EVOLUTION

Saverio Forestiero
Department of Biology, University of Rome "Tor Vergata," Italy

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Summary

The effects of biological evolution are the most amazing and spectacular phenomena observable in nature. The capacity to evolve is an intrinsic property of life and living beings, their variety, and their complexity, and their hierarchical organization is the output of the evolutionary process. Evolution is a manifold phenomenon producing both biological diversity and adaptation to the environment. Evolution is an historical process, too; sometimes it happens following deterministic ordered patterns, sometimes it happens in a probabilistic fashion; chance is important in evolution. So is time: evolution is a transgenerational phenomenon occurring at a rate depending on the kind of organism and on environmental circumstances. Evolution concerns both the products (the organisms) and the processes (the ways in which they work). Biological evolution is both a constructive process and a destructive one: species do not only originate, they

also go extinct. In spite of the appearances there is no progress in evolution; evolution simply occurs and sometimes it can be also progressive. Biological evolution is without intrinsic tendency to progress or to a purpose, an end. Evolution is an end in itself.

1. Introduction: The Nature of Evolution

The capacity to evolve, together with the capacity for organization, metabolism, and reproduction represents, from an overall standpoint, one of the four fundamental characteristics common to all living things.

In particular, biological evolution is the sum of all changes that occur along the lineages of living beings. Life means change: more specifically, change in the features of organisms; and evolution is essentially the history of such changes within the inherited features. The study of evolution entails also the description of the somatic modifications expressed by the various organisms over generations and of the various organizational hierarchies resulting from the relationships between information on genetic variation, phylogenetic constraints, and environmental variation. All of these modifications have influenced and have in turn been influenced by the way in which the flow of matter, energy, and information has affected living systems through generations.

Two main manifestations characterize the standing evolutionary changes; namely, the production of biological diversity and adaptations. Therefore, any theory on evolution must explain both the diversification of living organisms starting from the earliest forms of life and the fact that these organisms seem to have adapted to their environment.

Nevertheless, evolution is linked to time, to the continuity of the genome down along a lineage which has branched out over generations into many secondary lineages still linked to each other by their common ancestor. Such continuity is the basis for kinship among all living things.

One may therefore say that what actually evolves is the genome itself, i.e. the genetic information belonging to a given species. The genetic information is inherited, and the changes in the genome are the only ones to be inherited. Over time, genes and genotypes are preserved, whereas phenotypes embodied by the genotypes die at every generation. This causes the loss of any change carried by the phenotype, meaning that phenotypic modifications are not inherited.

1.1. Differentiating Replicators and Interactors

Although evolution is based on the continuity of genomes through generations, it is made possible by the phenotypes representing precise historical events. In other words, phenotypes are the actual products of the circumstantial relationships between genotypes and environment.

Evolution can therefore be described in two different ways according to whether emphasis is placed on the transformation due to genetic information or to the actual expression of the genetic information per se. Genes in which the genetic information is codified function as replicators, whereas organisms function as material interactors and represent the entities directly interacting with the environment. Interactors are confronted with the environment while developing, competing, carrying on their metabolic and reproductive activities, and dying; it is upon them that natural selection exerts its pressure, and it seems, therefore, that the object actually selected is the individual organism in its entirety. No environmental conditioning is exerted upon the genes themselves.

Given that there is no one-to-one relationship between genotypes and phenotypes, one may say that phenotypes, interactors, and organisms, on the whole, manifest new emerging traits which cannot be fully recognized as belonging to the genes that have produced them.

1.2. The Historical Nature of Evolution

Evolution is an intrinsically historical process characterized by a body of deterministic facts which are necessarily interwoven with probabilistic events. This actually means that the products of evolution and the modality of evolution could have been different from what they are, that things could have gone differently from how they actually went, and that the history of evolutionary changes could have turned out to be quite different. This is where the largely unforeseeable nature of evolutionary processes and the unpredictability of the same behavior over time in living systems stems from. Indeed, we can claim that living systems are not universally needed, in the sense that their structures and behaviors cannot be described by universal laws but rather by statements that apply case by case, or are at most valid in a limited number of instances. It is easy to understand what causes this behavior by way of an example illustrating the huge discrepancy between what is possible in theory, on a combinatory basis, and what has instead actually happened in history. Let us consider the case of genetic polymorphism at the population level. Starting from the 6000 structural genes (the average estimated number for *Drosophila* fruit-flies), and accepting the likelihood that half of them are polymorphic, we would have 3000 polymorphic genes. Assuming, then, an average of 2 alleles per electrophoretic locus, we would have 3 possible combinations of alleles for each locus which, multiplied by all the loci, gives a total number of allelic combinations equal to 3^{3000} (6^{3000} in the case of diploids). As we can see, the potential (whole) of all the thus calculated genotypes is represented by an astonishing total, not only absolutely larger than the total number of haploid genotypes already produced and which may be produced in the future, but much (even vastly) greater than the estimated number (approximately 10^{45}) of all the elementary particles in the universe. This example clearly shows that of all possible genotype combinations only some have actually materialized, and only some of the others may appear in the future. This represents clear evidence of the relative and contingent nature of biological systems. Such contingency seems to be at the basis of the nature of life.

1.3. Evolution Does Not Necessarily Mean Progress

Through the billion years of evolutionary processes, a number of genetic and phenotypic changes have been brought about which have produced different types of organization among living organisms. Therefore, prokaryotic organisms coexist today alongside eukaryotic organisms, and unicellulars coexist with multicellulars. We are also confronted with superindividual organizational levels, such as population-species and animal society, which have come into being during the evolutionary process. Each organizational level is endowed with properties which are new when compared to the previous, less sophisticated levels which are, in turn, simpler than the higher integration level.

There are many consequences of such an organizational hierarchy. The most crucial is that there are as many types of interactors as there are different types of levels. This means that selective mechanisms are different (i.e. the mode of selection is different) according to the level to which each interactor and its environment interact. Furthermore, the properties being replicated depend on the level of organization considered. Ever since the beginnings of evolution, the possibility of recognizing *a posteriori* the existence of evolutionary tendencies over wide time spans has encouraged the belief that there is an intrinsic tendency toward an increase in complexity and evolutionary progress. This is, however, a completely fallacious conclusion because simpler forms of organization have being coexisting over time and still coexist alongside more complex ones. Furthermore, it is well-known that, in the course of evolution, there have been several cases in which living systems have been affected by processes of drastic simplification in some subunits. A well-known case is the anatomical simplification of the eye, to the point of complete disappearance in blind cave animals. Another case is the regressive evolution of parasites living inside other animals.

Finally, one must distinguish between the concept of direction and the concept of progress. For example, many evolutionary trends represent a directional change without progress (e.g., the gradual reduction of the dermal bones in the skull roof of vertebrates from fish to man, or the gradual reduction of the skull forming the supporting structure of the jaws against the skull that encloses the brain in terrestrial vertebrates). Progress implies directional change but not vice-versa. To have progress means to have directional change with improvement over time. Evolution with progress means evolution characterized by improvement compared with some reference standard. The point is that the idea of progress necessarily implies judgment on value, and this implies in turn the adoption of a reference system, the adequacy of which is rarely founded on a solid theoretical basis. The idea of progress, therefore, cannot escape its axiological, intrinsically value-based, nature. The idea of progress is complicated also in the case of extrinsic opinions of an operational kind, as for example in assessing the increase in effectiveness of an adaptation. It might be possible to break out of this stalemate situation by replacing, as suggested by S.J. Gould, the notion of progress in a broad sense, with the idea of directionality, which is an informative notion with operational value. It might be possible to speak of evolutionary progress only in those hypothetical cases in which the existence of an objective improvement in adaptive performance has been proven.

From the standpoint of the history of biological theories, many of the concepts of evolutionary progress adhere to the forms of erstwhile orthogenetic doctrines. Persuasive arguments support instead the view that during evolution there has been some process of dissemination of biological complexity, in the sense that the ability of living systems to adapt to an environment presenting contradictory demands has being growing. In any case, it is indisputable that progress is not an inevitable result of evolution.

2. Major Transitions in Evolution

The earliest fossil evidence for life on our planet dates back about 3.5 billion years and is provided by microbial filaments in rocks of the western Australian continent. These fossils, however, already show the existence of rather complex forms of life. Therefore, one may hypothesize that these organisms must have originated hundreds of million years earlier. Since then a long period of time has elapsed during which a great many million different species have disappeared, new forms of life have appeared and have undergone diversification, and many properties of living organisms have changed.

The entire biosphere has been modified. Although these changes have left scattered and confused fossil traces, it is nevertheless possible to identify, in the long history of life on earth, the existence of major turning points. Surprisingly, these turning points can be read in the structures and behavior of extant organisms rather than by examining the fossil record.

The awareness of the presence of critical turning points in biological material as one moves from one type of organization to another stems from the observation that there is an organizational hierarchy of living systems and that, with time, some evolutionary lines have become progressively more complex. An increase in the complexity of organisms during evolution is indisputable, although one must remember that it may not always mean progress. As a matter of fact, there are times when one may witness an increase in the complexity of a particular structure or behavior during evolution; there are times, however, when the opposite occurs, i.e. simplification of a structure or reduction of the components of a biological system. Furthermore, there is no reason why an increase in complexity is to be considered a requirement to achieve adaptation and Darwinian evolution.

We may thus get a double description of evolution according to whether our attention is focused on genomes, the entities which replicate and pass on genetic information, or on phenotypes, the highly differentiated entities which interact with the environment allowing and conditioning the probability of replication of the genomes. Great evolutionary transitions can be detected both at the level in which changes in the modality of genetic information is transmitted from one generation to the next and in some remarkable phenotypic innovations in macroevolutionary perspective.

Examples are the highly complex adaptations corresponding to the appearance of new anatomical structures, to the evolution of new functions, or to the origin or redefinition of new architecture underlying physiological processes. Such adaptations fall into the category of phenotypic changes which include phenomena such as the origin of visual perception, the colonization of land by plants and animals, the control of body temperature, and the evolution of flight.

It is reasonable to hypothesize that the first evolutionary innovations of entities able to replicate must have appeared before the beginning of life itself (see *The Origin and Evolution of Early Life*). This event most likely dates back about 4 billion years ago, when in favorable chemical and physical environmental conditions those biochemical products and processes were improving which would eventually allow the production of the first cell. There is no direct proof of these first phases of pre-biotic evolution. Yet it is likely that at the beginning there must have been an evolutionary chemical stage with the appearance and accumulation of organic molecules of large size, such RNA, endowed with the capacity for self-replication. The capacity for self-replication of these molecules being imperfect, the process would yield polymer products not all capable of replication. The appearance of variation in the capacity for replication managed to trigger a selection process. Selection, therefore, in the sense of a cause or mechanism capable of producing evolution may have had an ancient origin, dating back hundreds of million of years before the first cell made its first appearance on Earth.

The second important evolutionary stage is represented by the origin of the progenote, the original cell which has come into being starting from the interaction between an informational RNA molecule, polypeptides, and lipids. The reciprocal interactions between these three types of molecules must have been so closely linked as to allow the formation of a super-molecular unit, the progenote, conditioning the behavior of the molecular components inside it.

Moving from the first to the second evolutionary stage, a transition from an “individual” to a “group” type of selection occurs. The first type involves the behavior and destiny of the individual molecules, while the second type favors the best interaction among the molecules constituting the different progenotes. These primordial cells differed from each other, although slightly, in their capacity to create and maintain integration within a supermolecular unit for a sufficient lapse of time. Once the production of a stable progenote is reached—which can be viewed as new type of individual at a higher hierarchical level with respect to the component molecules—the second evolutionary stage comes to its end.

At such a stage, integration between the molecular components becomes an irreversible condition. Therefore, selection becomes again of the “individual” type, the difference being that the individuals affected by selection are no longer represented by molecules but by progenotes.

The evolution of the progenotic type of primitive cells from which present-day bacterial cells would eventually stem, lasted for 2 billion years at least; an extremely long period during which the biosphere was populated only by microbes. What must have happened later on, about 1.5 billion years ago, is that some of these simple cellular individuals associated themselves and established symbiotic, mutualistic, or parasitic relationships. Probably, the association of progenotes cooperating and evolving in a progressively closer relationship was responsible for the production of a new type of organism characterized by compartmentalized organization and by the sharing of its working components.

The modern eukaryotic cell originates thus through symbiosis. Its constituents (nucleus, mitochondria, chloroplasts) derive very likely from as many cellular individuals, which were, at first, quite simple. Once again, moving from “individual” selection among simple cells on to a “group” selection may have allowed the appearance and establishment of a new level of integration. Although the mechanism has remained the same, it is noteworthy that the time span required to go from prokaryotes to eukaryotes was much longer than the time span between the availability of a “prebiotic soup” and the appearance of the first cell.

The next evolutionary step along the way from unicellular to multicellular organisms is based on the specialization of the inner parts, i.e. of the simple cellular components which lose their individual autonomy and favor the establishment of close interactions among the various types of cells. In this phase, the functional effectiveness of these interactions undergo “group” selection leading to “individual” selection once the new level of organization is established. With the appearance of multicellular organisms it was possible to form new types of comunitarian aggregations such as those pertaining to present-day insect society where interdependence among individuals is so strong that the biological autonomy of single insects is nil to favor the welfare of the beehive, or the ant, or termite nest. Among the strictly social insects, the new “individual” coincides with the society itself, while each bee, ant, or termite is a part of a super-organism characterized by highly functional specialization and rigorous labor sharing.

The main evolutionary transitions pertaining to the genomes and their mechanisms are shown in Table 1.

	initial stage	**final stage**
1	free replicating molecules	molecule populations confined in compartments
2	independent replicators	chromosomes
3	RNA as a gene and enzyme	DNA+ protein (genetic code)
4	prokaryotes	sexual populations
5	asexual clones	sexual populations
6	unicellular eukaryotes: protists	cellular diversification: multicellular eukaryotes: plants, animals, fungi
7	solitary individuals	colonies
8	primates society	language: human societies

(After Maynard Smith & Szathmàry, 1995, modified)

Table 1. Main evolutionary transitions (after Maynard Smith & Szathmàry, 1995, modified)

Table 1 shows the sequence of the hierarchical complexity of living systems. From a functional point of view, there has been an optimization of molecular and structural mechanisms (1–3), but only at later stages was an optimum also obtained in the cellular structures and therefore in the metabolic functions (3–4). Still later we witness the most effective use of organization at the level of organisms (and of the developmental processes in multicellular organisms) and populations (5–6) starting from a stabilization of all functions belonging to the previous levels. The origin of social groups and human language are the most recent evolutionary transitions.

The success in producing a higher level of hierarchical organization seems, therefore, to depend strictly on the most effective use of the immediately lower level. This hypothesis seems to be supported by the fact that basic molecular mechanisms (corresponding to the first three transitions in the table) are identically preserved in all living organisms. Furthermore, in pluricellular eukaryotes the developmental mechanisms and the differentiation modes (corresponding to the sixth transition in the table) are also identically conserved.

A relevant aspect in the reconstruction of the various stages of the major evolutionary transitions leads us to question the relationship between the role of natural selection and the level of organization. There is, however, a problem. In the biosphere, cooperative and noncooperative phenomena exist side by side. For example, meiosis is flanked by meiotic drive, and parthenogenesis contrasts with sexual reproduction. Considering that there are situations where there is a conflict of interest between the parts and the whole, how has the production of a number of levels of organization been possible?
An explanation of the mechanisms that would have allowed the transitions is based on the immediate advantage of the cooperative replicators during the transition itself. This advantage would result from the fact that there is a moment of strong genetic relatedness between the combining cooperative individual units in producing the new hierarchical level. These units are identical to each other or belong to few different genetic types. This explains the temporary advantage of replicators in cooperating in a transition to a higher level.

Let us now examine how the new level of organization can be maintained and what the dynamics are between the production of hierarchical systems and the surrounding environment.

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Biographical Sketch

Saverio Forestiero is senior researcher in zoology at the University of Rome "Tor Vergata." His work was mainly in the field of aposematism and mimicry in butterflies and moths by experimental methods. A second area of interest is theoretical and historical aspects of evolutionary biology; a parallel line of research is pursued in philosophy of science.