JULIAN HUXLEY: DEVELOPMENTAL GENETICS AND THE THEORY OF EVOLUTION

YASHA GALL

ABSTRACT. Julian Huxley was one of the architects of developmental genetics. Moreover, he was looking for the correlation between such developmental genetics and evolutionary theory. We have studied Julian Huxley's article "Natural selection and evolutionary progress" (1936). The textological analysis has led us to the conclusion that the article belongs to the fundamental works of the evolutionary synthesis.

KEY WORDS. Julian Sorell Huxley, developmental genetics, theory of evolution, neoteny, rate of gene.

In the memory of Armen Takhtajan (1910-2009),
the great botanist and evolutionist.

Julian Sorell Huxley (1887-1975)—a scientist and geo-politician—has earned several titles. Some call him the Great Huxley, some the founder or one of the founders of the synthetic theory of evolution. Ethologists and ornithologists suggest that his works lay at the basis of modern ethology. Historians of embryology maintain that Huxley brought about synthesis in embryology, or even wider, in developmental biology. In Russia, Huxley was admired for his embryological synthesis, although this was at a time when he was sharply restricted in America, where the founding of this synthesis was seen as being on a "feeble" basis. His experiments, conducted on the Mexican tiger salamander (*Ambystoma tigrinum*), were a genuine scientific curiosity. Everyone suggested that Huxley had made a fundamental discovery in the field of the life sciences, called gerontology. But then it seemed that he had been far from the first. However, for the occasional invalid, Huxley, the event did not provoke his depression. The salamander taught him an unexpected lesson: repeating any experiment can help to formulate an original investigatory program, even in more than one field.

Saint Petersburg Branch of the Institute for the History of Science and Technology of the Russian Academy of Science. 199034 Saint Petersburg. Russia. / Yasha@JG7549.spb.edu

Several historians of science still believe that within his scientific experience, Huxley had made no genetic investigation, and that he and R. Goldschmidt were heretics, or even committed a crime, since they had deviated from a pure Morganistic "transmission genetics" stance. While it is known that Huxley and Goldschmidt were standing at the source of modern developmental genetics, the works of these "heretics" opened up new possibilities and principles in the development of genetics itself, linking it to the classic problems of individual development and evolutionary theory.

Huxley's investigations on the problem of growth were as significant as the investigations of another well-known scientist, D'Arcy Thompson. Huxley joined the circle of founders of contemporary eugenics, and only he related its problems with those of evolutionary theory, which stood out as the foundation for this old and controversial science. Moreover, Huxley saw in eugenics not only a science for improving human beings, but also for preserving humanity's unity with the biosphere. It is entirely legitimate to call him the "Malthus of the twentieth century." The topics of population growth and continuous overpopulation were at the center of Huxley's focus, and here he also achieved a gigantic synthesis. Participating in that synthesis were such sciences as genetics, eugenics, demography, and the study of natural resources. Even if demographers had formally stated population growth in terms of exponents and discovered the field of increased growth, it was Huxley who had contributed the sharpest and most original methods to solve the problems. He suggested forming institutes for controlling the birthrate using sterilization. Huxley was strongly and sharply criticized, yet he was also actively supported; he was thinking of the fate of humanity as a whole. It was Huxley himself who formed the concepts of evolutionary ethics and evolutionary humanism, in order to gain a better understanding of human nature in the relationships between people, personalities, and the state. These concepts had a philosophical character, but in approach and even analytical style, the problem was principally different from academic philosophy. In this aspect, our author can be compared with Herbert Spencer. Huxley's ideas consistently shifted between materialism and idealism, and he suggested that even in such important field of philosophy there were no static relationships. The evolutionary approach permeated even the understanding of the foundation of philosophy. Within his circle of close friends, he called himself a vitalist. From his grandfather he learned the idea of popularizing science and accepted it as his right. Huxley showed the necessity of popularizing science, but in no way was he a founder of popular science. A series of his works, which were labeled, "lectures for the general public," had a deep scientific character. For example, one can boldly call his small book *Evolution in Action* (1953), like the lecture course delivered at Indiana University, a scientific masterpiece, since in it he predicts many future paths for the development of evolutionary theory. Such an intellectual result is possible only with the simultaneous combination of scientific and literary gifts. Julian Huxley's brother, Aldous Huxley, was the great writer, and his half-brother, Andrew Huxley, was a great physiologist and a Nobel Prize laureate. Julian also wrote poems, essays, and was even awarded a prize in literature. Beginning with Thomas Henry Huxley, the Huxley family was a most active participant in the intellectual progress of humankind. In 1968, Ronald Clark, the family biographer, wrote a book in which he extensively discusses all the Huxleys (Clark 1968).

As historians like to note, Charles Darwin lived at Down in Kent in isolated or semi-isolated conditions. Julian Huxley never lived in such circumstances. His creative scientific work through his entire life coincided with the equally creative and original organizational work in the areas of science and culture. Beginning in 1913, he was constantly in a state of stormy activity. In fact, he organized the Department of Biology at Rice University (Houston), headed the Union of Scientific Workers in Great Britain, was elected secretary of the London Zoological Society, and became head of the Department of Zoology at Oxford University and later at University College in London. He was secretary and then president of the London Eugenics Society, one of the organizers of the Society for the Study of Animal Behavior and the British Ecological Society, and the Society of Evolutionary Study. Finally, he served on the preparatory committee for forming UNESCO and wrote the Manifesto for the then highly prestigious organization. He became the first director general of UNESCO. But he was elected as a leader who had proposed the Manifesto of the organization, not as an administrator. In that regard, he is like the member of the French government, René Shmuel Kassen, who prepared the text of the World Declaration on Human Rights, which became the main document for the activities of the UN. Kassen was awarded the Nobel Peace Prize in 1968 in recognition of the twenty-year acceptance of the declaration, but Huxley was never offered such a high honor, although his Manifesto was written and accepted earlier. After leaving the post of director general of UNESCO, Huxley continued to work for the Organization, heading the commission for preserving wild nature and for human population, and also serving as an expert for many educational programs.

With the publication of his biography by his wife, Juliette, it became apparent just how sick a person Huxley had been through his entire life, and paradoxically, how very strong he must have been to live such a richly creative life. Here stands at the highest level the issue of personality, society, and state. Also connected with this is Huxley's persistent attraction to the problems of morality and humanism.

Huxley was a teacher in capital letters. He taught at the universities of several countries, and he taught biologists from a wide variety of fields through his books. Many were interested also in his work in the social sciences, although in these areas he had even more opponents and even outright enemies. Huxley himself preferred to have a small circle of students, with whom it was possible to discuss intensively and freely any scientific problem. His closest students and colleagues included E. B. Ford, Charles Elton, Gavin deBeer, George Baker and Peter Medawar. Subsequently, they all became members of The Royal Society in London, and Huxley always wrote interesting, and, in content, unexpected introductions to their monographs.

Huxley worried over the fate of Soviet biology. With enthusiasm he visited the USSR in 1931 to discuss systematics and evolutionary theory with N. I. Vavilov (even though it was already being concluded, Vavilov became the co-author of *New Systematics*, under Huxley's editorship, which was published in Oxford in 1940). Huxley was ready to believe in the successes of Soviet Russia in the social sphere, which, as Party agents declared, after the Civil War life quickly improved. Yet he viewed with hatred the rejoicing of Lysenko and the death of the great geneticists. Later with the same hatred, Huxley viewed the Stalinist regime and the later Soviet epochs. He knew well that many great Soviet scientists did not appear at international conferences for their political beliefs or nationality. He wrote about this in many publications including two monographs. It seems that it was he who introduced the understanding of "totalitarianism" as it applied to the Soviet regime. He never turned away from Marxism as a scientist, but was a fervent opponent of its incarnation in life.

In this paper I will discuss only one problem: The influence of developmental genetics on the evolutionary views of Julian Huxley before writing the famous book *Evolution. The Modern Synthesis*.

It is generally accepted that Julian Huxley had not delivered in his scientific heritage original genetic studies. Thus, his evolutionary synthesis was in this aspect a kind of scientific compilation. This opinion is absolutely wrong**.** Genetics and experimental embryology developed quickly at the beginning of the twentieth century. T. Morgan's school constructed the chromosomal theory of inheritance and, even more, obtained great successes in the study of the transfer of characteristics. At the same time, there was an active school of experimental embryology in the United States (F. Lillie, E. Wilson, E. Conklin, P. Harrison) and in Europe (H. Spemann, T. Bovery, O. Hertwig). The representatives of genetics and embryology regarded each other with great respect; however, regrettably, they could not find the bridges of collaboration—the abyss between them endured.

Morgan was both an embryologist and a geneticist. As the saying goes, he had the map in his hands to the synthesis of the disciplines. In 1934, he published a book entitled *Embryology and Genetics* in which one chapter discusses embryology, and another genetics, and there simply was no connection between them (Morgan 1934).

Although E. Ford and Huxley thought Morgan's investigations and his school great, they noted that themselves addressed only one aspect—the genetic basis of the effects that make one or several external traits in the adult organisms, at the time when the stages of development by which the result is produced remain in large part hidden from the investigator (Ford and Huxley 1927, p. 112). The goal of the investigation was to study how genes control the time and speed of developmental processes in animals and plants and, even more, to find information on the form of gene action.

The concept of "rate of gene" was first suggested in 1918 by R. Goldschmidt (Goldschmidt 1938, p. 51-78). He discovered that "genetic races" of the gypsy moth (*Limantria dispar*) differed in genes controlling the speed of the release of pigments in caterpillars. In several species lighter tones are maintained until the stage of chrysalis, and in other races coloring steadily becomes darker, the process occurring with determined speeds. He observed that the speeds were average in heterozygote hybrids with intermediary coloring. At the beginning period of his scientific career, he was an embryologist and united embryological and genetic explanations. The narrow differences between adult forms, for him, can be the result of weak variations in the early stages of development. These weak variations increase during individual development and growth. He identified the small quantity of genes that were related to the speed of their action.

In Goldschmidt's well-known book, *The Material Basis of Evolution*, there is a section of "mutations that influence early development" (Goldschmidt 1940). He wrote there: "I observed various compositions of several genes and connected that with a quantity of genetic material. This led to the idea that defined solitary mutations can quantitatively influence the early embryological process by changing its speed relative to other stages of differentiation. If such a mutation survived, it would attract to itself in a single-stage a significant deviation in development" (Goldschmidt 1940, p. 309).

Goldschmidt also wrote that: "My view that mutations are possible, which influence the early embryological development and produce great evolutionary changes, was accepted by other researchers and strengthened in the work of J. B. S. Haldane (1932), Huxley (1932), and especially of de Beer (1930), which worked the problem out in detail" (Goldschmidt 1940, p. 311). Goldschmidt described a panorama of proof for the idea of the importance of variations occurring in the early stages of embryogenesis. The authors of this idea were many zoologists and paleontologists (F. Müller, A. Kelliker, E. Kop, B. Garstang and to a great extent, A. N. Severtsov). Goldschmidt cited many times the German edition of Severtsov's book, *The Morphological Laws of Evolution.* Goldschmidt was just about the only foreign evolutionist who cited the famous Severtsov's work (1931). For Goldschmidt, it was novel that, first in his works and in the works of Huxley, the idea was expressed in the language of physiological genetics, and this united with the concrete study of the action of mutations in early embryological development.

Goldschmidt's investigations certainly influenced the work of Huxley and his students. Of course, such and influence primarily was related to the idea of gene speed and with the methodical side of genetics investigations. For Huxley, who simultaneously investigated growth, it was important to find the genetic basis of allometry. It is also interesting that Goldschmidt was factually a founder of genetics and developmental biology and Huxley's name was always place next to his. A better appreciation for his investigations, Huxley found difficult to imagine.

E. Sexton in Plymouth, around 1913, studied Mendelian inheritance in eye color in sand-shrimp (*Gammarus chevreuxi*). She investigated the entire range of its colors from red to black, proving that the red color is recessive (Sexton 1924; Sexton, et al. 1930). In 1921, Huxley became Ford's scientific advisor, and together they completed a series of investigations on *Gammarus,* using the results of the genetic experiments of their predecessors, but sharply "inclined" towards genetic development, realizing the goal mentioned above.

In the sand-shrimp, the black and red colors are alternative Mendelian traits. All eye colors in adult individuals at first appear red and then change to black according to the accumulation of melanin within a determined speed during development. Ford and Huxley discovered a network of genes, which form a series of colors by changing the rate and the time of releasing melanin into the facets of the eyes. The process partially occurs due to environmental control, since high temperatures favor the release of pigment. Nevertheless, there also exists an entirely complex genetic control over the development. This was best seen when animals were kept at 23 degrees celsius. In these conditions, the gene *R* makes black eyes, when in homozygotes *rr* the release of melanin occurs later and is equilibrium is achieved only when become deep chocolate. Ford and Huxley discovered that the recessive gene *S* so sharply slows the release of melanin that *rrss* individuals never achieve equilibrium even at 23 degrees. Stubbornly continuing the investigations, they discovered the recessive speed of the gene *m*, which slows the level of melanin release lower that the action of gene *S*; individuals *rrssmm* are more "white" that *rrssMM*.

Huxley and Ford also showed that body growth generally influences eye color. Moreover, this is also a combination of genetic and environmental factors. If the environmental factor slows body growth, then the eye color usually remains darker than in the case of normal growth. There is an interesting case of genetics in the homozygotes *mm,* in which the speed of melanin release is so lowered the eyes "whiten" in all variants of body growth. The formation of exact shades of eye color in adults can also depend on the correlation between factors controlling melanin release and factors controlling the speed of eye growth. During the normal formation of melanin, the greater the area of facets, the weaker their color. If this mutation makes the eyes small, then the thickness of melanin increases and the eye looks darker.

Surprisingly, Huxley and Ford immediately built a triad "genetics-development-evolution." If the genes influence the rate of individual development, then this allows for selection to slow down or speed up development in the dimensions the body, of the structural and physiological traits. Here is already the potential for a genetic explanation for allometry and neoteny. Neotenic explanations for the origin of human traits are related to the retardation of development, and have a genetic basis. The rate of gene action directly determines the correlation of parts in the developing organism or the time of appearance of structures in ontogenesis. These most difficult evolutionary problems were outlined by Huxley and Ford in several proposals (Ford, Huxley 1927). Ford recalled that during the experimental work, Huxley always kept in mind the general questions of growth, organism development, and evolution. The concept of gene speed was for him principally a new explanation for phenomena, which had already been studied by specialists. Ford also noted that when the time came to publish their collaborative work, Huxley told her: "You did more and your name should be go first" (Ford 1989, p. 45). Another of Huxley's student, Alistair Hardy, in a collective work devoted to the 65 year-old Huxley and entitled *Evolution as Process,* wrote of the collaboration between Huxley and Ford that: "The well-known work on the study of eye color in *Gammarus*, where Mendelian genes can influence the speed of various developmental processes, speeding up or slowing down the appearance of several traits or parts of the body in relation to others; this is also the explanation for neoteny" (Hardy 1954, pp. 126-127).

Huxley and A Wolsky showed that "albinos" and "colorless" mutants appear not from the absence of the genes *R* or *rr*, but from the fact that melanin cannot be deposited in them, because these mutants do not have the retinal part of the eye, where the melanin can be located. Thus, mutations cannot affect genes, which form pigments as in true albinos, but also hinder the appearance of area, in which pigment genes can conduct their action (Huxley and Wolsky 1932). John Baker, a student of Huxley's at Oxford, suggested an ultra-contemporary evaluation of the work by Huxley and Ford. He wrote: "Analyzing the work—it is one of the best examples of the interaction between genetic and environmental factors, which control gene expression (in this case *r*)" (Baker 1976, p. 220).

Goldschmidt generalized Huxley's and his students' investigations writing:

> Mutant genes produce effects, which differ from the effects of the wild-type, by changing the speed of developmental processes. This might be the speed of growth or differentiation, the speed of reactions which lead to defined physical or chemical situations in determined times of development, the speed of processes which correspond to the isolation of embryological potentials at a defined time (Goldschmidt 1938, pp. 51-52).

S. J. Gould saw in the investigations of Huxley and his students a good genetic basis for understanding the mechanisms of developmental speeding or slowing (neoteny, pedomorphosis). He posits: "This last I hope for universal recapitulation was dashed by discovery that genes act by controlling the *rates of* processes" (Gould 1977, pp. 204-205).

The investigations of Huxley and his students stimulated Haldane to unite the concept of the speed and time of gene action with evolution. Haldane wrote:

> In evolution there is a general tendency, related to individual development: the defined traits appear progressively earlier in the life cycle. This is connected with the time of action of defined genes. Another common tendency—is the retardation of defined traits in regards to the life cycle and, thus, the preservation of embryological traits in adult organisms. The phenomenon is known as neoteny (Haldane 1932, pp.15-16).

The concept of gene speed was widely used by embryologists and morphologists, and also evolutionists, who were both neo-Darwinists and "deviants" from orthodoxy (de Beer 1930, 1951).

The huge significance of the investigations of Huxley and his students subsequently became clear. Briefly, their results can be traced to the following: genes control the speed of developmental processes and can, thus, have a strong influence on the events during ontogenesis that depend on them.

If a given gene is able to influence the speed of growth of some define structure, then it will control the size of that structure regarding the size of the body (the genetic basis of allometry). In addition, one can imagine that gene speeds regulate the absolute times of the appearance of any given structure. Ontogenesis is composed of united and interrelated processes, e.g., the formation of each separate structure depends in time and space on the formation of other structures. Thus, changes in the times of the appearance of one morphogenetic event can have deep consequences, changing many subsequent, dependent levels of ontogenesis. Ontogenesis is always something different, and not a mosaic of developing structures. Huxley knew well the importance of changes in time of morphogenetic processes in evolution, especially in the case of neoteny, the presence rudimentary organs, and the formation of greatly specialized structures. All these ideas developed well independently of Huxley, Goldschmidt, and de Beer. Thus, Goldschmidt showed the program of development is something integral, which does not reduce to the interaction of genes or to gene balance. Here he cited the example of the phenomenon of regeneration, the internal property and tendency of embryological cells to actively to move and combine with other cells to form a new tissue (Goldschmidt 1940, p. 294). The logic of the integrity of ontogenesis is directly related to Goldschmidt's idea that evolutionary development can occur due to a special kind of heritable variations, systemic mutations, or macro-mutations, which affect the earlier stages of development and the character of the endocrine-hormonal status. Goldschmidt thought that chromosomes are an integrated regulated system and that definite infringements of its fields can lead to sharp changes in embryological development.

Huxley thought precisely the same, that regeneration is identified as "an internal property of life"; one cannot simply expound on its presence in lower forms, but on its limited distribution in higher forms (Huxley 1942, p. 418). The genetic foundations for regeneration also interested Huxley. With De Beer, he studied the hormonal control on frog development, suggesting that the action of the hormones themselves is under genetic control (Huxley, de Beer 1934).

In conclusion, it has to be said that Huxley was not inclined to recognize genetics as an independent science. But this does not seem strange or too paradoxical a claim. In genetics, Huxley saw the mechanism that should be used to clarify the facts and theoretical constructions in the framework of classical biology (morphology, embryology).This is seen clearly in his article written with Ford in 1927. The concept of the rate of the gene, developed to explain eye color, was easily extrapolated to the role of neoteny in the origin of humans. Neoteny is a general biological phenomenon, the study of which produced a wide evolutionary-biological construct, and the rate of gene is only a component of that structure.

The synthesis of genetics, embryology and morphology continues to be difficult today. From the position of molecular biology, it has become clear that to speed up synthesis, scientists are pressed to show that genes control ontogenesis. But it is even more important to explain how genes do this.

In almost all historical models on the formation of the evolutionary synthesis, the year 1937 is fixed as the date of the appearance the synthetic theory of evolution. In this year, *Genetics and the Origin of Species* by Dobzhansky (1937) was published. Prior to its publication, Dobzhansky's evolutionary research had a somewhat chaotic character, which had been dominated by Lamarckian, mutationist, orthogenetic, and directly vitalistic views.

In 1936, Huxley presented an address at the British Association for Collaborative Science on "Natural selection and evolutionary progress." The address was immediately published (Huxley 1936). His textual analysis leads to the simple conclusion: He was able to describe in a compressed form almost all the most important problems of evolutionary theory, which later became part of his well-known book, *Evolution. The Modern Synthesis* (1942). In this aspect, not a single publication on evolutionary theory in the 1930s-1940s could compare with his article. Moreover, in his 1936 address, he examined the now lively topic, which includes the triad "genetics-individual development-evolution," deeper and more clearly that in his later works. But it is most interesting that the theme of evolutionary progress almost completely disappeared from the works of the other authors of the evolutionary synthesis.

Well in tune with the spirit of the times, he wrote: "At present, biology is in a phase of synthesis. Before this time, new disciplines worked in isolation. There is now the tendency for unification, which is more fertile that the old one-sided views on evolution" (Huxley 1936, p. 81).

He considered mutations and natural selection to be processes which, taken separately, are not able to produce directed evolutionary changes. Using the historical approach, he succinctly evaluated the panadaptationist, mutationist, and orthogenetic concepts. He stated: "In the opposing views of Darwin and the Weismann school, natural selection by itself is not able to produce evolutionary change. In opposition to the more radical mutationist views and to orthogenecists, mutations by themselves are not able to produce directed changes or close off selective effects. Natural selection and mutations are complementary processes." (Huxley 1936, p. 81). None of the evolutionists had expressed it this clearly. Huxley's words exist literally in all works on evolutionary theory that discuss the synthesis of genetics and Darwinism.

"THE PLURALITY OF EVOLUTIONARY FORMS"

Huxley prefaced his address with a historical evaluation of the existing evolutionary concepts, entitled "The plurality of evolutionary forms", which was written without any dogmatism or bias. Since he sought in the address to present a sketch of the evolutionary synthesis, he first discussed the mistake most commonly made by investigators of evolution, i.e., the raising of a particular aspect of evolution, or the generalization of an evolutionary plan, to the level of a general law. Huxley wrote that: "Investigators of a particular aspect of evolution are inclined to think that their conclusions are true for the whole, but this is not so" (Huxley 1936, p. 81). Since it is not strange for paleontologists to look often on evolution as a gradual process, they think in series and claim that evolution can be adaptive and not adaptive. This conclusion is only partly correct, since first and foremost, it applies only to broadly dispersed species of animals. Therefore, the gradualness is not a universal characteristic applicable to all groups of animals and plants. He wrote: "For the majority of terrestrial plants possess the ability to be interrupted and the sharp formation of new species" (Ibid.) For Huxley, species represented by a few isolated populations demonstrate a completely different evolutionary path than the widely dispersed and dominant species. The latter species most often evolved gradually, but the small isolates are interrupted and not always adaptively.

THE RATE OF GENES AND THE PROBLEM OF ONTO- AND PHYLOGENESIS. NEOTENY

In his 1936 address, Huxley discussed all these important themes together in a section entitled "The rate of genes and selection." He was interested in many considerations. Earlier in fragments he had searched for evolutionary interpretations of the concept of developmental genetics, as suggested by Huxley and Ford. In addition, with such a formulation of the question, we should expect to a systematic outline of the evolutionary theme with the separation of the directions, or strategies, of investigation.

It is interesting that Huxley began his analysis not with his own original investigations, but with Haldane's theoretical article of 1932. In Huxley's opinion, Haldane had an interesting perspective on the time of gene action during the prolongation of development and neoteny, but left aside the question of the influence of genes on the intermediary stages of development and the speed of development in general. This is why the concept of the rate of genes, worked out by Huxley and Ford, has a broader character. The concept of the rate of genes is "forked," with one tooth leading to physiological genetics, and the other to evolutionary theory. To discuss evolution from the point of view of the rate of genes is difficult. Therefore, it is necessary to apply the concept of allometry. Hence, Huxley planned a valuable line of investigations: developmental genetics-growth-evolution.

Not surprisingly, his discussion of evolutionary themes began with the problem of recapitulation. A mutation, which produces an increase in growth speed, should have an influence on recapitulation. Moreover, the reverse, a mutation, which slows growth speed always has anti-recapitulation effects. He drew on De Beer's concept of the so-called *clandestine evolution* (evolution by neoteny, the juvenilization of ontogenesis and pedomorphosis) (De Beer 1930). The concept is essentially the idea that if fetalization, juvenilization, or neoteny took place, then old adult traits disappeared or were replaced by new ones. V. Garstang and de Beer suggested that such a process acted over a long span of time in the ancestors of vertebrates and gastropod mollusks. Huxley presented many examples that took place in evolution of a smaller scale and were related to the slowing of developmental speed relative to sexual maturity.

DEVELOPMENTAL GENETICS AND NEUTRAL TRAITS

The concept of genetically determined speed of growth and development, Huxley suggested, had a direct influence on the formation of adaptively neutral traits. At first, he used the example of *Gammarus*, in which mutations diminished eye size (it is difficult to find the adaptive significance of such a mutation) and in correlation changed the depth of pigmentation. The genetic basis for such a developmental path for Huxley was completely clear and, of course, provided a good foundation for extrapolations. He concluded that the work of systematics in diagnosing species is a project with correlated traits. Of course he did not forget about orthogenesis, although in 1936 he had a much different opinion than in 1930-1932, since Hersh's work had appeared in 1934 (Hersh 1934). Huxley suggested that concept correlated traits plus developmental genetics make it possible to view anew the material that he had discussed in the spirit of orthogenesis. Anticipating the analysis of the materials, he called the orthogenetic interpretation "simulated orthogenesis." Goldschmidt and Huxley unanimously interpreted Osborn's discovery that the horns of one and the same type appeared independently in four lines of *Titanotheres*, not having any kind of adaptive basis—an important fact. However, in 1936 Huxley suggested an allometric interpretation, different from the one in his 1932 book. This new interpretation was rather more interesting than the commentaries he made during the 1940s-1950s. The Titanotheria horns, he wrote, are similar to the majority of horns; they always grow in correspondence with the absolute size of the animal's body, that is, they are uselessly correlated with the useful traits (body size). Yet he elaborated on his new position, noting that the *initial uselessness* later becomes useful. He cited Hersh's research, which showed that in variable environments, natural selection acts intensively to increase the speed of growth. Huxley applied a similar allometric evolutionary explanation to the formation of horns of the Irish deer and to the fantastic horns of several beetles. Finally, he outlined the maximum limits of the evolutionary applications of the rate of genes. He suggested that the rate of genes "illuminates the evolutionary aspect of recapitulation, neoteny, fetalization, and, obviously, useless traits" (Huxley 1936, p. 94). Such a spectrum of applications of developmental genetics according to Huxley-Ford can appear exaggerated. But this is far from true. It is correct that Huxley himself did not manage to use his ideas so widely. Very simply, he accepted the most important role of neoteny in evolution only for the origin and evolution of humans. In all other cases, he admitted doubts, especially in the question of the origin of the higher taxa. Then, de Beer's evolutionary investigations of the 1930s-1950s were almost completely based on Huxley's ideas.

DEVELOPMENTAL BIOLOGY AND EVOLUTION: A GENERAL EVALUATION. NEOTENY AGAIN

We will look again at Huxley's evolutionary program in the 1936 address with regard to the development of evolutionary theory in general. In the framework of the synthetic evolutionary theory, there is almost no discussion of the connections between genetics and developmental biology, and evolutionary theory. Huxley worked on this fundamental problem, and it worried him throughout his entire research career. Actually, he was one of the first (independently of Goldschmidt and Haldane) to place genetics under the understanding of the evolutionary role of heterochrony, especially neoteny.

The conception of the rate of genes, suggested by Huxley and Ford, is most useful for discovering the genetic mechanisms of neoteny, which helps to explain the fast evolution of taxa found at the dead-ends of specialization. Neoteny results in the extremely specialized final stages of ontogenesis being *dropped off*, at the same time the *rejuvenated* taxon acquire a high evolutionary tempo; simultaneously, large gaps can form between major taxa. In this evolutionary pathway, the investigator's attempts to find intermediary simply hopeless.

Huxley's 1936 address was not simply one of the first investigations in the synthetic theory of evolution, but also significantly departed from the canonical framework of the evolutionary synthesis, a framework in which evolutionists attempted to extrapolate almost everything from population genetics or systematics at the level of small taxa in big evolution. Huxley's choice of the triad "genetics-development-evolution" in principle defined a new theoretical route. His concept was a hierarchical system in which population genetics, species formation, evolutionary trends (from family to phylum), evolutionary progress, precisely explained the formation of evolutionary novelty. No one had so consistently developed evolutionary views in the framework of this triad as Huxley in 1936 and Goldschmidt in 1940. The evolutionary views of these two great biologists differ essentially in the cardinal questions of evolution, and this indicates how great the possibilities were for this triad.

It can be said that Huxley had gone far ahead of the evolutionary synthesis even prior to its appearance. This has become quite apparent only now, when Evo-Devo (Evolution-Development) has become the center of evolutionary theory: genetics-development-evolution. In the synthetic theory of evolution, no one discussed this topic. Historians of science have asked: why was there such a poor relationship between embryologists and the evolutionary synthesis? Mayr answered that when genetics entered evolutionary theory, embryologists stopped taking an interest in such a non-orthodox "symbiosis" (Mayr 1991, p. 8). The historian of science, R. Amundson, completed a special investigation and concluded, not unexpectedly, that Mayr was right (Amundson 2000). Thus, the inclusion of embryologists in the evolutionary synthesis did not occur, and based on developmental genetics a parallel synthesis took place, which is called evolutionary developmental biology. Embryologists actively accepted developmental genetics and they occupied an important place in a new quickly developing synthesis. As far as classical and population genetics are concerned, they have no influence on the embryologists. These disciplines shared no elementary theme, and in fact, they became the "work horses" of the evolutionary synthesis. A new generation of comparative and experimental embryologists (e.g. Schmalhausen and Waddington) had already literally "devoured" genetics and made a huge contribution to the evolutionary synthesis and to Evo-Devo. But embryologists were neither ready theoretically nor psychologically to accept Huxley's evolutionary synthesis, the models of which included the entire complement of developmental biology, phylogenetics, and other close components.

The investigatory program introduced by Huxley in his 1936 address has until now not undergone an analysis regarding its place as the stereotype basis for the evolutionary synthesis without the genetics of individual development and embryology.

We wish to acknowledge Natalia Beregoy for the support in preparing this manuscript.

REFERENCES

Amundson R. (2000), "Embryology and evolution 1920-1960: worlds apart," *HPLS* 22 (3): 335-352.

Baker J. (1976), "Julian Sorell Huxley," *Biographical Memories of Fellow of the Royal Society* 22: 207-238.

Beer de G. (1930), *Embryology and Evolution*. Oxford: Univ. Press.

Beer de G. (1954), *Embryos and Ancestors*. Oxford: Claredon Press.

Clark R. (1968), *The Huxleys*. New York and Toronto: McGraw-Hill.

Dobzhansky Th. (1937), *Genetics and the Origin of Species*. New York: Columbia Univ. Press.

Ford E, Huxley J. (1927), "Mendelian genes and rates of development in *Gammarus chevreuxi*," *Brit. J. Exp. Biol*. 5: 112-134.

Ford E. (1989), *Scientific work by Sir Julian Huxley, FRS, Evolutionary studies. A centenary celebration of the life of Julian Huxley*, eds. M. Keynes and G. A. Harrison. London: Univ. Press, pp. 41-45.

Goldschmidt R. (1938), *Physiological Genetics*. NY: McGraw-Hill.

Goldschmidt R. (1940), *The Material Basis of Evolution*. Hanover : Yale Univ. Press.

Gould S. J. (1977), *Ontogeny and Phylogeny*. Cambridge-Mass.: Harvard Univ. Press.

Haldane J. B. S. (1932), "The time of action of genes, and its bearing on some evolutionary problems." *Amer. Nat.* 66: 5-24.

Hardy A. (1954), "Escape from specialization," in *Evolution as a Process*. Eds. J. Huxley, A. Hardy and E. Ford. London: George Allen and Unwin, pp. 122-142.

Hersh A. (1934), "Evolutionary relative growth in the *Titanotheres*," *Amer. Nat*. 68: 537-561

Huxley J. (1932), *Problems of Relative Growth*. London: Methuen.

Huxley J. (1936), "Natural selection and evolutionary progress," *Rep. Brit. Ass*. 106: 81-100.

Huxley J. (1942), *Evolution. The Modern Synthesis*. London: Allen and Unwin.

Huxley J. and G. De Beer. (1934), *The Elements of Experimental Embryology*. Cambridge: Cambr. Univ. Press.

Huxley J and A. Wolsky (1932), "Structure of normal and mutant eyes in *Gammarus chevreuxi*," *Nature.* 129: 242-243.

Mayr E. (1991), *An Overview of Current Evolutionary Biology. New Perspectives on Evolution*. NY: Wiley Liss.

Morgan T. (1934), Embryology and Genetics. NY: Columbia Univ. Press.

Severtzoff A. N. (1931), *Morphologische Gesetzmassigkeiten der Evolution*. Jena: Fischer.

Sexton E. (1924), "The moulting and growth-stages of Gammarus, with description of the normals and intersexes of the *G. chevreuxi," Journ. Mar. Biol. Ass.* 13: 340-342.

Sexton E, Clark A and Spooner G. (1930), "Some new eye-colour changes in *Gammarus chevreuxi* Sexton," *Journ. Mar. Biol. Ass. U. K.* 16: 189-190.

Takhtajan A. (1980), "Outline of the classification of flowering plants (Magnoliophyta)," *The Bot. Rev.* 46 (3): 226-359.

Takhtajan A. (1991), *Evolutionary Trends in Flowering Plants*. New York: Columbia Univ. Press.