organic evolution? Are we referring to Darwinian or to non-Darwinian processes or theories? Are there other selective processes than natural selection?

Thus, we should be careful not to misinterpret all kinds of evolution as being subject to the same law or set of laws. Although evolution is truly universal and the concept of "evolution" applies to all real systems, this is not the case for all concepts and laws of evolution. Many principles of evolutionary theory are restricted to particular domains. The application of the principle of natural selection to the evolution (sic!) of stars is as mistaken as is the view that the evolution (sic!) of scientific theories is nothing but a mere prolongation or extrapolation of organic evolution.

Unfortunately, these and similar errors are quite common. But whereas the transgression of the lower limit does usually no harm because it just signifies the application of complicated tools to a simple workpiece, the transgression of the upper limit may be quite misleading and even dangerous, leading to

oversimplification all too easily.

It would be worthwhile to inquire into some concrete examples of such backward and, even more important, forward applications of the theory of evolution. Cases in question are:

- a) the evolution of cognitive faculties (evolutionary psychology and epistemology),
- b) the evolution of scientific theories (history and philosophy of science, sometimes confounded with evolutionary epistemology),
- c) the evolution of machines in particular and of technical problems and technical solutions in general (history of technology),
- d) the evolution of social behavior (sociobiology),
- e) the evolution of moral behavior and moral norms (evolutionary ethics, as yet nearly nonexistent),
- f) the evolution of institutions (marriage, division of labor, market, law, democracy) (anthropology, sociology, political science),
- g) the evolution of art and of aesthetic standards (evolutionary aesthetics, nonexistent).

Interesting as they might be, such investigations must be left to another opportunity.<sup>26</sup>

In the light of these considerations, we should realize that the power of evolutionary concepts must not be overestimated or misused. The concept of evolution is universal, integrative, synthetic, heuristically fruitful, but it is not a panacea. It

is necessary to be aware not only of its strength, but also of its limits.

Notes

1. See, for instance, Jamal N. Islam, The ultimate fate of the universe. Cambridge: Cambridge University Press, 1983.
2. After August Weismann, Charles Darwin und sein Lebenswerk. Jena: G. Fischer, 1909.
3. For documentary purposes and without the slightest pretension to completeness, we list some pertinent titles exhibiting the universality of the evolutionary question. (SA stands for Scientific American.)

I. D. Novikov, Evolution of the universe. Cambridge: Cambridge University Press, 1983. - George Gamow. 1956. "The evolutionary universe." SA 195 (September): 136-154. - Maarten Schmidt and Francis Bello. 1971. "The evolution of quasars." SA 224 (May): 55-69. - Halton C. Arp. 1963. "The evolution of galaxies." SA 208 (January): 70-84. - J. C. G. Walker, Evolution of the atmosphere. New York: Macmillan, 1977. - Francisco J. Ayala, ed., Molecular evolution. Sunderland: Sinauer, 1976. - Articles in SA 239 (September 1978) have the following telling titles: "Chemical evolution and the origin of life." "The evolution of the earliest cells." "The evolution of multicellular plants and animals." "The evolution of ecological systems." "The evolution of behavior." "The evolution of man." -

- Konrad Z. Lorenz. 1958. "The evolution of behavior." SA 199 (December): 67-78. - Alison Jolly. 1985. "The evolution of primate behavior." American Scientist 73: 230-9. - W. D. Hamilton. 1964. "The genetical evolution of social behavior." Journal of Theoretical Biology 7: 1-52. - Robert L. Trivers. 1971. "The evolution of reciprocal altruism." The Quarterly Review of Biology 46: 35-57. - R. Axelrod and W. D. Hamilton. 1981. "The evolution of cooperation." Science 211: 1390-6. - Robert Axelrod, The evolution of cooperation. New York: Basic Books, 1984. - M. E. Bitterman. 1965. "The evolution of intelligence." SA 212 (January): 92-100 - H. J. Jerison, Evolution of the brain and intelligence. New York: Academic Press, 1973. - John Maynard Smith. 1984. "The evolution of animal intelligence." In Christopher Hookway, ed., Minds, machines and evolution. Cambridge: Cambridge University Press, 1984, p.63-71. - Tom Settle. 1983. "Evolution of moral and ethical behaviour." In: Absolute values and the creation of the new world. Proceedings of the Eleventh International Conference on the Unity of the Sciences (November 1982, Philadelphia). New York: The International Cultural Foundation Press, 1983, p.1209-31.
4. This story is told quite admirably in Stephen Toulmin and June Goodfield, The discovery of time. London: Hutchinson, 1965.
  5. Popper, Karl R. 1957. "The aim of science." Ratio 1: 24-35. Reprinted in Objective knowledge. Oxford: Clarendon Press, 1972.

6. See Salvador E. Luria, Stephen Jay Gould and Sam Singer, A view of life. Menlo Park: Benjamin/Cummings, 1981, p.582-586. - Articles by Ernst Mayr ("Evolution"), Francisco J. Ayala ("The mechanisms of evolution") and Richard C. Lewontin ("Adaptation") in Scientific American 239 (September 1978).
7. Darwin's autobiography is published in Francis Darwin, ed., The life and letters of Charles Darwin, Vol.1. London: John Murray, 1887.
8. For some of the reasons for this delay see Stephen Jay Gould, Ever since Darwin. Harmondsworth: Penguin Books, 1980, p.21-27.
9. D. S. Bendall, ed., Evolution from molecules to men. Cambridge: Cambridge University Press, 1982, an excellent volume whose several chapters cover the whole range of modern applications of Darwin's theory. See also G. Ledyard Stebbins, Darwin to DNA, molecules to humanity. San Francisco: Freeman, 1982.
10. This progress is lively documented in Carl R. Woese: "The primary of descent and the universal ancestor." In Bendall (Fn.9), 209-233.
11. See Carl R. Woese. 1981. "Archaeobacteria." Scientific American 244 (June): 98-122, and literature cited therein.
12. Charles Darwin, The origin of species (6th edition, 1872), ch.15. London: Collier Books, 1962, p.480 (and other editions).

13. Cited after Clair Edwin Folsome, The origin of life. A warm little pond. San Francisco: Freeman, 1979, p.VI.
14. Cited after Manfred Eigen. 1983. "Self-replication and molecular evolution." In Bendall (Fn.9.), p.128.
15. For an introduction see M. Eigen, W. C. Gardiner, P. Schuster, R. Winkler-Oswatitsch. 1981. "The origin of genetic information." Scientific American 244 (April): 88-118. A more comprehensive account is given by Bernd-Olaf Küppers, Molecular theory of evolution. Outline of a physico-chemical theory of the origin of life. Berlin: Springer, 1983.
16. Some speculations on possible first self-replicating systems are given in Armin Weiss. 1981. "Replikation und Evolution in anorganischen Systemen." Angewandte Chemie 93: 843-854. - Carl R. Woese (Fn.10.). - A. G. Cairns-Smith. 1985. "The first organisms." Scientific American 252 (June): 74-82, and literature cited therein.
17. From Glynn Ll. Isaac: "Aspects of human evolution." In Bendall (Fn.9.), 509-543, p.510.
18. The problem of self-reproducing machines is discussed by John von Neumann, "The general and logical theory of automata." L. A. Jeffress, ed., Cerebral mechanisms in behavior. New York: Wiley, 1951. Reprinted in Z.W.Pylyshyn, ed., Perspectives on the computer revolution. Englewood Cliffs: Prentice-Hall, 1970, p.87-113. See also John von Neumann, Theory of self-reproducing automata (ed. by Arthur



- W. Burks. Urbana: University of Illinois Press, 1966. For an introduction see L. S. Penrose. 1959. "Self-reproducing machines." Scientific American 200 (June): 105-114.
19. On punctualism see Niles Eldredge and Stephen J. Gould. 1972. "Punctuated equilibria: an alternative to phyletic gradualism." In T. J. M. Schopf, ed., Models in paleobiology. San Francisco: Freeman, 1972, p.82-115. - S. M. Stanley, Macroevolution: pattern and process. San Francisco: Freeman, 1979. - For neutralism see Jack Lester King and Thomas H. Jukes. 1969. "Non-Darwinian evolution." Science 164: 788-798. - J. F. Crow. 1971. "Darwinian and non-Darwinian evolution." In L. M. LeCam, ed., Proc. VI. Berkeley Symposium on Mathematical Statistics and Probability 1970. Vol. IV, V or VI, p.1-22. - Motoo Kimura. 1979. "The neutral theory of molecular evolution." Scientific American 241 (November): 98-126. - Motoo Kimura, The neutral theory of molecular evolution. Cambridge: Cambridge University Press, 1983.
20. Charles Darwin, The origin of species (see Fn.12.), last phrase of introduction and ch.15.
21. How traditional evolutionists try to integrate punctualism and neutralism into the "synthetic" theory of evolution, can be seen in Francisco J. Ayala. 1983. "Microevolution and macroevolution." In Bendall (Fn.9.), p.387-402. - G. Ledyard Stebbins and Francisco J. Ayala. 1985. "The evolution of Darwinism." Scientific American 253 (July): 54-54.

22. See G. Ledyard Stebbins and Francisco J. Ayala. 1981. "Is a new evolutionary synthesis necessary?" Science 213: 967-971.
23. For hypercyclic evolution (hyperbolic growth) see Manfred Eigen and Peter Schuster. 1977/78. "The hypercycle." Die Naturwissenschaften 64: 541-565 (A), 65: 7-41 (B), 341-369 (C). (Also Heidelberg: Springer, 1979) - Manfred Eigen. 1981. "Darwin and molecular biology." Angewandte Chemie (International Edition) 20: 233-241.
24. As an introduction to the discussion on the relevance of group selection use Edward O. Wilson, Sociobiology - the new synthesis. Cambridge, Mass.: Harvard University Press, 1975, ch.5 ("Group selection and altruism"), pp.106-129, or any other comprehensive textbook on sociobiology.
25. The importance of internal selection is stressed by F. Wolfgang Gutmann and Klaus Bonik, Kritische Evolutionstheorie. Hildesheim: Gerstenberg, 1981.
26. We just give some sources relating to the different extrapolations of evolutionary concepts, numbered a to g as in the text.
  - a) Donald T. Campbell. 1974. "Evolutionary epistemology." In Paul A. Schilpp, ed., The philosophy of Karl Popper. LaSalle, Ill.: Open Court, 1974, pp.413-463. - Gerhard Vollmer, Evolutionäre Erkenntnistheorie. Stuttgart: Hirzel, 1957, <sup>4</sup>1987. - Gerhard Vollmer, Was können wir wissen? Stuttgart: Hirzel, 1985/86. Vol.1: Die Natur der Erkenntnis. Beiträge zur Evolutionären Erkenntnistheorie.

- b) Stephen E. Toulmin. 1967. "The evolutionary development of natural science." American Scientist 55: 456-471. - Criticized by Paul Thagard. 1981. "Against evolutionary epistemology." In P. D. Asquith and R. N. Giere, eds., PSA 1980. East Lansing: Philosophy of Science Association, Vol.1, pp.187-196.
- c) P. Grassmann. 1985. "Läßt sich die technische Entwicklung mit der biologischen vergleichen?" Naturwissenschaften 72: 567-573.
- d) Wilson (Fn.24.). - Charles J. Lumsden and Edward O. Wilson, Promethean fire: reflections on the origin of mind. Cambridge, Mass.: Harvard University Press, 1983.
- e) Thomas H. Huxley and Julian Huxley, Evolution and ethics, 1893-1943. London: Pilot Press, 1947. - Antony Flew, Evolutionary ethics. London: Macmillan, 1967. - Michael Ruse. "Evolutionary ethics: a phoenix arisen." Zygon 21: 95-112.
- f) Friedrich A. von Hayek. 1984. "The rules of our morality are not the conclusions of our reason." In: Absolute values and the new cultural revolution. Commemorative volume of the Twelfth International Conference on the Unity of the Sciences, Chicago 1983. New York: International Cultural Foundation Press, 1984 , pp.35-42.
- g) Desmond Morris, The biology of art. London: Methuen, 1962 .