

Julian Sorell Huxley, 1887-1975

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Science editor: Academician AL Takhtajan

Preface by the Science Editor

The 20th century was the epoch of discovery in evolutionary biology, marked by many fundamental investigations. Of special significance were the works of AN Severtsov, SS Chetverikov, S Wright, JBS Haldane, G De Beer JS Huxley and R Goldschmidt. Among the general works on evolutionary theory, the one of greatest breadth was Julian Huxley's book *Evolution: The Modern Synthesis* (1942). Huxley was one of the first to analyze the mechanisms of macro-evolutionary processes and discuss the evolutionary role of neoteny in terms of developmental genetics (the speed of gene action). Neoteny—the most important mechanism of heritable variation of ontogenesis—has great macro-evolutionary consequences.

A Russian translation of Huxley's book on evolution was prepared for publication by Professor VV Alpatov. The manuscript of the translation had already been sent to production when the August session of the VASKNIL in 1948 burst forth—a destructive moment in the history of biology in our country. The publication was halted, and the manuscript disappeared.

I remember well a meeting with Huxley in 1945 in Moscow and Leningrad during the celebratory jubilee at the Academy of Sciences. He was deeply disturbed by the “blossoming” of Lysenkoist obscurantism in biology.

It is also important to note that in the 1950s Huxley developed original concepts for controlling the birth rate of the Earth's population. He openly declared the necessity of forming an international institute at the United Nations, since the global ecosystem already could not sustain the pressure of human “activity” and, together with humanity, might itself die. In this aspect, Huxley worked on programs involving eugenics. Eugenics was for him, as it was for our great biologist and evolutionist HK Kol'tsov, a noble science directed at improving the individual and humanity by means of deliverance from harmful or lethal mutations (“our genetic load,” to use G Müller's term), which had accumulated in great quantities. Huxley's Galton Lecture in 1962, “*Eugenics from an Evolutionary Perspective*,” ran into many editions. Comparing the ideas of this great scientist with contemporary programs in human genetics, one notes how far he surpassed his own time.

Even my short discussion leads to the obvious conclusion - Yasha Gall has written an interesting and important book. I am glad to have spurred the author to select the Huxley's creativity as the theme of his investigation. It has been interesting for me during the writing of this book to discuss with the author the historical, scientific, and theoretical problems of evolutionary biology.

Academician AL Takhtajan

Introduction

Julian Sorell Huxley – 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 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.

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, but 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, Huxley can be compared with Herbert Spencer. Huxley’s ideas consistently shifted between materialism and idealism, and he suggested that even in that 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, Huxley 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 Huxley's 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 a great writer, and his half-brother, Andrew Huxley, was a great physiologist and Nobel Prize laureate. Julian also wrote poems, essays, and was even awarded a prize in literature. Beginning with Thomas Henry Huxley (in Russia he was better known as Гексли), the Huxley family was a most active participant in the intellectual progress of human kind. In 1968, Ronald Clark, the family biographer, wrote a book in which he extensively discusses all the Huxleys.

As historians like to note, Charles Darwin lived at Down in Kent in isolated or semi-isolated conditions. Julian Huxley never lived in such conditions. His creative scientific work for 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, 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 UNO. Kassen was awarded the Nobel Peace Prize in 1968 in recognition of the 20-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 Huxley's work in the social sciences, but 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: EB 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 U.S.S.R. in 1931 to discuss systematics and evolutionary theory with NI 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. But 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.

The literature on Huxley exists in the form of articles, which treat separate questions. The majority of works analyze problems of evolutionary progress, ethology, and global views on the world. UNESCO published a small book with the complete bibliography of Huxley's work and an introductory biographical article, written by his student George Baker (Baker, 1978). In 1987, the London Eugenics Society held its 24th annual symposium entitled "Evolutionary Studies", which appeared in the centenary year of Huxley's birth (Evolutionary Studies, 1989). But this collection contains no historical reports or works, with the exception of a small note by Huxley's brother, Andrew, and a student, EB Ford.

The conference organized in 1987 at Rice University was entirely different. The participants of the conference were professional historians of biology and Huxley's friends. Presenters analyzed many aspects of Huxley's activities, and also attempted to reconstruct the spirit of the Huxley's times and theoretical style (Waters and Van Helden, 1992). Comparing the materials of the two symposia, however, it is possible to conclude that they did not produce a systematic analysis of Huxley's evolutionary views, which literally permeate all of his investigations and even appear as their theoretical organizing source.

In considering the figure of Huxley in the present work, it seemed desirable to combine the classic approach, which was best expressed in the scientific biography series of the Russian Academy of Science (RAS), with the theme of analyzing sciences, formulated in the works of the Harvard historian, G. Holton. It is worth noting that in response to recently increased interest in scientific biography, investigations have appeared standing somewhere at the junction between science and literature, or even works in which good literature and science literally blend. Janet Browne's biography of Charles Darwin and A Desmond's biography of Thomas Huxley serve as two examples.

The present work would not have appeared in the present form without the help of many colleagues. Most of all, I am truly thankful to Academician AL Takhtajan. It was Armen Leonovich who, during our long discussions, insisted I study Julian Sorell Huxley's investigations. I am eternally thankful to MD Golubovskii, DA Alexandrov, and Daniel Todes and Lloyd Ackert of the Institute of the History of Medicine at the Johns Hopkins University (Baltimore, U.S.A.) for their constant help in my literature searches. Working in London in 1999 and 2001, I discussed the difficulties in investigating Huxley's creativity with Janet Browne of the Institute for the History of Medicine at the Wellcome Institute. Possessing great experience in the area of scientific biography, Browne combines an invaluable gift for bright picturesque thought, with the ability to analyze scrupulously texts and archival materials. Fate gave me the

possibility to “live” her perception of the history of science for a month. Moreover, I have always received the “stimulant” of the work of American historian of science, G Holton, on thematic analysis. Valuable advice and observations while working on this book were given by: LN Seravin, AB Georgievskii, and KB Manoilenko. EI Kolchinskii, Director of the St. Petersburg filial of the Institute for the History of Natural Sciences and Technology, Russian Academy of Science (IIET RAS), closely followed the progress of this work and organized presentations of its materials at the Institute and at the St. Petersburg Society for Naturalists. MD Golubovskii, MB Konashev, and I co-authored several articles which had directly influenced this investigation. N Beregoi helped me to clarify the translation of several terms and took part in compiling the table of contents for the book in English. Claudine Cohen introduced me to rare French publications of Huxley’s work, which are held at the A Koyre Center for the History of Science (Paris), and persistently recommended that I visit the new building of UNESCO, where there is a bust of Huxley. SK Sokolovskaya inspired in me the hope that this book, if successfully written, would be published. My friends, S Smirnov and G Rednikin “nursed” my computer, getting it to function without stops and interruptions. Doctor Diana Zacharovna Zharnitskaya used her talent and persistence in maintaining my working form. And, finally, my wife, Liuba, Boruhzon daily found her original methods in order to help me work.

This book could not have been completed without the assistance of libraries and archives. MD Golubovskii assisted in receiving a copy of parts of Huxley’s archive, which are held at Rice University (Houston, TX). I am very grateful to the library of The Wellcome Trust (London) and British Library, where all of Huxley’s publications are preserved. The Edward Grey Institute of Field Ornithology of at Oxford University presented me with the possibility to become familiar with Huxley’s notes on observing birds since 1907. I also had the opportunity to read the correspondence between Huxley and David Lack. This invaluable archival material helped resolve difficult questions on the history of evolutionary ecology, which was widely discussed in connection with searching for the causes of the appearance of essentially new ideas in the well-known book by D Lack, *Darwin’s Finches* (1947). The Library of the Zoological Institute of RAS possesses unique works by Huxley’s students and colleagues. The Library of the Russian Academy of Science and its department at the IIET RAS collected the literature on evolutionary biology and I constantly used the services of these excellent and comfortable institutions.

Yasha Gall
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The Creative Path

Origin

Julian Sorell Huxley is a representative of an old family, which gave Great Britain and the world not a few great figures of science, culture, and social politics. His family traces its origins from the time of Richard 1 (1157-1199). At that time, the Huxleys thrived as farmers. At the end of the 18th century they worked as silk traders and well-to-do merchants in Wales. In 1810, George Huxley married Rachel Withers and they had eight children. The seventh child was Thomas Henry Huxley (1825-1895). In his *Autobiography* he noted that he received from his father hot-tempered disposition, stubbornness, and artistic abilities, and from his mother a liveliness of perception, which he valued most of all. His education began in an Ealing school, where his father George Huxley taught (for more on this, see Irvin, 1973).

When Thomas turned 11, the Huxley family moved to Coventry and his father became director of an impoverished bank. Then, in essence, school education ended for the boy. But thanks to systematic reading and independent study, Thomas Huxley made himself into one of the most educated Victorians. "His days were few," his contemporary wrote, "therefore he had the habit of burning candles until sunrise and, throwing a blanket over his shoulders, read in his bed." At twelve years old Thomas dreamed of becoming a mechanical engineer, but the possibility to realize that dream did not arise. He began to study medicine. Both of his sisters were married to physicians, and the husband of one, Ellen, helped him to master an elementary basis in medicine. In 1841 the parents moved to London, and Thomas began to study with a physician named Chandler, who practiced in the residential area near the docks. At first he did not like medicine, and he cheered himself up by spending the great majority of his time reading books in a wide variety of subjects—from chemistry to ancient history. Possessing an ability for languages, Thomas steadily perfected his knowledge of French, Italian and German (and in the process discovering Goethe). In 1842, Thomas became a student of the medical department of the Charing Cross Hospital Medical School. He was awarded a stipend. Lecturer in physiology, W Jones, strongly influenced Thomas's interests on physiology and anatomy, and with his help Thomas prepared his first research project and at the age of 19 actually discovered the existence of membranes in the roots of human hair, known now as the "Huxley layer." In 1845, Thomas passed his Master's degree exam in anatomy and physiology.

After passing the exam, TH Huxley served in the Navy (they needed doctors who were trained in science) as physician on the frigate, *Rattlesnake*. On December 11, 1846 the frigate left Plymouth for the shores of Australia and New Guinea with an expedition to inspect waters. On the trip, T Huxley worked to put in order the zoology of invertebrates, especially the systematics of molluscs, medusae, and tunicates. He also studied the systematics of appendicularia. Huxley presented weighty evidence that appendicularia should be ascribed to the tunicates. On board the *Rattlesnake*, he wrote an article "On the structure and ancestry of the family medusae." In this Huxley showed that medusae are related not to radiata, like starfish or sea urchins, but to a group quite unlike them, such as polyps and siphonophores (sea anemonies and jellyfish). He concluded the article noting that the principle of archetype structure in jellyfish forms according to the same plan as the chick embryo. In Sydney, he wrote four articles, three of which he sent to the London Linnaean Society, but received no answer. In 1849, he sent a large article on jellyfish

to The Royal Society in London. By the time he returned to London, this article had been published in Philosophical Transactions (Huxley, 1849). Based on this work, he was elected to the Royal Society. In 1850, at the age of 25, he became its youngest member. Twenty six candidates had competed for the spot, but TH Huxley apparently was helped by the recommendation of E Forbes, whom Huxley had introduced to the captain of the “Rattlesnake”.

On October 23 1850, the Rattlesnake returned to Plymouth. Upon arrival, TH Huxley gave a report on jellyfish to the Admiralty.

In spite of his membership in The Royal Society, he was never able to publish expedition materials in the same way that Charles Darwin and Joseph Hooker (1817-1911) had published their materials from the South American Antarctic expedition. But in 1851, Huxley’s materials were displayed at the Great Exhibition in London. From 1850 to 1854, Huxley published about twenty articles based on the materials of the expedition. After 1855, he began to study vertebrate animals. This switch resulted from his lectures in natural history and writings for the Geological Survey, which demanded a good knowledge of fossilized vertebrates. He made a principal contribution to morphology, showing that the comparison of adult structures is insufficient for demonstrating homology. Only a study of embryological development of various structures from the earliest stages, showing a general developmental path, would permit one to discuss their level of homology. Huxley conducted wide investigations on labyrinthodonts (an extinct group of amphibians) and tetrapods, and a census of Devonian fish. His great interest in birds led him to investigate Mesozoic reptiles, especially dinosaurs. Huxley rejected the prevailing idea of the close relationship between pterodactyls and birds, claiming that their similarities were only analogies and not homologies.

In 1863, based on a cycle of lectures he had presented, TH Huxley released the book *Evidence as to Man’s in Nature*—a strong statement against anthropocentrism (Huxley, 1863). Eight years before Charles Darwin’s *The Descent of Man, and on Selection in Relation to Sex* appeared, Huxley applied morphological, embryological, and paleontological evidence to show not only the similarity between humans and apes (which Linnaeus had already noted), but also their kinship, to support the idea of the origin of man from the apes. For proof of this position, Huxley used the entire arsenal of disciplines, the combination of which Ernst Haeckel called “the principle of triple parallelism,” adding also the evidence of biogeography—one of the cornerstones of the new biology.

The works of Linnaeus and Thomas Huxley are valued by specialists as “great events in the study of hominids” (Schwartz, 2002). In 1758, Linné introduced into his classification the “Order of Primates,” into which he placed human beings. In 1863, Huxley studied ontogenesis in humans (before Haeckel) and founded a complete hierarchical system of similarities between humans and vertebrates, humans and mammals, and finally between humans and primates. Man, Huxley reasoned, is more similar to the orang utan, chimpanzee, and even the gibbon, and should be included in that order of the primates. Later he came to the conclusion that there was a tighter relationship between humans and gorillas. He rejected the idea of the origin of man by means of a gradual evolution, defending saltationist views also in this key problem.

Huxley’s book, *Evidence of the Position of Man in Nature*, like his course of Edinburgh lectures, was a message to another person. This was Charles Lyell (1797-1875), who had written the books, *Principles of Geology* and *The Antiquity of Man*. Huxley’s book appeared in February 1863, and a year later it was published in the United States, and after two years, two publishers

competed for the rights to publish it. It is also important to note that Huxley's book appeared in two Russian editions.

Huxley's 1869 lecture "*On the Physical Basis of Life*" is for many reasons one of the most notable (Huxley, 1869). He searched for the connection between non-living and living matter, investigated the question of the interaction between matter and consciousness, which was widely discussed in relation to the growth of knowledge in the 20th century by Sir Robert Murchinson, who called Huxley's lecture "the most audacious action of his entire life." Although in an earlier work Huxley connected man with the apes, in this lecture he connected human life not only with the animal world, but also with non-living matter. Protoplasm, Huxley suggested, is the basis for plant and animal life, and its properties depend on the position and properties of matter. He wrote: "...molecular changes in living matter are the source for all other living phenomena." He concluded that "the fundamental doctrines of materialism and idealism, similar to the doctrine of spiritualism and the majority of other "isms," restrict philosophical knowledge." The years have made it clearer that Huxley was more than a scientist.

Immediately after the appearance of Darwin's *Origin of Species*, Huxley with pride called himself "Darwinism's bulldog". Huxley's review of *The Origin of Species*, published in the London *Times* on December 26th, 1859, served essentially as the public declaration of the scientific and public significance of Darwin's book. Huxley not only struggled for Darwin's theory, but revealed that the skirmish helped him to formulate his own concepts. The *Origin of Species* established Darwin's worldwide fame, and defending the book did the same for Huxley.

The first contact between Huxley and Darwin occurred when, upon returning from his expedition to Australia, Huxley sent Darwin a technical report on a series of specimens. A friendship arose and in 1854 Huxley became Darwin's expert on zoology (Darwin had noted Huxley's quick intellect), in much the same way that J. Hooker had served as Darwin's expert on botany and phytogeography. In 1856, when Darwin was already sorting out his notes on species, he invited Huxley and his wife to visit Down House. It is possible that this meeting was full of intrigue, due to Huxley's clear position on questions of zoology, which he discussed with Darwin. Working with molluscs during the expedition to Australia, Huxley noted that all varieties have a common ancestor or archetype structure. Through deduction he concluded that this phenomenon is probably the result of a modification of a single natural type, and the process was called "evolution." Of course, this was not evolution as Darwin understood it, but Huxley suggested that inside each particular group of organisms a gradual change through large intervals of time can produce different varieties or variants. But he did not go farther than variations within groups.

Huxley never was an orthodox Darwinian, however; as a matter of fact, he developed his own concept of evolution, based on a synthesis of Darwin's theory of natural selection and the idea of saltationist origin of species and taxa above the species level. Therefore, when speaking of Huxley's gradualism in evaluating variations in restricting large-scale taxa, one must also remember that before 1853 he had written to Lyell that: "the presence of strong and defined borders are bound with the theory of transmutation. In other words, I am suggesting that transformations can occur without crossings" (Irvin, 1973, p. 286). In 1859, Huxley wrote that Darwin burdened himself with the unnecessary difficulty by demanding that nature does not make leaps. "Nature from time to time makes leaps and recognizing that fact has considerable significance between species, types, and even larger-scale groups" (Huxley, 1859b, p. 142). The

natural selection of saltations clarifies the gaps between taxa and the paleontological record. Huxley, a future Darwinist in spirit, never followed literally Darwin's gradualism, which was more clearly formulated in 1859. Unfortunately, Huxley did not know that in the notes and manuscripts of the 1830s and 1840s, Darwin's position was completely different: he widely used the ideas of saltationist origin of species and large-scale taxa. But Darwin kept his manuscripts a great secret, they became known to the broad public only in 1909 (Gall, 1993; Browne, 1995, 2002). Nevertheless, there is a large scientific literature in which Huxley's devotion to strong evolutionism is contested, even after the publication of the *Origin of Species* (Lyons, 1995). Thus, M Ghiselin asserted that Huxley did not use the theory of natural selection in solving biological questions and remained the pre-Darwinian anatomist, which he had been for the large part of his life (Ghiselin, 1971). An analogous point of view was expressed by Mario de Gregorio, who noted that Huxley approved of evolutionary concepts only after 1868 when he encountered Ernst Haeckel's work (Gregorio, 1982).

It seems that Huxley's critique requires a special investigation. But several remarks need to be made. Huxley did not use the theory of natural selection for one simple reason: he never worked with biological material at the level of species. But the idea of the selection of saltations, actually, is new and lies at the base of Huxley's commentary. And regarding Haeckel's influence on Huxley, this is most likely true. But it is also true that Huxley developed his phylogenetic concepts somewhat earlier than Haeckel.

In 1864, Huxley showed that extinct reptiles have traits of birds, and many extinct birds have traits of reptiles. In 1867, he overturned the classification of birds themselves, having observed that for their narrow demarcation it is essential not webbed extremities or habit of living in water, but mainly several fine palatine bones, not worth attention at first glance. He raised an evolutionary paradox of birds descending from reptiles.

During his entire life, Huxley presented many lectures for both the aristocracy and the workers. However, the most important was the first lecture, which he read in 1852 at the Royal Institute called "Individuality in Animals." In the last years of his life, Huxley paid much more attention to the question of ethics, the social role of science, the philosophy of science, and reforming education.

Thomas Huxley worried about questions of ethics, especially in the light of evolutionary theory. In 1888, his article "*The Struggle for Existence*" was published in the February number of the monthly review, *The Nineteenth Century* (Huxley, 1888). In interpreting the "soft" Darwinian understanding of struggle for existence, Huxley placed his emphasis on bloody fights between organisms and predators. He also applied an understanding of the struggle for existence in such a narrow sense to human society. Naturally, this caused a negative reaction, although in evaluating social phenomena Huxley was not far from the truth. In 1890, in the same journal, appeared Prince PA Kropotkin's (1842-1921) article "*Mutual Aid: A Factor of Evolution*" (Kropotkin, 1890). [Most likely, Kropotkin's article simulated Huxley to publish several articles in the publication *The Nineteenth Century* in 1890. Among them were the articles: "*On Man's Natural Inequality*," and "*Natural Rights and Political Rights*."] This article was aimed against Huxley's work. In 1902, Kropotkin placed that article in his book *Mutual Aid as an Evolutionary Factor*, which was published in the United States. This book attracted such a huge amount of interest that it had to be periodically republished (Kropotkin, 1955). [Several important scientists in the United States sharply criticized Kropotkin's views. TH Morgan—the founder of the chromosome theory of inheritance—suggested that Kropotkin's book represented a collection of fairy tales for children (Morgan, 1936).] Kropotkin's book has also been published in several

Russian editions. It is widely discussed in scientific and public circles (Todes, 1989). Kropotkin not only spoke out against Huxley, but also against Darwin, striving to develop the concept of evolution based on cooperative processes (for more, see: Gall, 1976; Todes, 1989). Huxley did not stubbornly continue to defend his own “gladiatorial” ethics. This is sharply revealed in his second Romanes lecture entitled “*Evolution and Ethics*,” presented at Oxford in 1893. Huxley surveyed the progressive development of humanity, but did not make any analogies with biological evolution. Social achievements, he claimed, are connected with the development of more and more liberal laws and ethical principles. Huxley openly agreed with Herbert Spencer (1820-1903) that moral principles have evolved, but at the same time denied that the evolutionary process provides any basis for forming the very criteria of ethics. Fanatical individualism, according to Huxley, attempts to explain itself as analogous to, or in the application of, cosmic principles to society. As if already criticizing Spencer, Huxley wrote that in such analogies and applications, there is nothing new. In his correspondence, Huxley noted that “The essence of my lecture is to place Christian doctrine on a scientific grounding. The doctrine goes as so: Satan is the Prince of the Present World” (Bibby, 1960, P. 51)

It is interesting that the discussion between Huxley and Kropotkin influenced the views of Julian Huxley. Julian Huxley, judging by his texts, borrowed much from Kropotkin’s works when he worked through his concept of evolutionary ethics and humanism.

Thomas Huxley published many works on religion and teleology, delivered public lectures to the broadest audiences. All this interesting material shows that he was more anti-Church rather than anti-Christian. In the article, “*Agnosticism*” published in *The Nineteenth Century*, he openly wrote that he should be considered an agnostic (Huxley, 1889). Presumably, it is this—the antithesis to Gnosticism in accordance with church history, reflected his religious skepticism. (Agnosticism as a tendency in philosophy was entirely popular during Huxley’s time. There was even a constant publication: *The Agnostic Review*.)

Thomas Huxley was a founder of liberal education. He published a special article on that theme, in which he divided education into four parts: physical training and military matters; home economics, especially for girls; elementary laws of behavior; intellectual training, which should include reading, writing, and arithmetic, and also elementary science, music, and drawing. Huxley’s educational plan was sharply criticized, especially after he suggested that the hours for intellectual training be spent in the following ways: 10—ancient languages and literature, 10—contemporary languages and literature, 8—arithmetic and mathematics, 8—science, 2—geography, and 2—religious instruction. Huxley met with the Committee on Education on February 15, 1870, and from that date to the end of the following year, he had no less than 170 meetings. As a result, Huxley’s plan was accepted as the educational program, which prevailed over other plans for the next fifty years. All were surprised that Huxley included religion in the compulsory structure of education. He himself suggested that through reading the Bible children can acquire at an early age moral values, and religion itself in his educational system was a moral symbol (for more, see: Clark, 1968).

Thomas Huxley did not conceive of his life without family and friends. His close friends were Lyell, Hooker, Tyndall and Spencer. On Sundays, Huxley loved to discuss various scientific theories with Spencer. (The friendship between Huxley and Spencer arose after the publication in 1888 of the article on the struggle for existence in human society, in which Spencer introduced the expression “survival of the fittest” - Darwin had used this expression as

an analogue for natural selection - biologists and philosophers befriended the idea of a “struggle.”)

In 1847, Huxley met Henrietta Heathorn in Sydney, a 22 year old Englishwoman with blond hair and blue eyes, who was interested in German poetry. Henrietta and her father arrived in Australia in 1842 ahead of their family, hoping to begin a successful business. But at the start of the 1850s, the family returned to Great Britain, and Thomas Huxley began to prepare for marriage. They had not seen each other since 1847, and married on July 21, 1855. Their first son, Noel was born at the very beginning of 1857. Jesse Oriana was born in the spring of the following year, and the third baby was Marianna, who was born early in the spring of 1859. In 1860, Henrietta gave birth to Leonard Huxley (1860-1933), who from his first marriage became the father of Julian and the well-known writer Aldous Huxley (1894-1963), and from his second marriage the father of Andrew Huxley, who was born in 1917, a physiologist and Nobel Prize laureate (the first Nobel Prize laureate of the Huxley family).

Leonard Huxley at the age of ten studied at Univeristy College School in London, and later at St Andrew’s University in Scotland. It is difficult to find a simple answer for why his father made this choice because a year later Leonard was awarded a stipend to study at Oxford (he received it in the fall of 1879). Thomas Huxley now chose Balliol College, Oxford for his son and wrote to his friends that he had no doubts about his success. Actually, there was reason to doubt. Leonard, like many of the Huxleys, was quick of intellect and dreamed of popularity. In the company of friends, he always was the center of attention and original, and he loved to travel with students around Europe. In the summer of 1880, returning from a trip to Oxford, Leonard already was sure that he had chosen an academic life. In 1881, he was awarded a first (class honors degree) in a public examination for the Baccalaureate (Bachelor’s degree), and two years later, a first in *Litterae Humaniores*.

Leonard Huxley married Julia Arnold, a niece of Thomas Huxley’s friend, Matthew Arnold. The Huxley family had met at the Geological Society with Matthew’s brother, Thomas who was Julia’s father. It is quite probable that Leonard knew Julia before 1880, when both had been at Oxford. Julia Francis Arnold (1862-1908) was born in Birmingham and was the third daughter of Julia Sorell—granddaughter of the first Governor of Tasmania - and Thomas Arnold, who converted to the Catholic Church (he was a son of the famous Dr Thomas Arnold, headmaster of Rugby School, who remained Anglican). One of Julia’s sisters was the well-known writer, Mrs Humphrey Ward (1851-1920). Our hero Julian would take into consideration her opinion literally on all questions. It is natural that in such an environment, Julia steadily enriched herself intellectually. In the last years of her life, she came to the difficult conviction that religious study is simply “a Christian apprenticeship,” that it should not be sectarian, and should be open to question, on the basis of which it might be possible to cultivate humanity. Julia’s steel discipline surprisingly was combined with an almost light charm. She attended the High school at Oxford as a “home student”. There she again met Leonard Huxley. In 1855, they married and were happy until her death. The two years before their wedding that Leonard had worked as an assistant professor of Greek at Saint Andrews. They had four children. Besides those already mentioned, Julian and Aldous, there were Trevenen (1889-1914) and Margaret (born in 1899). Each of the children decided on their own careers independently. The happiness of this intellectual family suddenly was broken by the death of Julia in November 1908.

In 1912, Leonard Huxley married 23 year-old, Rosalind Bruce. Her father was William Bruce, whose genealogy goes back to the brother of Robert the Bruce of Scotland. The second marriage brought Leonard two sons: David (born in 1915) and Andrew (born, as was mentioned

already, in 1917). In 1939, Andrew and AL Hodgkin worked at a biological laboratory in Plymouth on the transmission of nerve impulses, and a year later they participated together in developing radar. Andrew joined the group set up by Blacket, which included three physiologists, two mathematical physicists, and representatives from three firms that made radar equipment. They completed their work by the late summer and early autumn of 1940. Andrew remained in anti-aircraft defense for the next two years and was then transferred to an operational department of the Admiralty.

Andrew Huxley married Jocelyn Richenda Gammell Pease, granddaughter of Lord Wedgwood (she was always known as Richenda), who was Darwin's cousin. In 1963, Andrew, AL Hodgkin, and JK Eccles became Nobel Prize laureates for their investigation on the conductivity of nerve impulses, which had been published in 1952. And three years after their Nobel article, all authors were made members of The Royal Society.

Leonard Huxley was not only a teacher, but also had an active, creative life in various areas. In 1917, he became editor of *Cornhill*, which regularly published short stories, poems, and articles, for example on Darwin and Hooker. In 1918, Leonard wrote a thorough biography of Hooker with the active assistance of Lady Hooker. This work was highly regarded. Leonard also published the diary of his father, Thomas Henry Huxley, which had been written during the expedition to the shores of Australia.

Childhood, school years

Julian Sorell Huxley was born on July 22, 1887, during the jubilee festival in honor of Queen Victoria (1819-1901), and only began his education at a preparatory school at the age of ten. Three years later he entered Eton College, where his grandfather, Thomas Henry Huxley, had been a governor. From his grandfather, Julian had inherited not only a great interest in the surrounding natural world, but also a quickness of mind. At Eton, the biology instructor MD. Hill had a great influence on Julian, as did the amateur ornithologist E Selous (1857-1914). Later, his teachers were E Goodrich (1868-1946) in comparative anatomy, J Jenkinson (1871-1915) in embryology, and G Smith (1881-1915) in zoology. Julian became seriously enthusiastic about biology. Upon completing college preparation, Huxley received a stipend for Balliol and in 1906 went to study there. He also studied zoology and German. Even during his summer vacation, he went to Germany to study the language in depth. In the Heidelberg library, he read deep into the literature in biology in the original German, and familiarized himself with the experimental philosophers of biology, Hans Driesch, the author of the well-known book on "*Vitalism*". Knowledge of German allowed him to read the ornithology of Ernst Haeckel. Huxley, however, was drawn to what he later called scientific, or evolutionary, humanism. He wrote in his memoirs that he could with great pleasure read Homer or Horace, reading their verses in Greek and Latin. It was not surprising, therefore, that he was awarded the Newdigate Prize for poetry. He spent the fifty pounds prize money on a binocular microscope. In Wales during a long holiday he made his first contribution to an original ornithological investigation. With his brother Trev, Julian observed the "play" (behavior) of estuarial birds, especially the Common Redshank. However, wanting to write about what he saw, he noted how little was written on it.

Naples and a Short Period at Oxford.

In 1909, Huxley was not only awarded a first-class honors degree zoology, but also received a stipend for scientific investigation at the Naples Zoological Station. It is significant that more than thirty years earlier, Thomas Huxley had actively supported Anton Dohrn in creating that station. On the way to Naples, Julian called on his aunt, Mrs Humphrey Ward, and then visited Florence. This is an interesting fact because on his return trip he informed his aunt about his work.

In Naples, he began to work in experimental embryology and conducted experiments on development in sponges. He investigated how sponges reform and continue to grow after segregation into individual cells or fragments. The results of the investigations were published and/or served as the basis for future work in experimental embryology (Huxley, 1912a).

The Naples, the biological station operated according to an ordinary regimen, in spite of the fact that it was constantly visited by continental Europe's best scientists. At the station, Huxley met the biochemist, Otto Warburg (1883-1970) from Germany * who in 1931 was awarded the Nobel Prize in physiology and medicine for "the discovery of the nature and mechanism of the action of respiratory ferments" (Friedman, 2000) [*Andrew Huxley, in reminiscences of his brother, noted that Julian studied biochemical methods of investigation. But unlike Joseph Needham, he never applied them to his own investigations (Huxley, 1989).] Huxley and Warburg, apparently, became friends because the latter loved to consider biochemistry and oncology from an evolutionary perspective. Warburg's biochemical and oncological investigations also influenced the work of Gause (1910-1986) (Gause, 1968; Gall, 1997).

Among the visitors to the Naples Marine Biological Station was Professor E. Conklin (1863-1952) from the U.S.A.—director of the biological station at Princeton University. At this time Huxley received an invitation from the Rice Institute in Houston, Texas, to organize a department of biology. He discussed this offer with Conklin at the final evening at the station. With great enthusiasm, the American scientist told the young Huxley about the advantages that would come from working at Rice. Huxley took it into consideration. That same year, he visited Oxford for a short time, where he received his D.Phil. and became a lecturer and demonstrator in the Department of Zoology and Comparative Anatomy at the University. He studied natural history, and also began a series of investigations into ornithology, which would continue for more than fifteen years. In fact, ornithology entirely captivated Huxley (Huxley, 1970). He observed the behavior of the common redshank, and these investigations resulted in the publication of the first in a long series of works on courting in birds in relation to the Darwinian theory of natural selection (Huxley, 1912b). To evaluate several actions of the male birds he used the word "formalized" (Huxley, 1970). It is now apparent that the majority of cases of behavior, actually, are stereotypical, and Huxley, in the words of Konrad Lorenz, made field natural history scientifically respectable.

In July 1909, the international scientific society at Cambridge celebrated the centenary of Darwin's birth and the 50th anniversary of the publication of his epochal work *The Origin of Species*. Huxley was invited to the celebration. Listening to the speakers he constantly recalled his grandfather who considered Darwin's theory one of the most liberal ideas in science. That theory freed people from the myths and dogmas existing in the science of life, and achieved a synthesis similar to that of Newton. Already at Cambridge, Huxley had decided that all of his

investigations should be conducted in the spirit of Darwin's research, i.e. connected to evolution in nature and to human evolution (Huxley, 1970).

The Rice Institute

The invitation from the Rice Institute led Huxley to think about emigrating to the United States. In November 1911, he sent a letter to Conklin in which he described briefly his plan for the Rice Institute. Before leaving for the USA, Huxley continued to study courting in birds. In the spring of 1912, thirty miles from London he and his brother Trev studied the behavior of the Great Crested Grebe (Huxley, 1914). In his memoirs, Julian noted that the area selected for observation, called Tring, was ideal (Huxley, 1970). Nearby was the Rothschild museum for natural history, which was home to the largest collection of birds in the world. It was natural that the ornithological department of the museum had an excellent library (Rothschild, 1983). Huxley's publication on courting in the Great Crested Grebe was a classic analysis of reciprocal play, and in it he introduced the idea of mutual selection. He discovered that the decoration of the sexes appears only in the spring, and identically in males and females—that their use in play was the same: courting was mutual and not one-sided like in most birds. In all games, rituals played the main role. He was the first to apply the term “ritualization” to the formalizing of ceremonial courting. It was an important moment in the scientific study of bird behavior and in the ethology of vertebrates in general. At that time, he also worked together with the well-known plant geneticist, William Bateson, founder of the experimental study of inheritance and variation at the agricultural institute in South London.

In February 1912, Huxley formally accepted the post of founder and director of the biology department at Rice, and agreed to the inauguration in fall of 1912. The president of the institute, E Lovett (1871-1957), agreed to Huxley's condition that half of his work time would be spent on scientific research.

Rice Institute was founded at the beginning of the 20th century. In 1891, William Rice began to organize it as an institute of literature, science, and art, hoping that it would continue to function after his death. He died in 1901 under mysterious conditions and all of his money was designated for the scientific, literary, and artistic goals of the institute.

In September 1912, on the way to Houston, Huxley visited New York, where many well-known biologists worked. He stopped in at the “fly room” of TH Morgan's laboratory at Columbia University. Huxley developed an especially close relationship with future Nobel Prize laureate, G Müller, whom he invited to Rice to be his assistant. Müller was a great specialist in genetics and was completely “uncomfortable” at Columbia. From his unordinary behavior and quick reaction to any new scientific question he had earned the nickname “the ugly duckling.” Huxley immediately valued the novelty of Müller's thinking and hoped for his help in demonstrating genetics experiments. In addition, in New York Huxley met with E.B Wilson, who was a great authority in cell biology, and he also visited the Museum of Natural History under directorship of the great paleontologist Henry Osborn (G Simpson's teacher). The New York newspapers announced that: “Huxley, zoologist, here.”

After New York, Huxley went to Princeton University in order to meet with Conklin, who had stimulated his transfer to Texas when he two had worked together in Naples. At that time, Conklin had begun to publish his new work on evolutionary theory, in which he outlined his extraordinary ideas on the finale of biological evolution. Huxley with great interest listened to this eminent biologist, and with him actively discussed many biological questions.

Huxley arrived in Houston in October. His room at the hotel was located next to that of the English chemist, William Ramsey and the Dutch geneticist, Hugo de Vries. The inauguration lasted four days and hosted the philosopher Benedetto Croce and the mathematician Vito Volterra, both from Italy, the mathematician Emil Borel from Paris, and Ramsey and de Vries. When the ceremony was over, Huxley visited the Johns Hopkins University in Baltimore, and Harvard University. In Baltimore he learned about the activities of the University's world famous medical school. It was there that he delivered his lectures on the origin of man, and on Darwinism in general. At Harvard, he met the young Norbert Wiener, who at the age of fifteen had earned his PhD in mathematics, and with the daughter of the Bulgarian philosopher, Chanov. Huxley was pleased to spend all his free time with her.

After his intensive networking in the U.S.A., he sailed to England for a brief period before going to Heidelberg and Munich. He received the money for his trip from the Rice Institute. He was filled with energy and spent every minute thinking about work. From Munich he wrote to Lovett: "I think that by March I will have seen enough German methods and universities that I can return to England. I can study specialized methods at home, and I want to get general training in physiology and physico-chemical methods. Some things are better to do in England, but after visiting American and Germany, I would like some time to take a new look at things" (cited in Clark, 1968, P. 168). However, Huxley's plans changed when his engagement to Kathleen Fordham was broken. He suffered his first nervous breakdown, and had to spend some time in a sanitarium not far from Godstone. His grandfather, Thomas Henry Huxley, had also suffered from depression (Desmond, 1997; Waters, 1992, p. 5).

Several months later in September 1914, after emerging from his depression, Julian returned to Texas and remained there for two years, except during his summer vacations. He spent one summer in England, the other at Woods Hole Oceanographic and Biological Station in Massachusetts, which was the largest marine laboratory in the United States and the official oceanographic institute. Many biologists (Morgan, Wilson, and Conklin) had built a series of small homes there. When there, Huxley could alternate between work and rest, as well as visiting interesting people.

When Huxley went to Rice, he took along his first book, which was still in progress, *The Individual in the Animal Kingdom* (Huxley, 1912e). In general, it continued the theme of his first lecture. I read that small book with great excitement when I was working at the Edward Grey Institute of Field Ornithology at Oxford, who was struck by broad zoological scope of this young scientist. Huxley wrote that he had tried to show the extent to which individuality in the animal kingdom shed light on the study of man. With his book he wanted to lessen the still extant gap between science, philosophy, and everyday questions. He noted first that humans, by using supplementary evolutionary mechanisms (he later called this psycho-social evolution), had left the framework of biological evolution. With the help of speech, and later writing, according to Huxley, man was able to escape death. It is also important that, thanks to words and actions a person's intellect could influence other people in space and time. The ideals of active harmony and mutual aid, he suggested, were the strongest means for progress. It seems that Huxley at this time showed that the ideas of humanism and evolutionary ethics, which Huxley actively reworked later, were already being nurtured in this small zoological book.

In the United States, Huxley observed the lives of many races and birds, which inarguably widened his worldview and influenced his subsequent humanistic perspectives. Of course, the humanistic ideas developed steadily, however, and by the end of 1915 he had already given six lectures in Houston on "Biology and Man," the first of which addressed the

relationship between biology and religion. Life in the U.S.A. gave him more than biological experience. He began to view humans and the world more objectively. He later wrote that all the institutions and ideas of his own country were not unavoidable and permanent things—they are relative, being the products of time, place, and circumstances, which interact with particular kinds of human nature. At the Colorado Springs laboratory he heard Lord Morley say that the next great task of biology will be the founding of the nature of humanity—these words reflect Huxley's own thoughts at Oxford. In "*Notes of a Humanist*" he wrote that it is necessary to widen general evolutionary behavior to the developments and processes of human nature, but at the same time he noted that it is dangerous to simply extrapolate biological principles to the human sphere (Huxley, 1964) [Huxley's ideas continue to "work" to this day, especially his ideas about social selection (Burrett, Dunmar and Lycett, 2002).]. Morley's words acted as a catalyst for Huxley and he began to formulate the ideas, which should have become scientific humanism, religion without revelation, to give hope to many people, but instead Huxley earned the title the "great antichrist." Over the years, naturally, the ideas should have evolved, spread, and been qualified. He described the fundamental question that he had solved and outlined clearly, at the end of a series of lectures he gave in 1915. They asked him to repeat the lecture under the title "*A Course of Municipal Lectures*." He did this, and introduced several innovations.

The concluding lecture covered the relationship between biology and religion. He asserted: "New ideas, usually classified as scientific, prevented a large part of society from access to some churches, belief in the sacrament, and from the revelation and authority of the Bible. A scientific view led to the emancipation of men and women from religion, and conveys the increase of education and its greater dissemination. The conflict between religion and science at the end of the second half of the nineteenth century emerged from the authority of the church over human intellect. The problem of emancipation is the question of the current day"(cited in Clark, 1968, p.173). A significant part of Huxley's life was devoted to the reconstruction this world view—a project that was widened by his experiences of two wars.

In 1924, he again visited the Rice Institute and delivered three lectures entitled "*Essays on Biology*." Biology was for him the uniting link between humanism and science. But we have moved ahead of our story.

The First World War was in progress and it dominated conversations in England. This bothered Huxley enough to make him leave Britain for two entire years, with the exception of short visits home. He sailed back almost secretly to Houston in the fall of 1914. His plans changed constantly. He had wanted to live there for 8-10 years, to remain in general in the U.S.A., and then return to England forever. He taught students and built laboratory. He also continued his experiments observing birds. He wrote that in Colorado where he was observing birds, the camp was situated among beautiful asps, not far from a mountain river. In one of the asps were nesting a pair of sapsuckers, which like all woodpeckers hollow out nests in tree trunks (Huxley, 1916). Huxley saw many new birds in Colorado including the western oystercatcher, the small blue-grey bird, and the only representative of the European warbler. His greatest delight was the white herons and herons in general, which lived on a small island in Louisiana. Here he observed two herons in physical contact with one another. He enjoyed observing that the herons—like the great grebe and all other birds that have the same developed sexual traits in both sexes—have mutual courting regimes. Moreover, the organs birds used when playing with one another were especially well developed in each species. He also took into consideration the emotional life of the birds. He noticed that when pairs reunited after one

partner returned with a fish, they entered a state of strong vocal excitement, turning their heads and flapping their wings. He later described the behavior of the birds in a profound, comprehensive article published by the Linnaean Society (Huxley, 1923c).

In the then small Texas city, Huxley first and foremost noticed the abundance of dark-skinned people; for every 100 blacks there were 10 whites. His first impression was not humanist for he said “I am beginning without any kind of process of logical thinking to understand why white people living in such conditions carry revolvers and developed a racist complex” (cited in Clark, 1968, p. 173).

At the Rice Institute, he carried out intensive scientific research on genetics with Müller, studying the relative growth in fiddler crabs and the abovementioned ornithological investigation. In the future, the investigations would be developed as monographs and articles, which were highly respected by the scientific community. The investigations on the fiddler crabs concluded by stating the formulas for allometric growth and a monograph on relative growth, which reported on the new stage of investigations on animal growth. With the ornithological investigations, Huxley advanced new conceptual structures (ritualization, formalized ceremonies, mutual aid), which in themselves and in Lorenz’s work provided the basis for an independent science of vertebrate ethology. Of course, this was not accomplished right away, but Huxley’s work at the Rice Institute undoubtedly was a fruitful period in his scientific career.

After almost a year in Houston, he developed new plans. In a letter to Lovett he wrote that “Finally I understand that in the circumstances, having left Rice, it would be better to not return there. It sounds sharp, but this is—the result of a long process of thinking and reflecting” (cited in Clark, 1968, P. 179). What kind of “circumstances” were these? Mostly, Huxley felt, that as an Englishman, he dreamed of working in English society, having his own special “group.” Besides that, he did not believe that his work went especially well in Texas, since he was more interested in general, not narrow questions. He also noted in a letter that to Lovett that in addition to the usual investigatory work, he should have time for general reading. “General reading” included studying sources in evolutionary theory, and teleology: Huxley saw how much it was possible “to grasp in terminology the evolutionary-naturalistic plans,” which he constantly had in his head. He left America with quite different feelings about the young country than those he with which he had arrived. He declared “A new country, which does not have a stable upper class, teems with chaos” (cited in Clark, 1968, p. 174).

Post-war Oxford

Many of the Huxleys served in the army. Julian’s own participation in the war began by serving in the censor committee, and soon he was commanded the Army staff corps, and a short time later he was transferred to the reconnaissance service was sent to Italy as a lieutenant. While serving in the army, he began meeting with Juliette Baillot, a young woman of French-Swiss origin who was ten years his junior. She was a governess for the daughter of Lady Ottoline Morrell. At first, he corresponded with Juliette and, in the Spring of 1920, three months after returning to Britain, he married her. She came from a family of hereditary Swiss who lived in a small town, which since the 18th century was a center of the watch business. Her father was a lawyer. His partner went to ruin and as a result, the family spent a large part of their fortune in wiping off the debt, considering it their moral duty. Since the beginning of the 20th century one of Juliette’s aunts lived in Britain, and at the age of 16 Juliette acted as the family courier. She

quickly reached out to the intellectual circles of Garsington, which was also visited by Aldous Huxley. She quickly befriended Aldous and through him met Julian.

Of course, Julian had returned for a short time to Rice, but all of his thoughts were on Oxford, where five positions had opened in the zoological department. One colleague had drowned before the war, two had died in France, and one left for another university. The most significant absence was that of the zoologist, Geoffrey Smith, who had died at the Front. Huxley was offered a stipend for investigatory work at Oxford University along, with the possibilities of becoming a preceptor of a new college and of working in the museum.

In post-war Oxford, he understood that over his three years service in the army he had lost touch with current biological thought, and began to doubt whether he would be able to handle the tasks before him. He became depressed and by the end of the first semester, he had his second nervous breakdown. Juliette took a train to Switzerland where they spent several months until Julian returned to health.

Returning to Oxford, he began actively to teach and research. During this productive Oxford period he organized a circle of most able students (John Baker, Gavin de Beer, Charles Elton, EB Ford, Alistair Hardy, and Peter Medawar). On vacations, this circle discussed actual problems in zoology and genetics. Huxley characterized his students as brilliant people each of whom became well-known figure (Huxley, 1970, p. 125). As a matter of fact, all of them subsequently became members of the Royal Society. It is enough to say that Elton was one of the founders of contemporary ecology, Ford conducted fundamental investigations in ecological genetics, Hardy was a great evolutionary morphologist, and de Beer was an embryologist, morphologist, and historian of science.

During the six years at Oxford (1919-1925), Huxley's scientific interests were highly varied. He generalized his ornithological research, describing mating in bird species, and analyzed the question of the evolutionary origin of these rituals. He began laboratory investigations, which continued through the 1920s and into the 1930s. The majority of these were aimed at studying the genetics of individual development, the allometry of growth, and experimental embryology. Perhaps, his most important contribution in experimental work was his simple allometric formula that expressed the relationship between the parts of an organism during the process of growth and development. His formula continues to be widely used today in many investigations on the correlation of onto- and phylogeny (Gould, 1977; Martin, 1989). Huxley taught lecture courses on experimental zoology, genetics, and animal behavior.

Already by the 1920s, he began to think about morphology and evolutionary theory. His short publication in *Nature*, which appeared during that period, touched on the induction of metamorphosis in the Mexican axolotl (salamander) by feeding it pieces of thyroid from a bull (Huxley, 1920). The popular press reacted in its own way to his publication. In the newspapers, articles gave the idea that he had discovered some sort of "elixir of life." He responded that if humanity desired an elixir of life, then it would be necessary to fund science, to open state and private funds to materially guaranteeing competitive projects.

His attempt to explain his work on salamanders for the wide public automatically brought him into the area of popular science. In his Oxford period, he wrote a series of popular articles and his first popular booklet on biology *Essays of a Biologist*, which was published in 1923 (Huxley, 1923d). This booklet was followed by more than twenty books on popular science. Already by this time, Huxley had become interested in the significance of biological knowledge for humanism and public politics. His views on these questions may be traced to his popular

works, however, his more mature statements on this subject came only later. His three volume book, *The Science of Life* enjoyed a wide success in the popular arena (1923-1930). In this work, which he wrote with the father and son H.G. and G.P. Wells, Huxley discussed the problems of evolution and phylogeny (more on this project below).

In this same period, Julian and Juliette had two sons: in 1920—Anthony, who subsequently became a botanist, and in 1923—Francis, who even in his youth took an interest in anthropology.

The Expedition to Spitsbergen

When it became clear that, in the summer of 1921, the Oxford University expedition planned to visit Spitsbergen, Huxley immediately joined. There were two other biologists on the team—Alexander Carr-Saunders and Charles Elton, the geographer and ornithologist Lonisteff, and also the bird photographer, Seton Gordon. The participants in the expedition arrived at Plymouth and there began to collaborate. Working at the Plymouth oceanographic biological laboratory, Huxley noted that several sea invertebrates grow primarily in the Winter, and several others mostly in the Summer; and this meant that in the cold Arctic life should be prolonged, but growth slowed. In West Spitsbergen, Huxley and Elton lived in isolation for eleven days. Huxley conducted a detailed study of mating in the red-throated diver, which gathered to nest and mate on that part of the island. Besides this, he continued his investigation of the greater crested grebe which he had started ten years earlier.

In 1925, he was invited to become the Professor and Head of Department at King's College, University of London. His field investigations were nearing completion, and he continued his experimental investigations at the new college.

It was during this period that HG Wells invited Huxley to write a combined encyclopedic work, offering him the job of editor. In the letter to Huxley, it is clear that Wells made great demands of his coauthor. Thus, he wrote that if by January 1, 1928 the authors could not present the basic amount of materials in an acceptable form, then the contract with the American publisher might be cancelled and the authors would not be paid. Wells expected sustained and quality work (Waters, 1992, p. 8). After being in London for two years, Huxley achieved the realization of that quite grandiose project. Practically all that was original on the project regarding genetics, evolutionary theory, and embryology was written by him.

Secretary of the London Zoological Society

By 1935, Huxley's contributions to zoology were so great that he was elected secretary to the London Zoological Society. Now work in the society became his daily activity. The society was opened in 1826 and from the very beginning it not only decided scientific debates, but also actively participated in education by popularizing scientific ideas in the field of zoology. Thus, the society's secretary directed the scientific work of the laboratory and disseminated scientific knowledge about how to understand the place of animals in the natural world. Huxley applied maximum effort in raising the education of youths in the area of evolution and more than once expressed the necessity for preserving wild nature with its vanishing fauna. He began to invite

young investigators to the society as curators. He wanted young people and experienced scientists to view animals not only as themes for research, but also as living illustrations of evolution. From photographers he demanded a scientifically planned chronicle of birds. Even though during Huxley's time there the society was in constant motion, he sought to broaden its activities. New pens were built for elephants, tigers, and lions. By the Christmas vacation of 1936, Huxley had organized two exhibitions on evolutionary themes. One illustrated the change in an animal's color (chameleons, frogs, toads) to match its background as a defensive ability that had evolved over millions of years. The second exhibit demonstrated Mendelian inheritance showing how the inheritance of color traits in rodents followed predicted lines. These exhibits, which were viewed by thousands of visitors, showed Huxley in his new role, and that of the Zoological Society in general in English life. Almost every day the London newspapers described the activities of the society, and with little money it became one of the most public institutes in Britain.

The Royal Institution invited Huxley to give a series of lectures for young people during the Christmas holidays. At one time the same invitation had been made to Thomas Henry Huxley. Julian chose the theme, "Rare Animals and Vanishing Wildlife." He showed how more and more species are becoming rare and disappearing. In one lecture, he addressed the problem of the disappearance of small populations of isolated people.

After this successful educational project in London, Huxley organized the European Zoological Society, which was modeled on the London society and soon opened in Berlin. His work on a wide public scale continued up until September 1939 when the Second World War began.

From the beginning of the war he intensified his humanitarian activities. In 1941, he published his earlier notes on humanism as a new separate book "*The Uniqueness of Man*" (Huxley, 1941b). In 1943, like his father had fifty years earlier, he delivered the Romanes lecture on "Evolution and Ethics" in which he claimed that ethics is not only the result of evolution, but also a factor in future evolution. In his words, "A man is able to inject his own ethics into the heart of evolution" (cited in Clark, 1968, p. 273).

In spite of the war, Huxley continued to become a well known figure in investigations on the relationship science and the philosophy of morals. The theme of man's place in nature captured his thoughts. He again began to collaborate with official organizations, making recommendations for improving education in colonial countries. When the end of the war approached, he more and more plunged into the preservation of animals and plants on the planet. He understood that industrialization had caused the death of many species and their environments. He asserted that "Man does not live like a machine. People need the beauty of nature, an interest in nature, even more than that—wild nature. They need contact with wild animals, which are living their actual lives in their habitual conditions. People should occasionally leave civilization and live in camps; they should travel" (Clark, 1968, p. 280).

In 1943, the Committee for the Preservation of Wild Nature in the British Ecological Society proposed a law for the preservation of nature. In 1945, the Biological Committee of the Royal Society made a similar recommendation. The government passed a law according to which both national parks were transformed into a consultative organization. In order to use the recommendation in the best way, two committees were formed, which dealt with national parks and wild nature. Huxley directed the Committee for Wild Nature and worked there right until he went to serve at UNESCO. He attracted such well-known ecologists and environmentalists as A. Tansley, Max Nicholson, and C. Diver to work at the Committee. Huxley assisted in forming an

information service on wild nature for the widest public. He published a series of booklets and brochures. Each booklet outlined one aspect of Britain's natural history.

Moreover, he continued his laboratory investigations at King's College and from 1925-1935 he published at least nine large articles and two original books on experimental biology. The first monograph, *Problems of Relative Growth*, treated allometric growth (Huxley, 1932b). In the second monograph, *Elements of Experimental Embryology*, written with de Beer, he generalized his research on experimental embryology (Huxley, de Beer, 1934b). Specialists and historians consider the latter volume to be a great synthesis in individual development (Filatov, 1936; Churchill, 1992). At the height of the war in 1942, he wrote what was perhaps his most important work, in which he laid the foundations for contemporary evolutionary theory. In addition to that foundational work, which was written for professionals, Huxley continued to popularize science and speak on the radio. He conducted many radio broadcasts and carried on polemics with Hyman Levy on the relationship of science and society. Huxley supported projects in science education in world society, visiting Eastern and Central Africa at the invitation of the Colonial Committee for Education.

But we will now return to family matters. According to Juliette's memoirs, her life in 1929 with Julian had entered a period of crisis—Huxley announced that he had a new love interest. He had met Ms Weldmeier, an 18 year old American, when traveling in Africa. In a letter written during the trip he told his wife that he desired to continue his affair and to remain married. Juliette fell ill and the entire Huxley family tried to find a way to fix the situation. But Julian himself found the solution—he finally wrote to his Juliette: “You are my wife, and I am your husband, we should take care of each other, we should do all that is possible to be reunited, this is—a true and great love . . . I learned a lesson; I know myself and you, and want to say only that which you already know: I do not dream of another woman, I think only of my life companion” (J Huxley, 1986, p. 162).

The First trip to the U.S.S.R: Science and Society.

In 1932, Huxley and Juliette were reunited. In her *Autobiography*, she wrote that: “We both needed to love each other and made to the same degree that which was desired” (Huxley, 1986, p. 163).

It is possible that the family reunited after Huxley's first trip with Julietta to the U.S.S.R. The trip was organized and supervised by NI Bukharin in 1931. One of the reasons to include Huxley in the British delegation of biologists and physicians was, probably, his friendship with Herbert Wells and JBS Haldane. Wells was already recognized in the Soviet Union as a progressive writer, who sympathized with the USSR Haldane was known for the publication of his book *Animal Biology* at the end of the 1920s (Haldane, Huxley, 1926f).

The ship *Rudzutak* was sent from the USSR for the English delegation and returned to Leningrad. Here the delegation anticipated a highly packed scientific program. Most of all, Huxley remembered visiting the plant-growing institute, where he met NI Vavilov and the collection of wheat he had collected from all around the world (more than twenty thousand specimens). The conversations with Vavilov made such a great impression on Huxley that he immediately invited Vavilov to collaborate on the study of the structure of species. In Moscow the program was even more intensive—they wanted to stagger the British not only with the

scientific, but also (and primarily) the medical and social achievements, in spite of Huxley's protests and reminders to eat lunch (Huxley, 1970, p. 204). The successes of the Soviet Russia really did impress Huxley—he wrote of them in a book and even insisted that Soviet Russia has a series of advantages over other countries and that it would not be bad to try to learn something from that country (Huxley, 1934c). The Russian experience is telling also because, upon his return home, Huxley participated actively in forming non-governmental planning organizations.

However, his impressions of Russia in no way were exclusively happy. He learned of the first traces of the future unpleasantness with Soviet geneticists, connected with TD Lysenko, from his American friend Müller, whom he had met in New York after working together at the Rice Institute. Judging by everything, Müller had been Huxley's primary informant on the following events in Soviet genetics (Huxley, 1970, Pp. 200-203). The eugenic ideas of Müller and Huxley were close (one can say that they formed them together), and their theoretical interpretation of many evolutionary problems practically were identical. In evolutionary discussions of the subsequent period they often supported one another, in particular in disputes with TG Dobzhansky on the understanding Darwinian fitness (Boothe, 1992). Naturally, the creative friendship of Huxley and Müller influenced the similarity of their approach to interpreting of events in Soviet biology in the 1940s-1950s. However, there was nothing special in their interpretation—they agreed with the understanding of any civilized person independent of their place of living.

Popular Science and Science Organization

The spectrum of Huxley's activities was very broad: experimental work, lectures, scientific and popular treatises, trips, radio broadcasts. He arranged a veritable industry of the production of films on animal life and wild nature. At the beginning of the 1930s he was directed the film *Cosmos, the Story of Evolution* and prepared for the Eugenics Society a film entitled *Inheritance in Man*. His greatest achievement in the film industry was the movie *The Personal Life of Gannets* made with J Grierson and R Lockley. The film tells the story of the nesting, feeding, and courting of the great white seabirds. He was awarded an Oscar for the best documentary film in 1937 (Clark, 1968, p. 209).

In addition, Huxley wrote several popular books on science, regularly submitted articles to such journals as *The Spectator*, and often appeared on BBC. As K Waters noted in May of 1930, *The Spectator* announced an offer to name the five best minds in Great Britain (Waters, 1992). The results of the voting were published in June of that year. Huxley came in 16th in that contest, Ernest Rutherford—24th, and Bertrand Russell—25th.

Soon after the outbreak of World War Two, the BBC invited Huxley to form a united radio program, *The Brain Trust*. It included program "C", the author of which was the philosopher E Joad, and the program director was "Commander" Campbell, who had experience of working with a wide audience. The master of the new program was surprised by the questions asked by the listeners, but it did not interfere with the work. The program was a complete success. Huxley later remarked that "The combination of arguments of philosophers and arguments of biologists was irresistible" (Huxley, 1970, p. 251).

Huxley's drew completely on his scientific experience, with his excellent position in society, in his work on education and the popularization of science. While working as secretary of the Zoological Society, he sponsored regular public lectures for children, organized special

children exhibitions and a Zoological Society for children. At the Society, he also published the journal *Zoo Magazine*, made many films, and opened a studio for the artistic representation of animals. All of this, undoubtedly, made possible the growth of interest in the animal world, and the popularization of science.

However, in 1942, when Huxley was in the U.S.A., he was removed from office. It is unclear why the members of the society expended so much effort to dismiss Huxley. It is thought that over the time of his work at the big administrative post the state and society as a whole gave too little support for scientific research (it is correct that Huxley accused the Members of the Society of a lack of desire to accept his progressive programs). However, there is a basis to think that not the least factor in his dismissal was his strict, one can say, authoritarian directorship (Waters, 1992).

Huxley was always interested in evolutionary questions and considered that area of investigation the most theoretically important in biology. Regarding evolutionary mechanisms, which lay at the basis of bird behavior, he leaned on Darwin's theory of natural and sexual selection. But the change from experimental investigations to the systematic study of evolution occurred in Huxley's first period of work as secretary of the Zoological Society. During that time, the questions of evolutionary theory were completely conceptualized.

From 1936 to 1941, he wrote several articles on evolutionary biology, introducing such a key understanding to the study of geographic variation, as, for example, "clines," and in 1942 the book, *Evolution: The Modern Synthesis*, which in scale surpasses, perhaps, even Darwin's *Origin of Species*. After many years of disagreement in evolutionary biology, Huxley's book made agreement possible. It is interesting that its central idea—the idea of a synthesis of genetics, ontogenesis in the broad sense of the term, and the theory of natural selection—was outlined by Huxley earlier in a popular form (for example, see Huxley, 1926d). Until his Presidential address at the British Association for the Advancement of Science in 1936, however, he had never presented his extremely clear views to a circle of professional scientists. Huxley's book of 1942 was, perhaps, his greatest contribution to biology. In spite of the fact that this book was written during the height of war when Great Britain was under constant air raids, he was able to concentrate completely on the work and produce a treatise, the appearance of which is often associated with the appearance of a new stage in the development of evolutionary theory.

In the 1930s, Huxley showed a great interest in eugenics and published several articles for both the broad public and for specialists. He was an active member of the Eugenics Society and served as its president from 1959-1962 (Allen, 1992). He played a key role in the transformation from an "old" eugenics to a "new" or "reformed" eugenics. The term "old" and "reformed" eugenics were introduced by D Kevles (Kevles, 1985).

The second trip to the USSR and the General Directorship of UNESCO

As early as 1942, after the defeat of the Germans in Stalingrad, the ideas of the post-war organization of the world were discussed in the English higher circles. Among the many ideas was one of an organization which united the nations. In the spring of 1944, the British minister of education, R Butler, proposed uniting the activities of the nations in the areas of education cultural reconstruction (which was soon put aside as a separate matter) and development. By the spring-summer of 1945 the United Nations Organization (UNO) was formed, but science was still not included in the plan of an analogous organization in education and culture. Then Huxley and Joseph Needham (an embryologist, biochemist and historian) insisted that it was not

UNECO, but UNESCO (United Nations Education, *Science*, and Culture Organization), with activities in the sciences being included. Each of them went their own way.

On 29th December 1943, Needham first outlined his thoughts on an international collaboration in scientific research. He declared “I think that the time has come that to achieve success there has been enough work by individual scientists or research groups at universities, associations, etc. and separate countries, and also through personal contacts of scientists from different countries. Now, when science and technology play such an important, accelerating role in the life of humanity, the question rises of the means of providing and effective international collaboration in science. In order to establish the necessary contacts, it is insufficient to introduce in all embassies the posts of “attaché in science,” since their activities will be forged by diplomatic formalities . . . I think that it is necessary to form a service of international scientific collaboration, the representatives of which would have semi-diplomatic status in all countries and would have the full support of the governments in questions related to the conditions of work and travel. One of the immediate tasks of such an international service would be to cooperate in the transfer of recent achievements in applied and fundamental sciences not only from highly developed industrial countries of the West, but also in the reverse direction.”(Huxley, 1985, p. 21). Needham’s creative energy between 1943 and 1946 was fully directed at forming an international organization in scientific collaboration. He outlined his ideas in three similar memoranda and sent them to a large number of diplomats, political actors, and scientists from the countries united in the anti-Hitler coalition. From Soviet, American, and British political sources, he received information on the creation of the United Nations Organization on education and culture. In his opinion, in the framework the new organization science could also function successfully. His third memorandum of 15 March 1945 entitled “*The Place of Science and International Collaboration in the Post-war World Organization*” became the first written document, in which the name UNESCO appeared. It is curious that it was Needham who suggested that the future organization should make a thorough investigation of *The History of Mankind* (Amytage, 1989). British scientists appealed for writing the history accentuating scientific and cultural progress, not military or political events.

In his own turn, in 1944 Huxley traveled to Western Africa as a member of the Commission for Higher Education in the British Colonies. Upon return to London, he suffered another nervous breakdown. He followed a course of medicine and shock therapy which, in Huxley’s own words, “went well” (Huxley, 1970, P. 280). He recovered and in 1945 went to the U.S.S.R., where he was invited to celebrate the 220th anniversary of the Soviet Academy of Sciences.

The effort of the Powers of the USSR to make propaganda of their achievements in science and of the Soviet system itself knew no bounds. The desired effect, at least regarding internal propaganda, was achieved: Western scientists came to say what they were expected to. However, Huxley was not among those who expressed their own positive opinion. He insisted on speaking with Lysenko, who refused under a species pretext, but came to his public lecture (Huxley, 1970, pp. 282-284). A short conversation with Lysenko after the lecture finally convinced Huxley that he was a “Savonarola” of science, not knowing and not wanting to know the international genetics literature. Upon return to London, Huxley first wrote a letter to *Nature* evaluating Lysenko’s activities, and then wrote an entire book analyzing Lysenkoism as a social phenomenon in science (the book was published in London and New York under different titles; Huxley, 1949a, 1949b). It is significant that in this book, Huxley suggested that Lysenkoism was not an exclusively Soviet phenomenon, but under the Soviet (Stalinist) conditions, it took on a

deformed hypertrophic form (Gall and Konashev, 1999). Huxley pointed out to his readers that into this deformed shape had been placed a series of important problems related to the interaction of science and society. Huxley's articles and book with the criticism of Lysenkoism together with the similar articles by his English, American, and other Western colleagues were sent to Spetskhranin the USSR, but were not given to Soviet readers until the end of the 1980s (Konashev, 1991). Moreover, from the criticism of Lysenkoism, Huxley's other works - especially those on social and humanist plans - were not available in the U.S.S.R.

The Stalinist purges and Lysenkoism cardinally changed Huxley's relationship with the U.S.S.R. and Soviet science. He always remained, however, a convinced supporter of the concept of social progress and scientific (evolutionary) humanism. In particular, in the works of the post-war period, he developed ideas which he had outlined during the peak of the war (Huxley, 1947, 1962). One can find many weighty arguments which prove that his trips to the Soviet Academy of Sciences became one of the premises for his social quests.

In the spring of 1945, he returned from the U.S.S.R. and began the post of secretary of the preparatory commission to form UNESCO. This post transferred to him from Alfred Zimmer, who had been director of the institute of intellectual cooperation at the League of Nations, but had become very ill. Huxley began the stormy organizing activity in the new post, with a letter to his colleague at the British ministry of foreign affairs, Philip Noel-Baker, on 14th August 1945. [The rapid inclusion of science in the Organization's plans was apparently related to the atomic bomb attacks on Hiroshima and Nagasaki in August 1945. It had become clear that scientific discoveries had acquired great responsibility.] This letter openly states that the United Nations Organization should have a clearer expression of scientific character when addressing questions of education and culture than was proposed at the present time.

The texts of Huxley's letter and Needham's memoranda, furthermore, were entirely similar in content. Huxley, however, wrote a conclusive program (manifesto) for the new organization. He quickly wrote a brochure *UNESCO, its Purpose and its Philosophy* in which he literally insisted that the organization could not resort to religious doctrines or on any kind of conflicting systems of academic philosophy. The organization should rely on "scientific humanism," which is based the proven facts of biological adaptation and social progress. All these phenomena were introduced by Darwinian selection and continue to act in the human sphere on the basis of psychosocial pressure, which in the final stage will lead to the growth of human control over nature and the preservation of natural forces.

Huxley saw the mission of UNESCO to be the dissemination of the ideals of mutual aid, the propaganda of scientific ideas, and cultural transformation. Members of the preparatory commission sharply criticized Huxley's ideas for being atheistic, and decided not to confirm his document. In November 1945, the creation of the organization was announced in London. UNESCO was inaugurated formally in the second half of 1946 and Huxley was nevertheless selected as its first Director General. But he stipulated a two-year time limit at a time when the position was to be for six years (Huxley, 1973). Huxley discussed his work on the organization's manifesto with his brother, the writer Aldous Huxley, who feared that the institute of intellectual cooperation was an ineffective establishment because of the disagreements in opinion of his colleagues and delegate-founders, and insisted that the majority of the delegates accept the manifesto. Otherwise the new organization might suffer the fate of its predecessor (A Huxley, 1946).

During his short period of work at the UNESCO, Huxley traveled around the world explaining to the political and academic leaders of the new organization's mission, accentuating

the future global world unity. As the secretary of the preparatory commission and General Director of UNESCO, he achieved much in developing a system of national parks, preserving nature, forming museums of science and art, and in applying science and technology to improve living conditions in developing countries. He also succeeded, although less remarkable, in forming institutes to control the birthrate. His ideas on the control of the birthrate seemed at that time far from liberalism and humanism, but they simply reveal how much he thought about the fate of humanity.

At the age of 61, he quit the post of General Director of UNESCO. In his farewell address, he discussed man's predatory destruction of wild nature and the search for a balance between growing and geometrically progression of population and the limits of natural resources. Huxley's depressing prognosis is constantly confirmed today by the World Commission on the Environment and Development (Food, 2000).

After leaving his high responsibilities, Huxley no longer worked in a steady academic position, but did not lose his key position in the scientific society. He gave lectures at scientific meetings, organized scientific conferences, and supported professional societies, including the Ecological Society, the Society for the Study of Animal Behavior, and the Society for the Study of Evolution. He continued to work with UNESCO, and was a member of international commissions.

He went on many wonderful trips with his wife. In his final years, he wrote a two volume autobiography and visited old friends. From all sides came awards and prizes. He was awarded the gold medal for great contributions in planning, for his contribution to preserving nature (from the international union for the preservation of nature and natural resources and the world fund for preserving wild nature), the Darwin medal, and Caling Prize for the popularization of science. During his entire life, however, depression haunted him, and from time to time he suffered a nervous breakdown (1951, 1957, 1966). Huxley died from pneumonia on Valentine's Day, 14 February 1975.

His Legacy

Ornithology and Ethology

In Huxley's rich scientific career, his early field investigations in ornithology have a prominent place. These investigations primarily focused on bird behavior. In the beginning of the 1960s Konrad Lorenz in a public lecture called Huxley one of the founders of ethology. In his autobiography, Huxley described his 1914 article on the study of the greater crested grebe "an important stage in the study of courting in birds and the ethology of vertebrates in general." He also suggested that "it made field natural history scientifically respectable" (Huxley, 1970, pps. 79, 83).

Here are two important historical aspects. First, Huxley very precisely recorded that in 1914, vertebrate ethology was not widely accepted as an independent science. Second, he said almost nothing about the conditions that influenced his investigations.

Today, ethology is a biologically oriented comparative and naturalistic approach to the study of behavior, associated with the names Konrad Lorenz and Niko Tinbergen. Until the 1930s-1940s (even later) the status of ethology was entirely problematic. In order to understand Huxley's place in this process it serves to examine his work on bird behavior in the context of

the theory and practice of his day. But most of all, it is necessary to outline the basic stages of Huxley's activities in ornithology and ethology simultaneously.

One can separate his research on birds roughly into three periods (for more detail, see Burkhardt, 1992). During the first period (1901-1911), he saw birds as a hobby. In the second (1911-1925) he carried out scientific investigations in the field and published a series of five important articles on courting in various species of birds. The third period (1925 to the end of his life) he wrote a series of general essays on bird behavior.

Such extended involvement by Huxley in ornithology and ethology, naturally, reflects the influence of the great English specialists and amateurs of that time. It is necessary to separate this influence in order to single out the individual contribution of a scientist. When Huxley described the development of his own thought in that field; first and foremost he noted his personal field experiences and natural development of ideas, but he recalled which of those ideas might have flowed from the works of other researchers. For example, he wrote that a good ornithologist becomes a good specialist over a long time, at the beginning losing much energy as an amateur (Huxley, 1930b).

In the early period of the development of ethology in Great Britain, amateur ornithologists included such investigators as William Broderick and Eliot Howard. The latter studied the breeding behavior of warblers. This new approach was first described in popular publications and was intended for the broad public. Fowler had a great influence on Huxley. He was an historian and classicist at Oxford, who published many works on the political, social, and religious lives of ancient Romans. He later met the patriarch of British ethology, Edmund Selous and together they took part in field investigations. Selous had, perhaps, the greater influence on Huxley. The investigatory activity of this ornithologist was as yet to receive its deserved attention. Selous, as Huxley wrote of him, could see even in the smallest divergences of behavior factors of variation, and thus material for the splitting of species. He always attempted to unite his observations with the Darwinian theories of natural and sexual selection.

Of the many ideas that Selous developed, the ones that had the greatest influence on Huxley were the ideas of courting in birds. Selous suggested that many behavior traits in birds are related to the higher organization of their nervous system and concerns about descendants. This organization provided all types of action, on which evolutionary forces acted with the help of natural and sexual selection. It is impossible to determine precisely what the young Huxley took from his reading of Selous's works. But Huxley's earlier conversion to the problem of bird behavior, most likely, was influenced by this eminent ornithologist. One might also think that owing to the influence of Selous, he broached the idea of a mind in birds. Most likely, Huxley's enthusiasm for Selous also determined his object of investigation: for ten years before Huxley, Selous made all his observations namely on the greater crested grebe—Huxley's basic research object. Selous actively defended Darwin's theory of sexual selection especially during the period when it was sharply criticized. And Huxley's discussion of sexual selection at the end of his article on the great grebe also flowed from the argument of his ideological teacher. However, the habits of the great grebe were studied by others than Selous. M Bartley had pointed out that they were also studied by W Pycraft in 1911 (Bartley, 1995, p. 92). J Durant presented a wider picture of the great interest in birds in Britain. He wrote "Birds were the Edwardian genre of the biography of animals" (Durant, 1992, p. 253). Durant cites the R Brooks' contemporary survey of the popular investigations of animals, written between 1900-1908, as proof that human morality is rooted in the social behavior of animals. Birds are especially interesting due to their

integrated behaviors of courting, cohabitational life, and care for their offspring. All these rituals were good models for humankind.

The earliest of Huxley's works on ethology is, primarily, a manuscript entitled *Bird Habits*. He wrote it in 1907, attempting to show how the investigation of birds informs evolutionary theory. He used details of bird behavior in order to explain natural and sexual selection. In addition, he explained bird singing as the expression of emotions, recognizing that individuals of one or another species can vary their own behavior. This showed that in birds there is often a compromise between the necessity of defensive coloring and the development of coloring for sexual play. In *Bird Habits*, he also broached the idea of the use of traits or actions by the species as a whole, as compared to its individuals. Subsequently that idea distinctly tracks into Huxley's behavioral and evolutionary works.

He made public his ornithological views in 1909 at Cambridge at a celebration of the centenary of Darwin's birth. He understood that to study evolution, one must find a connection between field and theoretical investigations. In September 1909, he worked at the Naples Zoological Station, studying the differentiation in the sponge *Clavellina*. It is correct that twelve years later he wrote to his student Alistair Hardy that he was not pleased with this work because it founded "on the ideas of other people."

On return to Oxford from Naples in 1910, Huxley came up with the basis for initiating the systematic study of bird behavior. After his first year of teaching in April 1911, he spent his vacation visiting Wells. There Huxley saw a black-bellied plover and great black-tailed godwit. He had never seen these species before and was happy for the chance "to study in favorable conditions the natural behavior and way of life of several widely dispersed species" (Huxley, 1912b, p. 647).

Most of all, he was interested in the courting of male and female redshank. The beautiful play of the males and also of the females, rejects the demonstrational display of the males one after another, and gave him a method for definitively expressing a theoretical explanation for the phenomenon. In a letter dated 10 April 1911, he noted that observations on the redshank confirmed Darwin's theory of sexual selection. He wrote "The very actions of the birds are explained by sexual selection or some modification of that theory. In the redshank, the obvious play of the males and the force of selection by the females is seen. Although males of that species demonstrate great initiative, the final decision must remain with the females" (Huxley, 1912b, pp. 651, 654).

During spring vacation in 1912, Huxley once again observed courting in birds. For ten days he aimed his binoculars at the greater crested grebe. That species had many traits characteristic in both sexes. He made the original claim that, since these structures are used only during courting, they must be the results of sexual and not natural selection. He preferred to use the term "epigamic" as coined by E Poulton. This understanding explains the traits of both sexes, which arise by way of sexual selection (Huxley, 1912d, pp. 601-602).

Huxley's original ideas about the great grebe were published immediately in 1912. Two years later, he published a large and now well-known article in the grebe. By then he had received much useful advice from amateur ornithologists and interpreted the behavior of these birds in a new light. He noted that the playful behavior occurs after the birds have mated. Hence it cannot arise from sexual selection (Huxley, 1919, p. 491). On the first page of footnotes to the article he wrote that the word "courting" in this case can be used mistakenly, since it suggests only a pre-marital behavior. He thought the best term was "love habits".

Considering the playful behavior of the great grebe once again, he concluded that play exists on for selecting a partner and not as a stimulus for mating. "The play serves, probably, in order to keep two birds in paired and the keep them constantly together with one another. From this view of species, apparently, it is important that the entire season between members of a pair is a form of marriage which should be constant" (Huxley, 1914, p. 526). He described a curious dance which the birds act out for one another, "shaking" their heads and bumping their faces; quivering their wings like excited penguins—males and females—dive under water and touch chests. In 1912, Huxley explained sexual behavior of the grebe as sexual selection, but two years later he understood that there exists, apparently, a kind of uniqueness in the actions of the birds with weak sexual dimorphism. Later, in 1920, in an archival note to a manuscript entitled *Island of Birds*, he noted that: "When I wrote about the great grebe, I was already surprised that in spite of the criticism of experimental zoologists, there was something to the Darwinian theory of sexual selection—nature simply does not make colorful plumage and energetic actions in the male without a genuine biological advantage" (cited in Bartley, 1995, p. 93). But if Darwin, built his theory of sexual selection on the study of birds with various colors and plumage then Huxley suggested that something new and stimulating can be done in zoology by studying the identical equipment in both sexes and symmetrical playing in birds (Ibid. p. 94). Huxley had observed that many actions and structures are seldom used in courting, although they are useful for a species as a whole and are supported by natural selection. Since the actions and structures of male and female grebes arose due to the sexual selection of males, therefore, Huxley suggested there was a steady transfer of secondary sexual traits from males to females and back. He called this property "mutual selection" or "mutual sexual selection" (Huxley, 1914, p. 524).

In the 1914 article, Huxley separated out the mating of the grebe, which occurs in the beginning of the season, from the vivid playing, which continues even weeks after the mating. He suggested a phylogenetic scenario by which mating over an entire season was replaced by mating limited to the earliest period. In the period of rest, however, the mating pair continues to perform the courting "dance," because, Huxley thought, "action keeps the pair together. Actions became the symbol of the birds' desire to remain paired and, connected with pleasure and stimulating emotion, might become a channel through which these emotions might expressed in and of themselves" (Huxley, 1914, p. 507). The happy "exhaustion" of the birds flows from the liberation of emotional energy during mating. He noted that "When everything is finished well the action is accompanied by vibrant and exciting emotions, which usually fade away or change, developing into completely different feelings" (Ibid. p. 95). He wrote further "the excitement of the birds is not always completely exhausted by the act of mating, and the act is usually repeated over a long or short period, thus it can be called an exciting courtship. General sexual excitement appears in both sexes"(Huxley, 1914, p. 526). The exhausted grebe is also common. Mutual courting "is a marriage" and the joint construction of the nest, noted Huxley, gives the species a huge advantage. In the article on courting in the great grebe, he repeatedly used the same terminology that characterizes sexual relationships in both humans and birds (for example, "sexual emotions" and "ecstasy"). Thus, he wrote "Courting action in a person is mainly predetermined inheritance. However, it is precisely these same actions that we observe in the great grebe. They are no different from one another"(Ibid. p. 510).

Huxley suggested that a bird's mind does not differ greatly from that of a human—birds possess emotions and desires, stormily expressing them in their mutual courting "dance." The historian of science, Mary Bartley noted: "It is clear that Huxley was interested in comparing the minds of birds and humans and revealed the evolutionary connections between organisms.

Evolutionary arguments were, for him, the main means of understanding the behavior of birds and humans” (Bartley, 1995, p. 91). At the same time, Huxley selected the traits for comparison which allowed him to theorize in the direction comfortable to him. Thus, he wrote: “The great grebe is a species in which both sexes are equivalent in all actions in the family life. From the point of view of the species, it is apparent that there is great value in the fact that “marriage,” when pairs stay together the entire season, provides a great advantage. A similar result of marriage is observed in such species as humans, but in a person the main reason for living together is the division of labor between men and women, when in the great grebe both sexes behave equally alike, as far as is possible” (Huxley, 1914, p. 516).

In Huxley’s archives, Bartley observed the manuscript for the lectures “*Biology and Man*” which the British scientist delivered at Rice in January 1916. It was a series of lectures on the sexual behavior of man, in which Huxley united human progress with the relationship of the sexes. Claiming that “the woman should be simply practicality,” he actively defended the beautiful model of the equality of the sexes, demonstrated by the great grebe (Bartley, 1995, p. 98). Huxley was convinced that mutual sexual selection uninterruptedly improves man. This type of selection is one of the leading paths to the emancipation of women. On the example of the grebe, Huxley felt that men and women as “members of a pair should be together and constantly support one another” (Cited in Bartley, 1995, p. 99).

It is interesting that after describing courting in great grebes and the stimuli that lead to the cohabitational life of pairs, he once again returned to the problem of man. He wrote “monogamy was the best decision and, of course, that monogamy when two partners in law also have the same rights and possibilities. Mutual selection, as we have named it, will actively participate in the growth of cohabitational life” (Ibid.).

As this did not appear paradoxical, constant parallels between the social life of birds and man was Huxley’s working analogy by which he had proof of human progress. Among the reasons for stating the question thus, possibly, was that many lecturers in the U.S.A. and Great Britain struggled for the rights and equality of women, for raising their educational qualifications. In these countries, however, there also existed the opposite tendency, which supported, for example, such authoritarian organizations as the Eugenic Educational Society. Their representatives claimed openly that women should sit at home and raise the children. Perhaps, according to the traditions of their mother Julia Arnold (founder of a school for girls) and grandmother on their mother’s side (Mrs Humphrey Ford) who were defenders of women’s education and the rights of women in general, Huxley became an active supporter of equal rights. The grebe led him to recognize how wonderfully organized are the cohabitational and social life of the “lower” animals. The analogy presented few difficulties for Huxley to move from birds to humans and back: the grebe provided a good example for the equality of the sexes, which women dreamed of achieving, and most important, birds showed the way for steadily improving man.

Returning to England after World War I, Huxley began experimental work on metamorphosis in the Mexican axolotl. He also continued to deliver lectures on ornithology, which were still focused on the greater crested grebe. The most interesting aspect of his lectures, however, was comparing the life of grebes and man. The idea of mutual sexual selection, which grew out of a study of common monogamous birds, he actively extrapolated to the life of man. This theme sounded especially loudly at the Royal Institution of London. In 1926, at the British Association for the Advancement of Science at Oxford, Huxley presented the near sum of his fifteen year study of courting in birds, declaring that the family life of birds has achieved the

highest level of development in the form of the equality of the sexes and that the remaining species in their evolution of this equality was “intercepted.” In the book co-authored with HG and GP Wells (father and son). *The Science of Life*, Huxley devoted an entire chapter to courting in birds, again making the connection between birds and man. (Wells et al., 1929-1930, p. 1233).

The question now arises of how observations on the greater crested grebe led Huxley to construct a theoretical relationship between natural and sexual selection. He repeatedly noted that even before writing the “large” article on the great grebe, he was convinced of the truth of the theory of sexual selection. The idea of mutual selection allowed him to take the first step towards the view that playful traits, which are used during courting is the inevitable result of sexual selection. From that idea also appeared his first use of the concept of the ritualization of behavior, to which he returned at the end of his career. Forty years after the publication of the article on the greater crested grebe, he organized a symposium on ritualization at The Royal Society in London.

Huxley’s 1914 article as a foundation in the development of ethology as a whole, served as a source for the most varied theoretical and historical-scientific interpretations. Durant suggests that the anthropomorphic tone of the article lies at the basis of all of Huxley’s explanations. Huxley directly extrapolated from humans to the behavior of animals (Durant, 1992, p. 255). What was the goal of his anthropomorphism? First, Huxley implied, as has already been mentioned, that the masterly conjugal life of the birds, monogamy, and defense of offspring serves as an example for the relationship between the sexes in humans. In the most real sense, he admitted morals in animals. Durant also criticizes Huxley for combining terminology that describes sexual relationships in humans and birds.

It was especially necessary to consider Nobel Prize laureate Lorenz’s evaluation of Huxley’s article. Lorenz, who had trained with Huxley at Oxford in the 1920s, wrote that: “When my teacher and friend Julian Huxley not long before the first world war undertook his pioneering, in the original sense of the word, investigation of the behavior of the greater crested grebe, he discovered the wonderfully engaging fact that distinct forms of action in the process of phylogenesis lose their own real original function and turn into a purely symbolic ceremony. He called this process “ritualization.” He used that term without quotes; in other words, without any hesitation he identified cultural-historical processes leading to the rise of rituals, with evolutionary processes, which generate so many surprising ceremonies in animals. From a purely functional point of view such an identification is completely justified, since we have not tried to keep in mind the difference between historical and evolutionary processes” (Lorenz, 1998, p. 101). The concept of ritualization that Huxley suggested occupied one of the central places in Lorenz’ creativity; he developed it into the most varied aspects.

Lorenz demonstrated the importance of evolutionary ritualization using the example of the forming of instincts that block aggression. He wrote “It is namely to instincts, arising from ritualization, that very often in the Parliament of Instincts the role falls to come out against aggression, directing it to a safe course and impeding its influences which are dangerous for preserving the species” (Lorenz, 1998, p. 108). Lorenz completely subscribed to Huxley’s ideas that rituals acquired by a cultural-historical path, and rituals acquired during biological evolution in spite of their differences are so similar that they can be used, as Huxley did, without quotations. “The functional analogies reveal,” Lorenz wrote, “how with the help of such completely different causal mechanisms the Great Designers achieve almost the same results” (Ibid.)

And finally, it is impossible not to include a long citation from Lorenz's book on the formation of rituals in the processes of the evolution of species. "Already more than a half-century ago," Lorenz wrote, "Huxley made the discovery of extraordinary importance, having proven that the mutual understanding between animals of one species, that is, in objective terms the coordination of their social behavior, realized with the help of "signals, which symbolize" completely the defined form of behavior. In his classic work on the great grebe (1914) he wrote, the way the male during courting gets for the female the materials for the nest from the bottom of the water, and then holding it in its beak makes on the surface of the water an action that undoubtedly reminds one of the actions made during nest building. In human language, the signal says "let's build a nest together." Already Huxley had clearly understood that many human methods of mutual understanding also appeared from symbolized representations of distinct methods of behaviors. Since in this case the process of their appearance is not evolutionary, but cultural-historical—this often leads to the free formation of original symbols in humans. But the analogy between both processes, and also between the functions that rise from them, goes so far that it seems justified in both cases to speak of "ritualization" and of ritualized actions; thus Huxley in 1914 also had embraced a complete understanding of the essence of the matter" (Lorenz, 1998, p. 426).

Excerpts from Lorenz's book are aimed at many thoughts. Probably, one can say that there is hardly any work on natural history published in the 20th century that can compare with Huxley's ornithological article in its significance for biology, sociology, and psychology. The great grebe, perhaps, is the basic source for thoughts and facts that encompassed Huxley's idea of the growth of biological evolution into psycho-social evolution, and, perhaps the reverse, Huxley's general reasoning which was tested on "bird" models. Moreover, the idea of both biological and social progress to a significant extent also flowed from the work on the greater crested grebe, but all this needs proof.

Along with the great grebe, Huxley also studied other birds, the behavior during mating of which less clearly related to the "model" of human behavior. In 1912, he described a case of "disharmony" in the mating of wild ducks (*Anas boschas*). He borrowed the term "disharmony" from I Metchnikov's treatises *On the Nature of Man* and *Studies in Optimistic Philosophy*. It is interesting that Huxley cited Metchnikov in the articles on ducks and the great grebe in public lectures delivered at Rice University in 1916, and a final time in *The Science of Life*. It is completely clear that Metchnikov had a great influence on Huxley's views on evolutionary progress. Metchnikov viewed life as a constant struggle with disharmony towards improvement (that term was used by Huxley as a criteria for progress), for harmonious conditions and relationships between people. Huxley completely sympathized with Metchnikov's thoughts on the continuous improvement of man by way of science.

In his manuscript on wild ducks, Huxley discussed "disharmony" as the absence of adaptations that counter the results harmful to species. He observed that in the period of mating in the set birds, crowds of males crush around one female trying to mate with her. As a result, each year seventeen percent of the females die—"an entirely significant loss for the species, and that loss is caused by the properties of that very species, that is, the consequence of the disharmony in the constitution of the species" (Huxley, 1912c, p. 622). He defined "disharmony" in the mating of wild ducks as the mission of adaptation to lead to harmful results for a species. He suggested the concept "disharmony" for the existence of various individuals and species, comparing disharmony with functioning structure, which "are poorly adapted" for life. It is possible because wild ducks exhibited narrow adaptability and could not provide proof for the

moral or physical improvement of the species, Huxley seldom mentioned them in his investigations.

Having encountered “disharmony” in wild ducks, Huxley immediately began parallel observations on the great grebe—they always acted on him beneficially on an emotional and intellectual plane. Thus in the course of investigations of bird behavior lay his broadest evolutionary constructions. On the “emotional” nature of the grebe, he based intellectual similarity of man and birds, although he suggested that: “birds diverge along their own real lines” (Huxley, 1930b, p. 105). It is interesting that, in spite of the absence of a direct connection between birds and man, he thought that such traits as, for example, emotions, should be used in arranging groups into “higher” and “lower” ones in regard to mammals. In an emotional relationship birds made up a higher “grade” in evolution, than several mammals, but structurally they do not belong to the same “clade” (Bartley, 1995, p. 101).

In 1921 during Huxley’s first period at Oxford, he organized an expedition to Spitsbergen. One of the results of the expedition was the publication of three large articles on bird behavior, and on courting in the red-throated diver. Although his articles are not as well-known as those on the great grebe, one compares with them in quality and significance. In this article, he came to the conclusion that “Darwin’s original theory of sexual selection in its time was completely adequate for explaining the origin of the majority of sexual ceremonies which are observed in monogamous birds” (Huxley, 1923c, p. 269). Here he accented the relationship of natural and sexual selection, viewing the organism as a whole. Therefore, he wrote: “The form of courting in several periods represents the consequences of causes which are connected with other fundamental biological needs regarding the yearly cycle of the animal” (Ibid., p. 273). The very idea that forms of courting are connected to other traits of the life history of species became the basis of the behavioral-ecological investigations of Niko Tinbergen and his students in the 1950s at Oxford. But let us return to Huxley. His cited article ends with the words that the Darwinian theory of sexual selection should be turned aside since a large percent of traits and actions used in courting cannot be explained in terms of competition for females. The development of an epigamic trait, according to Huxley, depends on the effect that the opposite sex has on the mind of the bird.

In the spring of 1925, Huxley completed an expedition to Holland. There he studied the behavior of the Eurasian oystercatcher (avocet). He was struck most of all by its singing. Probably, it was the first “simply accidental product of higher emotional tone in the breeding season. Later,” Huxley wrote “the ceremony became the stereotypical play” (Huxley, 1925c, p. 895). On returning from Holland, he began to consider a project that should have become a large monograph on courting in birds. But he never wrote such a book.

In 1925, Huxley went to London and his scientific interests changed. He published several new articles on bird behavior, but did not make any new observations. In Amsterdam he delivered a lecture on “*Biology and Courting in Birds.*” Four years later at the 8th International Ornithological Congress in Oxford, Huxley gave a lecture on coloring in birds. In 1938, he published long articles on the Darwinian theory of sexual selection in the light of contemporary investigations. For Huxley this was a wonderfully difficult and sneaky problem. On the one hand, Darwin insisted on that term, but since his first publication Huxley began to imitate him, and on the other hand, when sexual selection acts on an individual, a conflict often arises with the “good” traits of the group. He thought that, maybe, the most noticeable result of sexual selection is the appearance of poorly adapted traits such as bright, curled feathers in the males. But if poorly adapted traits are able to accumulate in a species, how then is progress realized? He

tried to solve this dilemma for over thirty years. At first, he looked at the theory of sexual selection as the female choice of a partner and competition between males, but later decided the theory of sexual selection should be looked on as the theory of natural selection (Huxley, 1938c, 1938d). This is not simply semantics. Avoiding this dilemma occurred in the following way. It was as if he accomplished a “synthesis” between compromising forces. He defended “the mutual sexual selection”—a process by which traits steadily move from one sex to another and both sexes become similar. In the great grebe he demonstrated that transfers existed which become symbols of cooperative and progressive change. He suggested that similar transfers are a mass phenomenon and therefore Darwinian sexual selection includes the competition between males, and act in monogamous families in sexually non-dimorphic grebes. Selection, therefore, acts in the direction of group improvement (species) and this falls under the action of natural selection.

The basic difficulty with the theory of sexual selection for Huxley was the mechanism of the female selection of a partner. Darwin strictly insisted that the females are able to select males as potential mating partners. But Wallace criticized Darwin’s theory. Huxley with doubts accepted the idea of selection, but not as the main factor, since, for example, in the grebe the males and females exhibit similar functions during courting.

By 1938, Huxley had changed his opinion of the theory of sexual selection. Female choice and competition among males, he suggested, are not affixed to many traits. But at the time, he had not yet observed birds and his change of view is related primarily to reconsidering his earlier experiences. In 1926, he had abandoned empirical investigations because he began to write *The Science of Life* with the Wells. In 1921, in a short article in *Nature*, he described several important arguments on which basis he placed the idea of sexual selection in doubt. His central argument was that grebes and other birds often form pairs prior to the mating ceremony takes place; that is, the mating ceremony has very little influence on the actual selection of partners. Besides, competition between males for mating accompanied by any form of selection by the females is not a common phenomenon, as Darwin had postulated, but apparently, a relatively rare phenomenon, characteristic of a few polygamously structured species (Huxley, 1921s, p.566). This idea precisely in the very same species was conveyed in Huxley’s 1938 publication. He wrote that sexual selection is a secondary factor of evolution. Bartley suggests that this critique of the theory of sexual selection in unison with electing to investigate monogamous species (the greater crested grebe) established the avenue of Huxley’s future transfer of these ideas to the question of man. Durant also confirms that all Huxley’s investigations on birds were imbued with the spirit of anthropocentrism and therefore the transfer of ideas from one sphere to another was his investigatory norm (Durant, 1992).

Durant was one of the first to unite Huxley’s ethological and evolutionary investigations as a whole (Ibid.). This was not difficult to do. For Huxley, evolution was not a simple biological fact, but more of a central philosophical principle which equally applies to biological, intellectual, and social phenomena. However, Durant traced the formation of Huxley’s fundamental evolutionary notions, and in light of these notions, discerned the relationship of sexual and natural selection in his articles of 1938. A line of monist evolutionary philosophy ran through Huxley’s entire life, according to which matter, life, and reason were only different expressions of a single dynamic world system. In 1923, he outlined these ideas of a new evolutionary philosophy, which did not contain a conflicting beginning (Huxley, 1923d). In his view the elements materialism, idealism, rationalism, and romanticism were linked. He was simultaneously an atheist and a religious person.

In ethology, the mixture of elements was even more apparent than in Huxley's views on the evolutionary process. His worldview formed under the influence of Darwinism but its roots are located in scientific humanism that looks at the evolutionary process as the source of moral principals and even spiritual inspiration. A future Darwinist, Huxley clearly understood that the evolutionary process is materially and morally progressive. The question lay in the combining of Darwinism and humanistic ideology. With such an approach, none of the evolutionary biologists took on the problem of producing a synthesis on such a high level. Already apparent in an address of 1936 is the influence of ethology on Huxley's evolutionary position. In it, he talked about the general delusion according to which natural selection always helps a species, or even life as a whole. However, intraspecific selection often leads to destructive results (Huxley, 1936a). This evolutionary conclusion undoubtedly follows from Huxley's observation on the greater crested grebe and wild ducks.

In his 1936 address, he also noted that: "If we cannot discover the purpose of evolution, we might at least trace the direction of evolutionary progress. And this previous direction can serve as a key for determining our goals for the future" (Ibid., p.100). It is interesting that such a balance between the aimlessness of evolution and evolutionary progress is present in all of Huxley's works on evolution. To survey this question more completely, it is more expedient to analyze his general evolutionary opinions.

Huxley stands out from contemporary evolutionary biologists in steadily reducing the theoretical status of individual selection and simultaneously increasing the role of group selection in S Wright's interpretation. The reason again lay in ethology. For Huxley the classic case of individual selection was Darwinian sexual selection. But Huxley regarded it always entirely indefinitely, since Durant suggested that he separated the philosophy of biological and social progress - he also knew that individual sexual selection can produce traits which do not give an advantage in the struggle for existence. Huxley wrote "Interspecies selection, on the one hand, should lead to the biological improvement of the species. Intraspecies selection, on the other hand, should act to aid the evolution of traits that are useless or even harmful for species as a whole. An example is the competition between males" (Huxley, 1930b, pp. 22-23). Therefore, according to Huxley, sexual selection can act in a direction opposing natural selection, not producing primarily an individual and a species in the struggle for existence. To follow all the discussions of the main reason for intraspecies competition which lead to harmful adaptation, it is best to search in Huxley's work on wild ducks (Huxley, 1912c). First and foremost, such successful and clear material simply does not exist in any other field of natural history.

Huxley's concept of intraspecies selection was developed by Lorenz. "The cycles with positive reverse connections," Lorenz wrote, "always carry with them the danger of an avalanching accumulation of any generation away from equilibrium. The special case of positive reverse connections is met when individuals of one and the same species join themselves in competition, influencing the development of the species by way of *selection*. This *intraspecies* selection acts completely otherwise from selection that occurs from environmental factors: it produces changes in the heritable material, not only lowering the perspective of success in corresponding species, but in the majority of cases appreciably reducing them" (Lorenz, 1998, p. 16). Lorenz cited the following example of an act of such a type of intraspecific selection (his point is correct, although not completely clear)). During the period when they make their mating call, the male argus pheasant (*Argusianus argus* L) unfolds its wing feathers and they return to the female's side, like the tail of the peacock, where such a role is played by its upper covering

feathers. The choice of partner, as reliably established in the behavior of the peacock, depends exclusively on the females.

Durant suggests that Huxley's abrupt attacks in defense of sexual selection might not have happened if he had analyzed it in the framework of "little" evolution (Durant, 1992, p. 159). But Huxley himself understood that it was impossible to "omit" completely individual selection, and came to the conclusion that many traits which Darwin attributed to sexual selection in reality were the result of natural selection. Huxley never denied sexual selection and only considered it a secondary evolutionary mechanism. The wide evolutionary view and the social philosophy of humanism in large part determined the path of Huxley's theorizing in ethology. By rights, Huxley belongs to the founders of evolutionary ethology, and at this point we must search for the transition from classical to contemporary ethology. Before Huxley, no one introduced into descriptive natural history so many new dimensions, based on the deep understanding of Darwin's evolutionary theory. One of the leading ethologists of Great Britain, R Dunbar, wrote: "In the very best of traditions of explanatory (in opposition to purely descriptive) science, Huxley used Darwin's theory in order to understand the behavior of animals and to use the behavior of animals to develop new views of evolutionary theory" (Dunbar, 1989, p. 61).

We should not forget, however, that Huxley began to discuss the problem of social progress at the very beginning of his scientific career. For example, he discussed the "disharmony" of Metchnikov in his first scientific booklet *The Individual in the Animal Kingdom* (1911-1912), that is, a year before his investigations on the great grebe. The idea of evolutionary progress is briefly outlined in that booklet. Therefore ethological constructions were not only a source for Huxley's general biological and philosophical conceptions, but they themselves formed in the broad context of the interaction of biological and sociological thought.

In 1936, Huxley was involved in the founding of the Institute for the Study of Animal Behavior and became its first president. Selecting him for this duty provides the best evidence of the recognition of his huge contributions in developing the entire complex of behavioral science. An ethology itself rose with such speed that it occupied a place in the hierarchy of sciences next to molecular biology. Huxley's efforts to develop an approach for studying animal behavior, which would be based on the interplay of observation and theory, was taken up by all contemporary ethologists and formed the cornerstone of so-called functional analysis (Tinbergen, 1963). Darwin and his contemporaries expressed the idea that behavior might be studied from an evolutionary point of view, precisely because morphology is studied by comparative anatomists. This was a new idea based on principle. With time, however, it proved to be speculative and in reality its application no longer worked. Huxley sought an approach that would provide a result, an approach in which "structure precedes function" (Huxley, 1914, p. 492).

He asserted that if we search for sense in animal behavior, then the deciphering of what would make the act to survive or flourish more effectively would become more decisive. Thinking over the problem of inheritance in evolutionary explanations of behavior, Huxley consistently came to see that any biological fact has three different senses (Huxley, 1942). Discussing behavioral (or morphological) traits he underlined that one can suggest a mechanistic (or physiological) explanation, which describes how the studied phenomenon works; one can give a functional (or adaptive) explanation by identifying that which the given peculiarity allows the animal to undertake; and finally, one can suggest evolutionary (or historical) explanations, in which the sequence changes occur. Huxley's methodology in explaining a biological fact was wholly adopted by Tinbergen in his discussion of the status of various ethological methods. To

the three dimensions of a biological fact suggested by Huxley, Tinbergen add a fourth—the study of development or ontogeny (Tinbergen, 1963).

It is worth considering specially one of the very last theoretical constructions that Huxley introduced. Ethologists immediately took great interest in it. We are speaking of the term “grade.” Huxley employed this term twice: in 1958 for solving the problem of classifying phylogenetic structures (Huxley, 1958a) and in 1959 at a Chicago jubilee in a speech on Darwin and the fate of his study for characterizing the style of animal life (or species), which occupied a special ecological niche. Huxley was able to look upon the role of ethology in the development of evolutionary theory in a new way (Huxley, 1960). His ideas were developed in a series of well known publications by J Crook, on the evolution of social system in weaver birds and primates (Crook, 1965, 1970). Crook showed that adaptation to the needs of specific niches can have predictable consequences for patterns of dispersion, which are favored by mating. The assumption that ethology can offer a decisive force in social evolution, simulated field investigations over a twenty year period. Huxley fully described how his ideas influenced ethologists in the 1930s-1940s (Huxley, 1966). Practically no journal that published articles on ethology managed without an analysis of the phenomena of rituals in the most varied animals and humans.

Contemporary investigations on animal behavior, suggests Dunbar, are different from the investigations completed by Huxley and his classical ethologists in three important aspects. The first is the transition from studying behavior as such to studying relationships in which animals use behavior as an intermediary. This step lead to the higher dimension of functions, to the analysis of the nature of the relationship between functions, and to the understanding of the functional “end,” included in the behavioral pattern. The second aspect is the highlighting of quantitative data. Although numerical data was introduced by Tinbergen in the classical stage of the development of ethology, they carried an episodic character and concerned field experiments. The third aspect is closely related to the second and is the use of powerful theories for making detailed working hypotheses on the behavior of animals that can be verified (Dunbar, 1989, p. 62).

Contemporary theories in ethology are actually different from Huxley’s early ideas. His early ideas, however, formed the foundation for many key contemporary investigations. Ethology even today constantly returns to Huxley’s work on the study of the behavior of the great grebe. “Julian Huxley, even today, remains a young person, the same enthusiast and the same leader in ethology” (Dunbar, 1989, p. 76).

Experimental Embryology

The study of embryology in the 19th century mainly was concerned with the study of phylogeny. The data of embryology was used to inform phylogeny according to Haeckel’s biogenetics laws or other theories of recapitulation. Experimental embryology, however, completely turned away from the phylogenetic direction. Even J Jenkinson, who had been Huxley’s teacher in embryology, shunned it. Huxley always supported Jenkinson’s view that individual development was not a simple repeating of an ancestral series. For Huxley embryology represented a particularly experimental discipline and he never related his own experimental investigations with phylogeny.

His experimental investigations were devoted to ontogeny in the widest sense of the word. He began these investigations in 1909-1910 at the Naples Marine Biological Station, and then continued them in Oxford and London. A part of the investigations was completed at Woods Hole Oceanographic Biological Station in Massachusetts.

In 1907, Wilson had shown that if a sponge (*Microciona porifera*) is pressed through sterile gauze it disintegrates into separate cells which lose their ability to differentiate and change into a mass which is like a syncytium (a multi-nucleus protoplasm which is not separated into cells), from which a new sponge can develop. In Naples Huxley worked with two species of the more primitive family *Sycon*, which were able to live in the station's aquaria (Huxley, 1912a). Investigating differentiation, he used the same technique as Wilson. He succeeded in showing that when cells are isolated they form particles that were incompletely differentiated,, failing to form a syncytium. Afterwards the cells congregate into groups, each of which develops into a completely new individual. It is surprising but he tried to speculate on the significance of regeneration for evolution. The article containing this speculation was published when he was 23 years old (Huxley, 1970). Here he suggested that the protozoa were the predecessors of sponges, but later was careful in confirming that the development of *Volvox* was not the result of phylogenesis, but the result of the special conditions in which the cells are living. He, of course, felt that his results could not be used against the theory of choanoflagellate. If this theory was correct, the cells of these spheres should be able to grow into other types of sponge cells and they all should all come from a choanoflagellate parent.

Huxley's next experimental step was with *Ascidiella* (*Clavellina lepadiformis*). Studying the speed with which its organs underwent differentiation, he concluded that *Ascidiella* are seemingly not the only anatomically complex organism to any significant extent which are able to regenerate after complete de-differentiation (Huxley, 1926a). However, he found no clear phylogenetic result to answer the question that arose during the sponge investigations. He practically repeated Jenkinson word for word, that the experimental study of ontogenesis is a weak key for understanding phylogeny.

In 1912, Huxley published a work on the sponge about cellular differentiation resulting from his investigations in Naples. Wilson in his own investigations on hydroids suggested that specialized cells give a beginning to "totipotent regenerating tissues." and Huxley did not think that, at the time when all tissues become morphologically dedifferentiated in the process of reduction, cells would not physiologically dedifferentiate (Huxley, 1921a). After the first "shock" of dedifferentiation produced by the unfavorable conditions of the culture, the cells are still able to dedifferentiate, and their state inside the cellular mass is determined by their abilities to develop sooner than their state which determines their differentiation. His 1921 article differs from his 1912 article in that he was able to compare normal and abnormal development. In this regard, he discussed the importance of experimentation in embryology. He knew that the understanding of anomalous paths in development permits for more effective understanding of normal development.

In his collaboration with de Beer, Huxley studied the effects that result from the influence of poisons or starvation in *Obelia geniculata*. Investigations showed that under the action of poison, hydroids are inclined to dedifferentiate; however, in various parts of the body processes continue at different speeds (Huxley, de Beer, 1923a). Huxley became more interested in differentiation processes than in subsequent morphogenetic changes. He completed the work, however, as if it was contrary to that which he had done before. Together with P Murray, Huxley studied how in many cases separate characteristics acquired by the cell are functions determined

by the area or environment in which they are located. The epidermis, which is similar to the epidermis chorioallantoic envelope of the bird embryo, does not normally display horns, but it can become horny if some tissue is transplanted on it (Huxley, Murray, 1924b). But in known environmental conditions of environment an apparent loss of specific characteristics or differentiation can occur, and then the tissue reverts to its non-differentiated type. Such dedifferentiation is, however, reversible.

In a long series of experiments, Huxley investigated in particular the effects of the so-called temperature gradient in amphibians. The essence of the experiments was to add another gradient to those already existing in the early stages of development. With his assistant D Kempson, he made an apparatus that allowed for the simultaneous maintenance of one embryo at a high temperature and another at a lower temperature. These experiments on cell division achieved interesting results. Often it was noticed that in two portions of the eggs of one lying where part of the cell was at a higher temperature, and part did not, no principle difference was observed. The cells of the anomalous hemisphere acted differently: the heated cells divided faster, stimulating division in the other parts of the egg. Huxley gave a lecture on that theme in the U.S.A. This was before 1927, when V Vogt had published his article outlining similar experiments - he had investigated higher temperatures and focused on the later stages of development.

The American embryologist Charles Child showed the existence of “dominant” regions of high metabolic activity. They were revealed by studying the reactions of embryos to metabolic poisons. These dominant fields establish physiological gradients, which give differentiated sensitivity to poisons. The gradients are responsible for determining the polarity and symmetry of organisms or organs. Huxley drew on Child’s ideas and methods in order to evaluate the relationship between the zooid and stolon, when the colonial ascidian, *Perophora*, undergoes reduction in response to unfavorable culture conditions. He concluded that his results supported Child’s claims.

Besides his experimental work on morphogenesis, Huxley conducted theoretical and popularization activities in this field. He published a short article in German in which he attempted to interest German biologists in Child’s theory of axial gradients. Moreover, he strove to prove that G Spemann’s “organizer” is a special case of Child’s gradients (Huxley, 1930a). This is interesting since in the 1921 article, Child’s gradient theory increasingly dominated Huxley’s investigations and occupied a central place in the book written with de Beer.

Experimental embryology was one of Huxley’s greatest scientific interests during his early creative period. In 1924, he published a general article entitled “*Early Embryological Differentiation*” in which he surveyed analytically the progress in embryology from the time of Jenkinson’s 1909 book. In the article, it is clearly seen that the work and ideas of Child and Spemann had a great influence on Huxley (Huxley, 1924c). Huxley wrote “Allow me at the beginning to give a formal explanation of the early stages of development. During gastrulation, every part of the fetus has a defined relationship the system of metabolic gradients. There is, firstly, spinal-abdomen, that is, the main Spemann organizer. The chromosomes provide both the complexity and also specificity of development, at the time when two main gradients provide the differences between the parts of the fetus, which are necessary for the beginning of differentiation and the activity of the spinal lip, in order to activate the energy for the network of processes of action” (Huxley, 1924c, p. 278). Eight years later, Huxley and de Beer collaborated in writing one of the best books on embryology. In that book they focused on neither the problem of growth (Huxley had already written a book on that theme) nor of metamorphosis. Their goal

was to describe the basic discoveries in the investigation of the causes for differentiation. Their book differed principally from other books in that they did not merely describe their own research. They attempted to extract general principles from a wide survey of contemporary knowledge. They broadly interrogated embryological material with developmental genetics. But prior to discussing their book, it is necessary to examine Huxley's other experimental, analytical, and theoretical activities in order to see the scope of the synthesis in relation to development.

The Salamander: The Elixir of Life

"The Elixir of Life" is in fact related to salamanders. In February 1920, Huxley presented a report to the London Linnaean Society in which he outlined the results of his investigations on how thyroid iron from a bull stimulated metamorphosis in the Mexican tiger salamander (*Ambystoma tigrinum*), and in that same year published a short note on it in *Nature* (Huxley, 1920). The newspapers quickly reacted to the report, publishing stories about the "elixir of life."

The reaction of the popular press could be understood only in the context of the investigations of hormones in the 1920s (see the survey of newspapers: Witkowski, 1986). The idea from the 17th to the 19th century that the functions of an organism were controlled by trace chemicals, led to clinical observations concerning the activities of specific glands. For example, in 1849 the Edison syndrome was described, which was explained by the destruction of the adrenal gland. In this research, important significance was given to work with animals, in which the new ways of studying the function of glands and their secretions progressed. Investigations were most intense on the thyroid gland and in 1891, for treating a patient. Murray used injections of the thyroid gland of a sheep. By the end of the 19th century the existence of internal secretions was completely accepted and anatomical, physiological, and clinical investigations became the independent science called endocrinology. Society waited for news about the hormone study and wanted to believe that Huxley would turn the dream into reality.

Perhaps the most interesting aspect of the history of metamorphosis in the tiger salamander is that Huxley was not the first to study it. By 1865, it had been discovered that tiger salamanders are larvae that breed without metamorphosis. In 1912, F Goodernatch reported that tadpoles that ate thyroid glands underwent premature metamorphosis making fewer but normal frogs. Not one of the other glands produced a similar effect (see Huxley, 1970). In 1942, a Cold Spring Harbor Symposium was organized on the theme - the relationship of hormones to individual development. In his report, E Witschi called Goodernatch's work "an intriguing discovery" (Witschi, 1942). It was not by accident that after its publication, the investigation of the role of thyroid glands in the metamorphosis of tailless amphibians acquired a wide scope. The most varied methods of experimental embryology appeared, including also surgical manipulation of embryos.

Huxley actually was not original in his experiments on hormonal control of metamorphosis in tiger salamanders. However, his experiments on the essence of the topic became a large investigatory program, which can be called "morphogenesis and evolution"; and maybe, an even broader program—growing from biology into sociology. In amphibians, metamorphosis can be partly or completely suppressed, nevertheless the larvae achieve sexual maturity and breed. The phenomenon known as neoteny is not rare in amphibians, and is also widely spread in invertebrates. Huxley began to consider the role of neoteny in the origin of great taxa and in human evolution (the naked ape), which preserves juvenile traits in adult life,

for example continuing the growth of the brain in the post-natal period. Humans have an extended period of maturity and an extended childhood when they succeed in receiving from the previous generation what Karl Popper later called the third world, or the products of human intellect, such as science, art, weapons, and etc.

Huxley's work with tiger salamanders was instructive also for historians of science. The "unoriginal" experiment can be a stimulus for entirely original thoughts and experimental investigations, which end up far away from the theme of the concrete experiment. However, it is worth noting that the role of hormones in the process of morphogenesis is not analyzed in the monograph Huxley wrote with de Beer, *Elements of Experimental Embryology*. Perhaps this is directly related to the fact that Huxley did not discover, but only "rediscovered" that field.

This small work on tiger salamanders, however, led him to a broad investigation of hormonal control on morphogenesis (Huxley, 1925a). In vertebrates, there are several structures under control of hormones, these being made in special glands. In frogs, the hormones of the thyroid gland were of great interest that was related to the development of many structures. Huxley claimed that the difference in the development of animals enumerated below can be explained by differing speeds of the development of the thyroid gland.

Bufo lentiginosus (toad) – metamorphosis occurs at the beginning of Summer.

Rana temporaria (grass frog) – metamorphosis occurs at the end of Summer.

Rana clamitans – metamorphosis occurs in the next year.

Rana catesbeiana – metamorphosis occurs in the third year.

Huxley was concerned with the connection between the speed of metamorphosis and the size of animal bodies. Before metamorphosis, toads obtain the smallest body size in comparison to the other animals listed above. In the future embryologists directly connected the time of metamorphosis with the concept of the speed of genes, and de Beer was one of the first (de Beer, 1951, p. 21).

And thus the line of investigations known as "genetics in development" found a concrete incarnation in the investigation of metamorphosis.

Genetics and Development: The Rate of Genes

In the first quarter of the 20th century, both in genetics and the biology of development, more and more investigations took place. However, little was done to synthesize them. Embryologists were absorbed in the mechanics of the process of ontogenesis and geneticists were occupied with explaining the laws by which the transfer of traits occurred. The two fundamental biological fields developed for the most part independently. It is correct that genetic discoveries influenced evolutionary theory, but experimental embryology did not have any influence on it. The strange alienation of disciplines from one another has several causes. S Gould showed that the most important reason was the denial by experimental embryologists of the biogenetics "law" (Gould, 1977). D Ospovat claimed that this denial emerged from the fundamental works of K Baer (Ospovat, 1976). As much as geneticists accentuated the transfer of characteristics, it made it completely natural for them to be isolated from embryologists.

In the article "*The Gene and Orthogenesis*" F Lillie wrote: "At the present time geneticists postulate that over an entire life of a given individual, its genes at any place and at any time are

identical, if one does not consider the appearance of mutations or anomalous crossing of chromosomes, which in the future will follow the very same laws. The most important problem of development is namely differentiation in space and time over the entire life of a given individual, which geneticists are apparently ignoring. The successes of genetics and physiology of development can be applied only to the most narrowly limitations of these two fields of science, and all hopes for their unification (in the Weismanian sense), in my opinion futile. Those who want genetics to lie at the foundation of developmental physiology need to explain how certain and unchanging complex can direct the flow of the regulated stream of development” (Lillie, 1928, p. 368).

It is clear that such a categorical denial of the role of genetics in the developmental biology of individual development and in the forming of a synthesis between disciplines was due to several important reasons. First, early Mendelians thought of the gene as a kind of particle, transferred to offspring in the spermatozoa and egg. Namely these corpuscular factors (genes) provided for the development of the individual in the process of ontogenesis. Naturally, similar views were completely denied by experimental embryologists, since they reeked of preformism, a theory that had been “buried” long ago. Second, Mendelism openly admitted that chromosomes and genes are precisely regulated and all cells precisely receive completely identical sets of them. The fact of experimental embryology disputed the conclusions of the Mendelians. It was well known that ontogenesis consisted in the successive distribution of the egg’s cytoplasm between cells that accompany the constant judging of its morphological potential. Embryologists unanimously asserted that genes in general cannot direct ontogenesis. Thirdly, as has already been mentioned, there was a primordial divergence between geneticists and embryologists: Mendelian genetics was interested mainly in the transfer of characteristics from generation to generation, when embryologists studied the development traits in the limits of one generation.

Genetics and experimental embryology developed quickly at the beginning of the 20th 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 USA (F Lillie, E Wilson, E Conklin, P Harrison) and in Europe (H Spemann, T Boveri, O Hertwig; see Bagley, 1979). 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 1932, 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, 1932).

Although Ford and Huxley thought Morgan’s investigations and his school great, they noted that they 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, 1927f, 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 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, however the process occurs 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 this 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 noted in his 1920 book his understanding that "genes which control development act by way of changes related to the speed of the integrated process of differentiation" (Goldschmidt, 1923). He wrote: "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 JBS 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, AN 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 Severtsov's work). 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 an 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 placed 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 with 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. But 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 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 than the action of gene *S*; individuals *rrssmm* are more “white” than *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 become, 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 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 it came time to publish their collaborative work, Huxley told her: “You did more and your name should be go first” (Ford, 1989, p. 45). [In Keller’s monograph on the history of the gene concept completely ignored the developmental genetics of Goldschmidt-Huxley, and does not have a single citation from either of these authors (Keller, 2000). This is quite strange since Keller loved heresy in science and wrote an entire book on Barbara McClintock, who traditionalists branded just like the investigators of developmental genetics. But compensation came in 2003, when the historical-scientific and philosophical book, *The Concept of the Gene in Development and Evolution*, appeared (eds: P Beurton, R Falk, and R Rheinberger, 2003; see also Moss, 2003)]

Another of Huxley’s student, Alistair Hardy, in a collective work devoted to the 65 year-old Huxley and entitled, *Evolution: The Modern Synthesis*, 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, 1932a). 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 investigations and his students, 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).

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 wrote: "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, 1923b, 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. Adapting the ideas of A. Gurvich, Goldschmidt thought that chromosomes are an integrated regulated system and that definite infringements of its fields can lead to sharp changes in embryological development (for more, see Golubovskii, 2000).

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). And this seems clearly in his article written with Ford in 1927. The concept of the rate of 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 it is pressing for scientists to show that genes control ontogenesis. But it is even more important to explain how genes do this (Neifach and Timofeeva, 1997). Recently many laboratories have focused on the regulation of insertion and deletion of gene action in development, which is called “epigenetics.” The name indicates that in regulating processes at the level DNA, DNA itself is not affected. Namely the suprar-genetic mechanisms (due to environmental factors) decide which genes act in the synthesis of protein and cell processes, and which genes “repress.” [The leading role in these decisions are played by chromatin the most important component—histones.] Epigenetics has so quickly developed the field of cell biology that it should shed light on the entire genetic-molecular mechanism of individual development (Karpov, 2003).

The Question of Growth

In the field of relative growth, Huxley probably made the most important discovery. His work on that subject was purely analytical. It was based on the actual measurements and also the generalizations made by other investigators. In his first article on relative growth Huxley that his teacher in zoology, Geoffrey Smith, made measurements of the claws and absolute body dimensions in crabs and concluded: that “on the whole, species of large size have secondary sexual traits which were not only absolutely, but also relatively, large” (Huxley, 1924d, P. 469). It is thought that Smith’s work influenced Huxley, but in the introduction to his *Problems Regarding Growth* (1932), Huxley wrote that his investigations were stimulated by the classic book of D’Arcy Wentworth Thompson *On Growth and Form* (Thompson, 1917). Thompson was the first zoologist to apply mathematics to solving the problem of form. The goals of the investigations were to understand the forms of living beings and parts of living material based on physical concepts and to prove that organic forms which would oppose physical and mathematical laws do not exist. Using the transformation of Cartesian coordinates, Thompson

showed how it was possible to depict the evolutionary changes of forms of such complex objects as skulls, fish, and copepods. He focused on the physical forces acting on organisms as the direct factors which determine morphology, but said nothing definite on the change of forms which occurs during growth.

The formula of heterogenic (allometric) growth

In 1971, in the introduction to his republished book of 1932 *Problems on Relative Growth*, Huxley wrote that he began his investigations on the fiddler crab in 1913 (the first of his publications from these investigations appeared in 1924) by comparing the growth of the abdomen of the male crab (*Uca pugnax*). In 1924, Morgan conducted and published his analogous work on the fiddler crab (Morgan, 1924). He studied the variation in the width of the abdomen in males and concluded that male crabs with abnormally small abdomens grow more slowly. Huxley noted that in very young specimens width of the abdomen section grew to a similar index in both sexes, but subsequently due to relative growth (in relation to the body) the index of abdomen width in males went higher. Moreover, the abdomens always grow faster than the general dimensions of the body, even in males with very small abdomens (Huxley, 1924d). In the 1924 article, he wrote nothing about the law of relative growth, although he had already arranged all his material for that. Where did the idea come from? The question remains open. In 1924, he published a two-page article on the growth of claws in females of the very same species of crab. He showed that the size of claws in relation to body size (or in a more general form—the size of the differentially growing organ) x can be expressed by the formula

$$y = bx^k$$

where k – the measurement of differential growth of the claws in comparison to body growth (the correlation of proportional growth), b – the scalar factor. The size of x and y usually progresses on a logarithmic scale. When $k = 1$, the correlation of the dimensions of the structure do not change, the growth occurs isometrically, though rather seldom. In the majority of cases k differs from 1 and the proportions change with the variations of dimensions (Huxley, 1924e). The existing theoretical peculiarities of Huxley's formula of relative growth are that the constant k is not the relationship of two sizes, but the relationship of two speeds of growth. He wrote his formula as the logarithmic equation:

$$\log y = k \log x + \log b$$

The logarithmic equation easily proves the existence of heterogenic (later called allometric) growth. The heterogenic growth of an organ will be demonstrated by a straight line with the slope $k / 1$.

It is interesting that, in *Nature*, Huxley cited the work of A Pezard and H Champy. These references were apparently not accidental: both authors studied the brain/body relationship, using the function of correlations. But Huxley did not cite Pezard and Champy as predecessors. In *Problems on Relative Growth*, in passing he also cited the work of E Dubois and L Lapique, who studied intraspecies and interspecies correlations. However, Huxley found it necessary to write: "I was the first to show that there are important relationships between the two variables [the growth of some organ and the growth of the body]" (Huxley, 1932b, p. 4). Such a historical situation, naturally, requires a return to this question.

After formulating the equation for growth, Huxley doggedly accumulated factual material in order to demonstrate heterogenic growth in the most varied aspects, which in the future earned a special name or even transformed into an independent direction of investigation. Specialists note that Huxley's work on this field was more systematic, than works on de-differentiation and morphogenesis (see for example Baker, 1976, p. 218). Huxley showed that joining of the claw ends in crabs *Maia squinado* demonstrate the varied meanings of k . The finger grows faster than the body, and the body faster than the ends (Huxley, 1927a).

He claimed that the meaning of k was not always constant over an animal's life. In collaboration with O Richards, he revealed that in male green crabs (*Carcinus maenas*) the abdomen width was positively heterogenic ($k=1.26$) relative to the length of thorax, until the thorax had reached 17-22 mm, and then $k=1.42$. Probably, this occurred in a period when the crab had reached sexual maturity (Huxley, Richards, 1931c).

Huxley encountered a more complex situation in the study of the size of claws in the common earwig (*Forficula auricularia*). He showed that the claw length in relation to body length demonstrated positive heterogenesis. The species, however, is bimodal in claw size. He separated all specimens into two groups: those with large claws and those with small claws. In each of these two groups the meaning was close to the isogenic growth ($k=1$). He concluded that there are two equilibrium points, but in one of the groups the claw size fell (Huxley, 1927b).

Huxley's 1932 Book, Problems of Relative Growth

In this book, he outlined the huge amount of factual material on differential growth, which in the future was used by investigators in most varied ways. He effectively applied the concept of relative growth to the analysis of phenotypic polymorphism. It seems that, although soldier ants look different from other workers because of their huge heads and jaws, all the variety of their forms are grouped into one distorted cast in the ant family. This means that although larger workers look different from the small ones, their entire series on the whole reflects the display of a genetically determined law of growth.

Huxley discussed in particular the question of negative heterogenesis as related to the phylogenetic significance of reduced structures. For a long time he thought that the result of reduction from the point of view of phylogeny produces changes of relatively little systematic significance. This widespread view was opposed by Goldschmidt in his research during the 1920s. He supported Huxley on the importance of the investigations of growth in relation to the reduction of structure. Huxley's logic led to the following: if the initial stages in structure reduction included a lowering in the activity of rate of genes which control growth (the case of negative heterogenesis), then the simple fact of the existence of rudiments of extremities in chick embryos is not proof of any kind of recapitulation of traits in the ancestral adult form, but is proof of the repetition of embryological traits. Huxley noted that since size reduction of the heterogenic organ is related to body size, then the level of the reduction of structure or organ can be explained independently of their functional significance.

de Beer used the idea of heterogenic growth and rate of genes for discussing phylogeny of reduced organs as related to recapitulation and K Baer's law on the great level of similarity between early stages in the development of various animals, than between the stages of young and adult animals (de Beer, 1951, pp. 72-73). He wrote: "Human evolution is accompanied by the progressive reduction in the size of the pre-maxillary teeth, and it was not understood why the ideal correlation between it and the upper maxillary was not attained in comparatively contemporary human ancestors" (Ibid., p. 73).

In his investigations of intraspecies heterogenic growth Huxley used basically his material on invertebrates. Therefore, it is interesting that he drew on the example of skull development in the bear baboon (*Papio ursinus*) to illustrate the change in form relative to the change in size. The example illustrated the extremely fast growth of the face relative to the brain (Huxley, 1932b, pp. 18-19). In this case Huxley used throughout the graphical method of Thompson (Cartesian transformation), having completed the measurements on the baboon bear. Later this work stimulated many investigations (see Martin, 1989, p. 98).

The concept of differential growth was entirely productive in the analysis of paleontological material as well as in the comparative morphological analysis of closely related species. Moreover, the variants of directed orthogenetic growth, which were obviously adaptive trends, were determined by the principles of differential growth and were only slightly related to adaptability. As an example Huxley (and after him Goldschmidt) drew on the gigantic horns of the *Titanotheria*. He wrote: “the relative growth of the horns, or other heterogenic [allometric] organs, was automatically defined as a secondary result of the general mechanism of growth and therefore *had no adaptive significance*” (Huxley, 1932b, p. 214). Huxley and Goldschmidt were inclined to think that the evolution of these great horns represented the acquisition of a new type of morphogenesis. Goldschmidt thought that evolution in this case is a classic example of macroevolution on the basis of systemic mutations, and leaned towards accepting the orthogenetic ideas of G Osborn (Goldschmidt, 1940, P. 319). Huxley also mentioned Osborn’s name, but more carefully. In *Problems of Relative Growth* in the section “Heterogenesis and Evolution”, he returned again to the *Titanotheria* example. He wrote: “Theoretically the most interesting case is the titanotheres, studied by Osborn in 1929. Osborn interpreted the material in the spirit of strong orthogenesis, that is, using the idea of predetermined variations in the germ plasma, although it is more precise to say – the idea of directed evolution. It is extremely difficult to find an adaptive significance for horns in the early stages of their evolutionary development, when they are represented only by simply growing bumps, and even more difficult when they simply exist as potential!” (Huxley, 1932b, pp. 219).

At the end of *Problems of Relative Growth*, Huxley wrote simply that the study of differential growth has a direct relationship in solving the problem of non-adaptive traits in orthogenesis (Ibid., p. 244). However already in 1934, A Hersh noted that Eocene ancestors of the titanotheres were smaller and their horns were either absent or shorter. The size of titanotherian horns grew radically with the growth of the general size of the body and in the process of their evolution during the Oligocene. Hersh produced a graph on a logarithmic scale: on both axes, titanotherian species were one and the same, as it was later called an allometric curve with a highly significant k . Therefore, the regulation of growth in the ontogenesis of the titanotheres occurred when an increase in the size of their skull was accompanied by an even greater nasal area. Apparently, the greater size of the entire body and horns provided a selective advantage, and therefore the given allometric tendency was preserved. The theme of “allometry—paleontology—evolution” will be continued later.

The slope of the curve of allometric growth of some organ can either change in ontogenesis or differ in various species. The regulation of the size of embryo, from which organs develop, can essentially change the character of the allometric correlation. In its turn, the embryo size can depend on the speed of cell division and on gene mutations that control that speed. So Huxley made it easy to build a bridge between the evolutionary importance of allometry and the importance of the variation of genes that regulate the speed of growth and development.

The concept of rate of genes was applied to the correlation of onto- and phylo-genesis. This concept was generally important for Huxley and his students (for example, de Beer), and it led them to search for connections between genetics, embryology, and morphology (Churchill, 1980; Waisbren, 1988). Huxley attempted to show that all these cases, which had earlier been described in terms of Haeckel's terms of recapitulation, could easily be explained in terms of rate of genes. If the gene produces a speeding up of growth then the given trait will appear earlier in the life cycle and biologists will discover a progressive combining of structure of the adult organism in the embryological stages. If the same gene slows the growth of the trait, then that trait will appear later in the life cycle and this a classic case of neoteny, that is, the reverse of what the biogenetic law states. Huxley wrote: "Undoubtedly, many cases of recapitulation will be discovered not as the mysterious secret of a phyletic law, but as an embryological convenience (Huxley, 1932b, pp. 234-240). He focused on the importance of the connection between allometry and genetics in explaining the reduction of structure. Any structure reduction at the early stages includes a lowering of the activity of genes, which control growth, and this is a typical example of negative allometry. de Beer discussed genetic control in the case of negative allometry in an interesting way (de Beer, 1951, pp. 72-73). To Thompson's words, Goldschmidt added the following prophetic words which appeared in his 1940 book: "...*highly differential growth can be initiated by the formation of specialized hormones (of determining materials) in the defined time; it is possible to imagine a majority of evolutionary processes, which are produced by small quantitative changes of the base genes, which lead to displacements in the ordered time of the coordinations*" (Goldschmidt, 1940, p. 311).

These ideas were proved experimentally by Goldschmidt and Huxley. For that reason Huxley called Goldschmidt's connection of evolution and developmental genetics an "excellent discussion" (Huxley, 1942, P. 513). But at the same time Huxley separated the investigatory line of Goldschmidt-Huxley from the investigations of Morgan's school, which was trying to underestimate the evolutionary importance of changes in genes which control growth and morphogenesis, and the importance of the coordination of their action in space and time.

In *Problems of Relative Growth*, Huxley has two sections on taxonomy: "Heterogenesis and taxonomy: subspecies and taxonomic forms" and "Heterogenesis and super-species groups" (Huxley, 1932b, Pp. 204-215). This is important for the following thought: Huxley was the editor of *New Systematics*, and the mentioned gaps indicate that he was always driven to solve the problem of systematics. In these sections Huxley generalized the extensive literature and completed his own original analytical investigations. He especially completely analyzed the cases of Scottish deer (*Cervus elaphus L*). In this species, the significance of b and a is constant, but in different organisms body size varies greatly. In the Scottish deer, the body weight can reach 125 kg and in the Carpathian deer, 250 kg. He claimed that the antlers grow by the same methods and their final size relative to body weight is strictly allometric ($b = 0.00162$, $a = 1.6$). He concluded that genetic facts practically do not determine the difference in weight in the two forms. The second confirmation was the fact of the introduction of the Scottish deer into New Zealand, where it lived as the Carpathian deer. He understood that the typical mistake of the systematists was that they determined the percentage relationships for the parts and the whole body. The concepts of allometry created a great interest in Huxley for systematics, with which he had little to do until 1932.

He searched for a connection between differential speeds of growth and evolutionary theory. He wrote: "The existence of gradients of growth make it possible for mutations and selection to influence a series of parts in a correlated way, and this is how the selection process

works” (Huxley, 1932b, p. 222). He attempted to clarify the great changes in structure and not run to the idea of a great reorganization of the genome (see Waisburn, 1988, p. 320). He wrote: “It is clear that the main genetic factors which control any organ, which demonstrate heterogenic growth, should be the rate of genes, or genes which determine the speed of the processes of individual development” (Huxley, 1932b, p. 224). Morphology, embryology, and evolution were well supplemented by the ideas of the genetics of individual development. Naturally, working out the concept of differential growth led him to the conclusion that not all evolution existed on the basis of small mutations and moreover constantly has an adaptive character. This idea appeared earlier in his collaborative work with Haldane in 1926. But now Huxley possessed a huge amount of material, and in his conclusions was very carefully.

Goldschmidt discussed the evolutionary consequences of allometric growth significantly more broadly than Huxley (Goldschmidt, 1940, pp. 308-323). First and foremost, he noted the similarity of his concept of the rate of gene action, which grew out of his experiments on the butterfly *Limantria*, and the analogous concept of Huxley and Ford, which was the result of experiments on *Gammarus*. In 1912, Severtsov worked out the theory of arhallaksis, which showed the important evolutionary role of early embryological changes and closely related concept of systemic mutations (hopeful monsters). Goldschmidt examined three groups of facts and observations, which showed the special evolutionary importance of the changes of relative growth and developmental speed: facts and generalizations, which were collected in *On Growth and Form* by D’Arcy Thompson (1917), homeotic mutations, the phenomenon of rudimentations, and finally, macromutations which Goldschmidt called by the scandalous metaphor, “hopeful monsters.” The examples collected by Thompson on the changes in form of living organisms due to the transformations of the speed and intensity of growth in the Cartesian coordinate system greatly influenced the views of both Goldschmidt and Huxley. When evaluating Thompson’s ideas, Goldschmidt focused on the idea that the transformation of forms during evolution can occur without natural selection, and moreover, not on the basis of small mutations, with which Huxley agreed.

Goldschmidt recalled the example of titanotheres and returned to the concept of orthogenesis. According to orthogenesis, the evolution of one or another line is channeled in a defined direction, from which it cannot deviate even when the direction stops being adaptive; subsequently its extinction is unavoidable. Similar ideas gave directed evolution a teleological sense and carried a mystical character. Nevertheless, in evolution such directions do exist and should be investigated. The concept of relative growth, for Goldschmidt, suggests many kinds of explanations without mysticism and Lamarckism (Goldschmidt, 1940, P. 322). It is interesting that Goldschmidt suggested several evolutionary mechanisms: selections of small mutations, systemic mutations without selection, gene action, which controls growth. After Goldschmidt analyzed the concept of orthogenesis regarding the level of relative growth, many publications appeared on the topic (see for example, Gould, 1977).

It is not by chance that much has been said about Goldschmidt. In his 1940 book, he gave more evolutionary significance to allometric growth and discussed it in even more detail than Huxley—the author of the monograph and equation on allometric growth. However, this is not surprising since the coming into being of allometry with all its deeper interpretations of the parameters and their correlations took decades. Gayon (2000) drew an interesting historical picture of the formation of allometry, fragments of which will be discussed below.

The origins of the term “allometry” and its history until Gould

Until 1936, the term “allometry” did not exist. In the English language the French term “heterogenesis” was used, and in the French literature the term “disharmony” was used. The term “allometry” was introduced by Huxley and the French zoologist and geneticist George Teissier (1900-1972) in their co-authored article published in English and French (Huxley, Teissier, 1936b, 1936c). What led to this collaboration? Teissier was better known in Russia as a geneticist-populationist, and not as a classic zoologist (see Nazarov, 1984). He was fifteen years younger than Huxley and had begun his scientific career as a systematist and biometrician. When Huxley discovered the law of heterogenesis, Teissier was only 24 years old and had written nothing on biometry. Teissier published his first article on relative growth in 1926 on entomological material. Naturally, the French zoologist-biometrician knew very well the French literature on relative growth; in the article mentioned above he cited the work of Louis Lapicque (1866-1952), who compared eye size and body size in vertebrates (Lapicque and Grioud, 1923). Like Lapicque, Teissier suggested determining relative growth with the help of a law. In the following publications on differential growth, he continued to cite Lapicque, and also Huxley, using the formula for differential growth (Teissier, 1928a, 1928b, 1928c). In his 1931 dissertation, Teissier devoted an entire chapter to the history of relative growth, where he noted the importance of Huxley’s work, but said nothing about Huxley’s discovery of the law of differential growth and logarithmic coordinates. Teissier wrote that the method of describing relative growth was discovered in 1897 by Dubois and in 1898 by Lapicque (cited in Gayon, 2000, p. 753).

In 1897, the Danish naturalist Eugene Dubois (1858-1940) published an article on the relationship between brain weight and body weight in mammals. He wanted to develop a quantitative method for express the correlation between two factors, which determined the volume of the brain: “the level of ‘cephalization’” (the reflection of the position of a given species on the scale of evolutionary progress) and the size of the lobal section of the roof of the brain in related species. These indexes were at the foundation of Dubois’s formula (Dubois, 1987, p. 368) expressing the relationship between brain weight, e , and body weight, s :

$$e = cs^r$$

where c is the coefficient of cephalization and r is the coefficient of the ratio (Dubois thought that the relative size of the brain was roughly proportional to the surface of the body, that is, $r = 0.66$). He used the coefficient r for comparing ratios between closely related species.

A year later the young French physiologist, Lapicque, applied Dubois’s formula in a comparison of the relative brain weight of dogs belonging to one species. He received significance for the coefficient ratio of 0.25 (Lapicque, 1989). Over the next decade he wrote a series of articles on the relative brain weight both within and across species. With enviable constancy, he obtained a coefficient of 0.25 for intraspecies variation and 0.5-0.6 for interspecies variation. In 1907, he represented Dubois’s formula graphically, which he called a law for interspecies variation. Since he accepted Dubois’s conclusion that the coefficient ratio was always equal to ~ 0.55 , his graphical representation of relative brain weight in related mammals produced a series of parallel lines. Lapicque called these “isoneural lines”. In a graph with strictly parallel lines, he also included a series of lines that went at an angle of 45 degrees, which were purely theoretical. These corresponded to the support of an absolute ratio between brain and

body weight. It is interesting that this dependency was discussed by Gould (1977) some sixty years later.

And so, at the end of the 1890s and beginning of the 1900s, Dubois and Lapique investigated the relationship between brain size and body size, including mathematical and graphical means, which precisely correspond to what would later be called allometry (intra- and inter-species allometry, or, for Gould, “statistical” allometry). But neither scientist was interested in the question of individual growth, which was central to Huxley’s investigations. Moreover, the Dubois and Lapique-derived formula was regarded as an empirical law with a vague theoretical status.

The line of investigation of Dubois and Lapique was biometrical and included experimentation. Beginning in 1900, several biologists began to observe the secondary sexual traits over the duration of individual animal lives and concluded that they develop at different speeds. Albert Pezard (1875-1927) made the first experimental and quantitative investigation on that theme. He conducted investigations for many years, but only in 1918 did his first publication appear. He studied the development of sexual traits in cocks, and observed that they have a discordance between body size and comb size, at the time when growth of the spurs nearly follows the general development of the bird. He suggested new terminology, writing that: “Growth, which follows the general development of an organism, can be called *isogenic growth*, and growth, which is special can be called *heterogenic growth*” (Pezard, 1918, p. 23). Right up until 1936 the term “heterogenic growth” was widely accepted especially in the English language scientific literature for designating individual relative growth. Pezard’s monograph influenced many investigators who studied the physiology of sex, and also embryologists, endocrinologists, and biometricians. But there was an essential omission in his work; he did not suggest an algebraic term for the law of relative growth in cock combs.

The French physiologist, Christian Champy, published a book in 1924 on *Sexuality and Hormones*, in which he suggested a formula for heterogenic growth. He introduced the expression “disharmonic growth” to designate the phenomenon of constant growth of relative sizes in secondary sexual traits like the functions of body size. This book included many illustrations, primarily from entomology. Champy explained how his discovery of sexual hormones which produce the intensification of cell division in a defined part of the body arose. “Disharmonic growth” was expressed by the following formula:

$$V = at^2$$

where V is the measurement of secondary sexual trait, t is the body size, and a is a constant (Champy, 1929). In this formula, the relative growth of an organ is a function of body size. Champy’s equation is hardly a law, since it expresses, primarily, a particular case.

It was thought that the work of Pezard and Champy was decisive in the appearance of the general concept of allometry.

Since the status of Teissier’s investigations on allometry and the investigatory line of Huxley’s predecessors in France is well-known, it is necessary to discuss the connection between Huxley and Teissier.

In 1935, Huxley and Teissier decided to standardize the terminology for relative growth. Over several months they exchanged letters in which they searched for acceptable solutions regarding the lexicon and symbols. In 1936, two coauthored articles were published in France (*Comptes Rendus de la Societe de Biologie*) and in Great Britain (*Nature*). Unanimously they

decided on the changes in terminology that authors had used until then. Huxley's term "heterogenesis" and Teissier's term "disharmony" were replaced with "allometry", and the corresponding "isogenesis" and "harmony" were replaced by "isometry." Huxley and Teissier also agreed on the symbols in the formula for allometric growth":

$$y = bx^a$$

Comparing the French and English versions of these articles shows that they differed on one principle issue — the constant b . For Huxley this constant had no biological meaning. In his essay, b was no more than the change in y , when $x = 1$. The constant depended only on the selection of a unit of measurement. Since this unit might be such that the allometric ratio did not exist for a given significance x , then the parameter b had no biological significance. Teissier did not agree with this. He felt that b could have a biological significance if one focused on the statistical nature of the factual material. On this basis he introduced into the French article the following note: "From the statistical point of view b has significance and expresses the ration y/x for all observed individuals" (Huxley and Teissier, 1936c, P. 936). Huxley did not include this note in the English version of the article. However, the article did include Teissier's example, which illustrated the biological significance of the coefficient b . He showed that local populations of a species can have an allometric equation for a defined organ and differ only by the coefficient b . If, for example, the growth of the abdomen of a lobster can be described by two allometric equations and the difference in b is observed in the second equation, which signifies that the growth in young animals in one of the races began earlier.

The agreement between Huxley and Teissier had a great impact on the future history of allometry (Gould, 1977).

As has already been noted, Goldschmidt was one of the first to analyze allometry in a broad evolutionary context. But his analysis was mostly directed against Darwinian orthodoxy. It is thought that he made it possible for allometry, along with embryology and morphology in general, to be part of the evolutionary synthesis. Gayon (2000) suggested that all this occurred sometime around the beginning of the 1940s. It is surprising that Huxley in his 1942 book, *Evolution: A Contemporary Synthesis* wrote only nine (generally descriptive) pages on allometry (and this was after Goldschmidt's analysis). Of course, all this requires special analysis. Perhaps, Huxley suggested, if allometry is an important phenomenon in evolution, will it then disturb the general adaptive orientation of the synthesis? This latter explanation completely disappeared since there was in general no strong adaptationism in Huxley's book. Maybe Goldschmidt's macromutationism on the whole frightened Huxley somewhat, so that he displayed great diplomatic caution. Perhaps it was much simpler to explain? The concept of allometry, as much as it was associated with ontogenesis and evolution, seemed outwardly "hidden."

G Simpson in his classical monograph, *Tempo and Mode in Evolution*, published in 1944 (which incidently was a foundational book for the evolutionary synthesis), devoted one section to allometry in paleontology (a Russian edition appeared in 1948). This section was entitled "Relative tempos in evolutionary genetics regarding single traits." He used allometry to prove something opposed to Goldschmidt's claims. Simpson wrote: "Paleontology noticed long ago that two similar traits can evolve so that the direction and speed of the changes in one of them can be the function of changes in the other. Various theories of orthogenesis, directed evolution, etc., were founded on observations of this type. The analytical methods of relative growth were

basically worked out and described by Huxley in 1932, shedding unexpected light on these phenomena” (Simpson, 1948). Several researchers quite independently of each other discovered that changes in relative size of various structures can often be determined by steady ratios of the speeds of their growth. Paleontology was at the beginning of the road in this aspect of the research, but it had already shown that changes in proportion occurred in just this way in many cases.

Drawing on R Robb’s generalized works, which investigated a series from the ancestors of horses to contemporary horses (*Hyracotherium* – *Equus*), Simpson discovered that an increase in the general size was accompanied by a relative lengthening of the muzzle in comparison to the skull (Robb, 1935, 1936). Robb studied and described this phenomenon of “progressive predominance of pre-optical parts” in the terms of relative growth. It seems that the absolute speeds of muzzle lengthening and of the whole head are different, but have a tendency to remain steady. Analogous work was completed by Robb on the proportions of toes on horse feet, but with a much more pronounced genetic perspective.

On the basis of Huxley’s formula, Robb and Simpson concluded that the transformation of horses from three-toed to one-toed, was not a simple product of a change in size or length of legs; it was related to defined heritable changes, or mutations, which affect that trait as an independent unit. In a later work he did not exclude an interpretation of growth in terms of Goldschmidt’s ontogenesis (Robb, 1937). Simpson wrote: “In distinction from the skull proportions the toe proportions evolved by themselves, but this process occurred in only one stage of the evolution of the horse and, as far as we know now, happened in one leap” (Simpson, 1948, p. 31). He used all the material of horse investigation to criticize orthogenetic structures, many of which were based on the idea of the similarity of onto- and phylogenesis. Moreover, he asserted that allometric growth eliminated all direct analogies between ontogenesis and phylogenesis because the structure of each adult organism in an evolutionary series is the result of its ontogenesis, and ontogenesis is heritable” (Ibid., p. 28).

In 1949, the zoologist and paleontologist, Norman Newell, published an article in *Evolution* (a journal for evolutionary synthesizers) on the phyletic dimensions in invertebrates, in which he devoted several pages to allometry. He denied the common view that allometry explains neutral and orthogenetic evolution. He used three kinds of evidence related to the constant parameters of the allometric formula. First, the constant a (the constant of the correlation of relative growth) really is modified only by natural selection. Secondly, the constant a may simply be the property of natural selection. Following Simpson, Newell used the example of the width of bone extremities in large surface vertebrates. This example gives an allometric curve where the constant $a = 1.5$. Such a width, in the researcher’s opinion, can be only due to natural selection. With other values of a , the animals simply do not survive (Newell, 1945, p. 115). And thirdly, the constant b can also change the consequences of natural selection, as in the example of joint length in several lines of ammonites. Commenting on allometric curves, he wrote that: “Regression in successively young genera shifts to the left. I interpret this in the following way: natural selection made an ammonite with progressively smaller values of b in the allometric ratio. These cases are the speeding of evolution” (Ibid.). He sought a way to reveal the gradual change of the constant a , since the change of that constant leads to the modification of the organism’s proportion due to a change in the character of growth. The shift of allometric dependence between length of the hinge and perimeter of the shell during the evolution of one line of fossil bivalve mollusc genus *Myalina* served for Newell as proof of the

constant increase in size and allometric change. Yet he still did not produce systematic proof of the adaptive significance of allometry; he only offered examples.

Newell's work, however, influenced subsequent investigators who saw in it proof of the adaptive significance of allometry. For example, one of the founders of the evolutionary synthesis, Dobzhansky, in the third edition of his monograph, *Genetics and the Origin of Species* (1953) did not discuss allometry. Only by that time had he escaped from his pluralism of 1937, and became, one might say, a deeply consistent adaptationist (or, in Gould's words, a panadaptationist) and mentioned the subject (Dobzhansky, 1953, p. 99-101). Describing the work of Simpson, Rensh, and Newell, Dobzhansky wrote in the section of his monograph on 'Correlative responses to selection' that: "All these authors have shown that evolutionary trends can be explained by the "orthoselection" for several adaptively useful traits, for example, the progressively growing size of the body" (Ibid., p. 100). And furthermore, in the spirit of the young Huxley, Dobzhansky wrote that: "The growth of body size, however, can produce numerous correlative changes in traits which by themselves have no adaptive meaning" (Ibid., p. 101).

In terms of evolutionary synthesis, allometry was more deeply and originally worked out by Stephen Gould in 1965-1971. In all of his articles, written as complete monographs, he investigated the following three interrelated themes:

- 1) the value of the constant b in allometric equations,
- 2) the relationship between allometric and adaptive evolution,
- 3) the relationship between various forms of allometry.

Following Teissier, Gould suggested that the constant b has great biological significance. In the case of intra- and inter-species allometry, a change in b indicates the formation of a new regression, which moves in parallel to the old one. He became interested in how defined species are able to "give up" the previous allometric curve and "jump" to another. In 1965, in a collaborative article with the mathematician, White, Gould completed an algebraic analysis of this question; but it was not until 1971 that he produced a graphical representation (Gould, 1971). By what law (or rule) did the coefficient b change? Two evolutionary mechanisms are possible. Dubois suggested that a move from one allometric line to another occurs by way of a sudden change in ontogenesis, since in mammals the absolute brain/body ratio increases by way of an increase in the number of neurons during early embryogenesis. The second possible explanation is the speeding up or slowing down of development during phyletic evolution. This hypothesis does not suggest sudden and sharp changes, and includes the idea of intraspecies selection or selection between closely related species. Gould chose the second explanation, which is typically gradualistic, adaptationist and selectionist. He also proposed that changes in the constant b depend on the form of allometry - the allometry of growth, phyletic allometry, and static intraspecies and static interspecies allometry. Gould conducted investigations of all these relatively independent subjects.

In combined investigations on allometric growth and interspecies allometry, Gould tried to explain whether the constant a changed in value. He depicted the allometric dependence between brain mass and body mass in closely related species of insectivorous mammals from Madagascar as a broken line, and the allometric dependence within the limits of each species in the process of orthogenesis as unbroken lines. Ontogenetic curves had lower slopes than the curves for groups of species; however, the reverse picture was just as probable because in the process of individual development the value of constant a is often greater than 1. Gould noticed

that the characteristic value of a for ontogenesis differs from the value of a for the comparison of adult individuals from different species, but is still the same for all these species. However, the value of constant b differs for all species.

If the interspecies $b = 1$, then in this case the adult individuals of larger species are the bigger variants of their own smaller relatives (or ancestors). Gould hypothesized that this could occur in the process of evolution where the progeny of the larger species preserve the value of constant a of their smaller ancestors. But allometric growth of the surveyed structures begins in it from the larger embryos, i.e. with a higher value of constant b . In order for the size of the structure to change, this requires that either embryo growth begins at an earlier time (acceleration), or is delayed. This allows for the alternate possibility of increase in size during evolution, which does not require changes in the laws of growth. If the curve of ontogenetic growth of its ancestors is preserved in an organism, and the allometry of growth is very different, so that $a = 1$, then the proportions of the body can sharply change from an increase in size. By preserving allometry, but beginning growth from other embryo sizes, an organism can avoid large changes in relation to the sizes of different parts.

Gould's research on the growth of gigantic antlers in the extinct Pleistocene deer, *Megaloceros giganteus*, became well-known (Gould, 1974). In large males, antler reached 3 to 3.5 m. Gould showed that the antlers of this deer follow the same law as the antlers of other deer. Since this was a very large deer, it was quite expected that its antlers would also be especially large. But was this the only cause of the gigantic size of antlers? Gould suggested that the selection of strongly favored such huge antlers since the deers' breeding behavior depended on them. Up to Gould's analysis, both the example of Pleistocene deer and the example of titanotheres had served as a classical proof of orthogenesis. His research was an open attempt to build a bridge between evolutionary synthesis, allometry, morphology, and embryology. It is interesting that all these are characterized by the systematic use of biometric methods, and in this approach, by the related early investigations of the brain/body relationship. Gould used Huxley's formula of allometric growth as the basis for perfecting the apparatus of quantitative analysis (see Gould, 1977, pp. 238-241).

Unfortunately, it is not possible to explain the mechanism of regulatory processes lying at the foundation of allometric growth. "We are freed from the concept of the evolution by the formation of new genes due to the constant substitution of nucleotides and need to search for evolutionary mechanisms at the level of gene organization and their expression in ontogenesis, in order to explain fast and deep changes in morphology" (Raff, Kaufman, 1986, p. 74). Related to this, apparently, the time has come to reinterpret the concept of the rate of genes advanced by Goldschmidt, Huxley, and Ford. In the framework of its experimental verification, the first data on gene expression were obtained.

Elements of Experimental Embryology: A Synthesis in the Question of Individual Development

The "generalist" and "synthesizer" as Huxley's usual characteristics

These labels relate not only to the Huxley who wrote his 1942 book, *Evolution: The Modern Synthesis*, but also to the Huxley who wrote articles on biology, and also the Huxley who wrote together with the two Wells the book, *The Science of Life* in 1929-1930. Without doubt, the book *Elements of Experimental Biology*, written in 1934 by Huxley and de Beer is also a great

synthesis, as has been noted by historians of science (Filatov, 1936; Witkowski, 1992; Churchill, 1992).

When *Elements of Experimental Biology* was written, embryology was an extraordinarily varied and complex discipline. It combined experimental and descriptive methods. It included many subfields, beginning with heteroplastic transplantations, tissue cultures, experiments on regeneration which completed on almost all representatives of the animal kingdom and at all stages of development, the transplantation of organs in medicine, teratological and pathological observations, the action of separate physical and biochemical factors in development, and the attempts to unite genetics with individual development. Obviously, Huxley and de Beer clearly understood that embryology needed unification. Together they searched for theoretical constructions that would allow for unification of all parts into a single whole.

They had met after World War I at Oxford, where Huxley had received a job as senior demonstrator in the Department of Zoology and Comparative Anatomy, and de Beer had become his assistant. From the very beginning, they had a warm and very creative relationship. In 1924, they published two co-authored articles on the differentiation and reabsorption of embryological material.

The principle elements of the future synthesis were not solved at Oxford, however, but in Freiberg and Chicago. In Freiberg, Hilder Proefscholdt was successful in transplanting the spinal lip of the blastopore in salamander embryos in 1921. She showed that the transplantant was able to induce development of the secondary axial of the germ on the abdominal side of the embryo. Proefscholdt's scientific advisor, Spemann, added a conclusion to her article, which contained a description of the technique of the heteroplasmic transplantation, and first used the term "organizer" (for more details, see Hamburger, 1988). In 1924, Spemann and Proefscholdt (her married name became Mandofold), published a well-known article on the organizer (see Spemann, Mandofold, 1924; Willer and Oppenheimer, 1964). In a special article on the organizer, the German authors showed the wide participation of the dorsal lip of the blastopore in the program of the development of new embryos. Here they introduced the formation of plan of bilateral symmetry, placing a part of a cell into the structure of the transplantant, and the induction of the development of the central nervous system (for more information, see Gorodilov, 2003). At the same time on the other side of the Atlantic, in Chicago, Charles Child was writing his books on axial gradients.

Huxley now kept in mind two lines of investigation in embryology—the line of the organizer and the line of gradients—and recognized the need to synthesize them. In January 1924, he began to correspond with Spemann. Over two years they exchanged seven letters in which they did not discuss theoretical aspects of embryology. Huxley invited Spemann to deliver lectures at the British universities, but the German colleague politely declined due to his poor understanding of the English language (Churchill, 1992, pp. 110-111). In Amsterdam during March 1924, Huxley and Spemann met briefly. In 1930, Spemann translated a note by Huxley into German. It is interesting that in the last years of his life, Spemann criticized Child's interpretation of metabolic gradients (Spemann, 1938).

de Beer also was preparing for the future synthesis. In 1926, he published a long article on "*The Mechanics of Vertebrate Development*," which mostly laid the basis for his later collaborative book with Huxley.

Huxley's list of investigations was presented in the previous section, but it is worth briefly recalling it in order to understand the novelty of this monographic work. It is incorrect to claim that the upcoming embryological synthesis developed from the work of Spemann and

Child. Huxley had his own embryological interests, and it was they, primarily, that influenced the scientific synthesis of Huxley-de Beer. Huxley's creative list included: work on dedifferentiation, partially completed with de Beer; experiments on morphogenesis and investigations in temperature gradients; the study of early embryological development and hormonal control of morphogenesis; allometry and experiments on the rate of genes in *Gammarus*. All these themes were represented in the 1934 monograph. Huxley's experimental investigations were not accidental, isolated, or a simple bibliographical survey. From 1920 to 1932, he investigated the majority of the separate segments that would directly enter synthesis constructed by him and de Beer. However, reading *Elements of Experimental Embryology*, it is difficult to imagine that this work came as the result of a purposeful strategy that was realized over a decade. It is correct that specialists in embryology who know Huxley's work in the original, most likely, think otherwise.

We return now to the structure of *Elements of Experimental Embryology*. The book is very well organized, and rich in examples and references. The clarity of the text, the numerous and well-chosen illustrations made *Elements* the textbook and compendium of experimental work for many years. It can be divided logically into four parts. Part one—Chapters 1-3—is an introduction to morphogenesis, with a focus on the normal development of amphibians and a survey of the classical work in that field. Part two—Chapters 4-7—discusses the stages of individual development, designated at the “organization of completely different types.” The thesis of Huxley and de Beer was that the types of organization influence successively (the same succession that determined by the polarity of the egg) the movement of its cells from the blastule stage to the neural stage and, of course, the morphological and histological differentiation. Part three—Chapters 8-11—discusses the demonstration of embryological fields and gradients in normal ontogenesis, the regeneration of functional structures in pre-histological differentiated embryos and in post-embryological life, and the differentiation of nervous systems in amphibians. In other words, this part is a survey of the proof for the existence of morphogenetic gradients. Part four—Chapters 12-13—is devoted to the relationship between development and Mendelian factors, that is, between development and genetics. The basic text is followed by a brief review.

In *Elements*, Huxley and de Beer considered axial gradients to be the primary factor determining the stages of development, and saw that they are initiated external agents such as the orientation of oocytes, the influence of gravitation, or the point of entry of the sperm. In the authors' words, for example, a frog's egg is “the mechanism for realizing the complete normal bilateral symmetry” when “even the weak differential action of various external agents can act as triggers which allows a particular plan of symmetry.” Huxley and De Beer showed that the level of viscosity, and chemical or other cytoplasmic differences are organized around the axial gradient, and not around the nucleus, and at that stage play a defined morphogenetic role. In studying the blastula stage and neutralization, the authors discovered Spemann's organizer and inducers which direct the subsequent stages of development inside established gradients of the egg system.

Huxley and de Beer established that after the neuralization stage the gradient system “returns” to the mosaic parts of the field, in Gurvich's terms, or to the field of differentiation in organs. The localization of each field is determined by the axial gradients and the organizer. The formation of the field is a gradual process, guided by invisible “chemical” differentiation and later by now visible morphological and histological differentiation. That which initially was the quantitative part of the egg steadily became a qualitative process of differentiation. Only at the

stage of histological differentiation did Huxley and de Beer identify the action of factors of nuclear inheritance. But it was at this stage, when “genes come into play,” that the difficult problem arose of the interaction of genetics and embryology. How did the genes begin to act? Huxley and de Beer thought that genes begin to act at the stage of histological differentiation, an idea that would prove to be prophetic and is now widely accepted in developmental biology.

If in the second half of *Elements*, Huxley and de Beer presented and documented the succession of types of organization, then in the third part they related them to fields and gradients. The authors began with Child’s experiments on regeneration. They offered the convincing argument to prove that the rule, established in studies of regeneration in adult amphibians, should also be correct for normal ontogenesis. On the basis of the analogy, Huxley and de Beer investigated the organizing and regulating steps in the early stages of ontogenesis. They saw a tight connection between ontogenesis and regeneration, but noted, that these processes are not identical. Development and regulation in the egg are early embryological reactions; they take place because the general field-gradient “informs” the embryo. In the early stages these fields play a dominant role in development and initiate the embryo’s plasticity. As the field-gradient loses dominance, the embryo becomes less plastic and loses its regulating ability. Regeneration occurs only at the end of development, after morphological and histological differentiation. Based on this, Huxley and de Beer proposed a completely new idea; genetically determined responses in the process of development allow different organisms to regenerate defined structures to different extents. Regenerative responses should be guided by gradients of different levels of universality, and this was proved by Child. In part four of *Elements*, Huxley and de Beer attempted to show how the data of contemporary genetics and physiology can be interpreted in their model of early development. This was especially important because Morgan’s efforts in that direction had been unsuccessful. Huxley and de Beer tried to build some kind of boundary for the action of heritable factors. Early embryological development is the result of such effects as the initial gradients, gradient fields, and only the last stages of development, especially morphological and histological differentiation are the results of the activation of genes. They wrote: “When genes by themselves are not able to initiate the process of development and differentiation, it is completely apparent that they play an active role in controlling these processes at the very start of development, and their presence is essential” (Huxley and de Beer, 1934, p. 403). The specific activity of genes is stimulated by external triggers of the type of gradient-fields and chemical induction in histogenesis. Their research on the rate of genes and relative growth played an important role in this argument. It is thought that the study of the genetic bases for allometric growth was the decisive argument in the promotion of the concept of genetic control of morphological differentiation.

In the words of the well-known embryologist, Churchill (1992, p. 119), *Elements of Experimental Embryology* was a stimulating network of generalizations. It is best to consider the book from its historical perspective. V Roux was the first to insist that experimentation is the only key for obtaining precise and reliable conclusions in embryology. H Driesch, T Boveri, and J Jenkins, on the basis of experiments, claimed that epigenesis is the true description of developmental phenomena. Spemann, R Harrison, and Child provided general principles for theorizing, and now had come the time to search for the physico-chemical basis of these principles. Huxley and de Beer combined the principles into a unified whole—this was, truly, a synthesis. Naturally, the real heroes were Child and Spemann in this synthesis.

Child and axial gradients

Child developed the theory of axial gradients after completing experiments on regeneration in adult hydroid and flatworms. The basis for his views were visible already in his earliest works in cytology, conducted in the tradition of American scientists, to be exact—in E.B. Wilson's school. But in distinction to his colleagues - Wilson, Conklin, and Frank Lillie - Child concluded that cell division was more of a quantitative than qualitative isolation of the egg, and that blastomeres are not the early steps in differentiation. He literally attacked the classic cell theory and supported Driesch's conclusion that differentiation is a function of position. At the same time, Child denied Driesch's mysticism (vitalism), maintaining mechanistic views.

In 1900, Child began an investigation of regeneration and over a decade successively developed the concept of the connection between regeneration and axial gradients. He noted that axial gradients organize forming processes of the entire organism and express the physiological unity of the individual. Child's experiments showed that organization can be manipulated with the dominant fundamental axials, and that in favorable experimental conditions the axes come together or are formed anew in fields which were not under the influence of the old gradient axes. By 1915, Child completed many physiological experiments showing that developmental speed is related to metabolic gradients, and directly correlated with axial gradients. He came to a paradoxical conclusion, which none of the specialists in embryology or cell biology took seriously. He proposed that formative processes should emerge sooner from an organism's physiology, than from a specific structure of protoplasm or contents of the cell. Across all his scientific research, Child consistently thought of inadequacy as a strong biochemical and cytogenetic (chromosomal) approach to the study of development and even for understanding organic form. The theory of axial gradients simultaneously suggested both a dynamic and physiological explanation: the initial organic form is a product of integrated processes which from the primary axis of formation.

Child's approach opened up a wide perspective. First, it became apparent that there is no connection between correlations and causes. His experiments proved that metabolic (or physiological) gradients are often determined by the need for oxygen or the products of carbon, but the experimenter was not able to demonstrate that they were the causal factors of axial gradients and other stages of formation. Second, his experiments on regeneration of adult organisms served as the primary proof for the theory of axial gradients. Many investigators were completely justified to doubt whether Child's conclusions could be extrapolated to earlier stages of development. Thirdly, Huxley and de Beer, approving of the theory of axial gradients, tried to join it with their own theory of gradient fields and concluded that chemical differentiation precedes morphological or histological differentiation. But why did they not conclude that gradient fields might be simultaneously activators and the result of formative processes (for more details, see Weiss, 1939, pp. 186-189)? It is difficult to explain Child's deeply anti-cellular and anti-genetic position. A year later, when Morgan's collaborative book, *Mechanisms of Mendelian Inheritance*, appeared, Child was able to write the following: "Even the most contemporary discussions attempting to reduce everything to the position of heritable factors on the chromosomes, completely ignore the complexity of the problem of regulating these same factors, and all this is assumption. Actually, if we subject this group of theories to logical analysis, then we unavoidably come to the assumption of the existence of some similar superhuman intelligence, which lies in everything and controls everything. These theories do not solve the problem, but their application is anthropomorphic and teleological" (Child, 1915, p. 23).

Huxley and de Beer closely followed Child's work, and it seems that they approved, at least internally, of his organismic, anti-cellular, anti-chromosomal interpretation of forms.

Spemann and the organizer

Spemann's theory of the organizer formed another support for Huxley and de Beer's theory of gradient fields. At the turn of the 20th century, Spemann was inarguably the leader of experimental embryology in Germany. He began his experiments with the study of bilateral symmetry and polarity in salamander embryos. Spemann and his coworkers obtained an intriguing result, which actually made duplicate larvae. They demonstrated the dominant dorsal field and the importance of gastrulation in determining the axial organs. It is interesting that the historian of embryology, V Hamburger has conducted such a deep interpretation of Spemann's experiments (Hamburger, 1988, p. 33).

Between 1901 and 1922, Spemann worked out the method of microsurgery and conducted a series of experiments on the transplantation of nuclei in frogs. The most important series of experiments was completed in 1917 when he was absorbed in the investigation of the structures determining gastrulation. Using heterotransplants (transplants between different species of the same genus), Harrison discovered the fate of various pigmenting cells. Spemann saw in the technique a method for identifying the nervous and epidermal segments of early gastrulation, and the experiments helped him to explain the significance of the upper lips of the blastopore as the "organizational center" of the latter structure. As has already been mentioned, then came the experiments of Spemann and his students, which made it possible for embryologists of the across the world to evaluate the formative processes of gastrulation and neuralization. It took an entire decade in order to establish that the formation of axial organs consist of complex and numerous interactions. Later, using the embryos of tritons, Spemann tried to explain the equivalence of potential in somatic cells by transferring the nuclei of subdivided blastomeres into the ooplasm (Muzrukova, 2003).

Spemann insisted that a hierarchy of organizers exists, which act as a chain of successive processes. In 1930, the result of intensive investigations led him he advance the idea that the principle of the organizer allows for simply asserting that: the formation of axes produces alternative possibilities, but in the end a standardized result is achieved. He showed that the formation of gastrulas, neurulas, and primitive brains cannot be understood in terms of the single pathway "action—response." The historian of Spemann's research has written: "How should we evaluate the experiments on the organizer? They were simply unique. No new principles appeared from the experiments of Spemann and his students. But something more significant did appear: the constellation of important phenomena at a critical period (integration, self-differentiation, induction, regulation, and self-organization). Here, we should add the origin of the axes of the organ and the maintenance of the organ's activity over a relatively short critical period, and also the precise study of the process of gastrulation" (Hamburger, 1988, p. 86).

Among the embryologists, there began to grow the recognition that processes in individual development were varied and interacting. The ideas of the Spemann school came to Great Britain. Huxley, de Beer, Needham, and Jenkins began to investigate the biochemical nature of the organizer. Thus, Huxley and de Beer accepted the contributions of the German school of embryology. But for them, it was necessary to combine the theory of organizers with Child's gradient theory. Finally, they had to do something with their own concept of gradient fields. However, in *Elements of Experimental Embryology*, the successes of the German scientists in embryogenesis found no place: Huxley and de Beer changed almost nothing in their monograph when compared to their earlier publications.

It was Spemann himself who translated Huxley's article into German and made a short commentary on it. The German scientists associated Huxley's name with Child's and made a sharply critical evaluation of the theory of gradients. Spemann repeated this critique in his monograph on embryological development and induction. He wrote: "On the basis of contemporary facts, I cannot admit in any way that the theory of gradients of Child, de Beer, and Huxley can be applied to the early development of amphibians" (Spemann, 1938, p. 345).

The great embryologist, Paul Weiss, critically assessed Spemann's organizer theory (Weiss, 1939). But Weiss also criticized both Child's gradient theory and the synthesis of the great British scientists Huxley and de Beer for having a "feeble" basis.

On the nature of the Huxley-de Beer synthesis

Not a single scientist was able to implement a synthesis in their area of investigation, which would be able to envelope all its questions, facts, and opinions. A synthesis suggests a choice of defined initial principles, around which is formed a general model. This model fills the function of the hypothetico-deductive method, paving the way for the search for and generalization of factual material. Child's theory of gradients, Spemann's organizer theory, the gradient-field theory of Huxley and de Beer, and finally classical genetics and the genetics of individual growth all this went into the general model, or synthesis, of Huxley-de Beer. Witkowski (1992) attentively collected and analyzed the reviews and testimonials of *Elements of Experimental Embryology*. Literally all reviews criticized Huxley and de Beer for the broad use of Gurvich's idea of field and the genetics of individual development. The first idea seems too idealistic, and it was thought that it was necessary to "cut it out" of science. Regarding genetics, "classical" embryologists were almost in a state of shock. Why did embryologists need genetics? But such an example serves as evidence of the radical novelty of the synthesis in the field of individual growth. And only one Russian embryologist understood this, DP Filatov. In 1936, under his editorship, Huxley and de Beer's book was translated into Russian by TA Detlaf and was published under the title, *Osnovy Eksperimental'noi Embriologii* (Foundations of Experimental Embryology). The title was successful—the book was accepted and even now there is used as a textbook at the universities. Actively working in the genetics of individual development on the molecular level, LI Korochkin noted that this book remains one of the best and is always ready at hand on his desk.

It is interesting that the main themes Huxley worked on received the greatest development in de Beer's work, but it is necessary to document this claim. de Beer made a huge contribution to study of segmentation, and the development of the skull and pituitary gland. In his comparative anatomy, research on vertebrate embryology always dominated. He widely used the concept of neoteny when discussing the origin of taxa of any range. Moreover, he made the widest survey of the phenomena of neoteny in invertebrates and vertebrates (see de Beer, 1951, p. 52-69). All of his investigations were related to comparative embryology. At the same time, de Beer had the experience of an experimental embryologist and improved that field (for example, he traveled to Germany and, working with Spemann, mastered the method of embryo transplantation). He collected a series of books which can easily be called classical: *Embryology and Evolution* (1930), *Embryos and Ancestors* (1940, 1951, 1954), and *The Atlas of Evolution* (1964). All these books had one goal—to combine embryology and evolutionary theory. The problem of heterochrony and homology dominated all de Beer's works, but he also presented himself as a historian of science. He prepared Darwin's notebooks on evolutionary theory (1837-

1839) for publication, republished Darwin's manuscripts of the 1840s, which predated his writing of the *Origin of Species*, published A Wallace's articles on evolution, and finally wrote a monograph and a series of articles on Darwin. Undoubtedly the powerful growth of Darwinian historiography in the 1970s-1990s was made possible in many ways by de Beer.

Huxley's influence on de Beer's views can be traced even to the discussion of heterochrony when de Beer tried to accomplish a synthesis of genetics and evolutionary embryology. de Beer widely used the concept of the rate of genes in explaining the phenomena of heterochrony, neoteny, pedomorphosis, and also in the study of the general principles of individual development. In his book, published in 1951, there are eight references to Goldschmidt and eight to Huxley.

On the relationship between the concepts of heterochrony and the rate of genes, de Beer wrote: "We...can conclude that by way of the action of different rates genes can change the time of appearance of defined structures, as is described in the case of eye color in *Gammarus*. This conclusion is of huge interest, since it allows us to see changes in the order of the appearance of structures can occur. This phenomenon was appropriately named heterochrony" (de Beer, 1951, p.20). He saw how the genetic and evolutionary advantages in organisms arose, when heterochrony moves into pedomorphosis. He wrote: "Only those species undergo pedomorphosis which possess the genes able to control the loss of adult old traits in neoteny, and the exchange with lines of organization. It is possible that genes make possible the formation of new developmental paths. Pedomorphosis in that way can directly contribute to the growth of genetic and evolutionary plasticity"(Ibid., p. 93). Finally, all of de Beer's thoughts on heterochrony are presented in the following four conclusions (Ibid., p. 88):

1) the evolutionary novelty of any quality appears at any stage ontogenesis and often in the adult organism (analogy to AN Severtsov);

2) the time and order of appearance of traits in the ontogenesis of offspring compared to their ancestors can be changed (here de Beer actively used genetic explanations);

3) the qualitative difference between traits emerge from heterochrony and play an important role in phylogeny in the addition of qualitative novelty;

4) an organism's traits evolve at different speeds and not in the same way (mosaic evolution).

de Beer's genetic repertoire significantly broadened in discussing homology. Regarding the genetic basis of structures that should be homologous, he analyzed phenocopies, homeotic mutations and the mutation "eyeless". He came to the following conclusion: "Traits which are controlled by homologous genes are not always homologous. Therefore, homologous structures are in no way invariably controlled by identical genes, and the homology of phenotypes does not suggest the similarity of genotypes" (de Beer, 1971, p.15). The question of the relationship between genetics and embryology arose in de Beer's research and was influenced by Huxley. Even now there is still much to be done in that field.

It remains to say that the synthesis of Huxley-de Beer included a deep contradiction of the core problems of evolution. This contradiction became especially obvious after 1942 when Huxley's monograph *Evolution: The Modern Synthesis* was published.

The Science of Life. A System of Evolutionary Views

Analysis of Huxley's research makes it possible to introduce a correction in historical dates. In the 1920s, he had not a simple neo-Darwinian view in considering natural selection and chance variation as the main traits of causes of evolution. In 1926, Huxley and Haldane published the book *Animal Biology* in which they claimed that natural selection acts the same on small mutations and saltationist changes. The authors clearly broadened the theoretical possibilities of selecto-genesis, applying the theory of selection to explain the gap between the great taxa (Haldane, Huxley, 1926). This problem worried Huxley all his scientific life, and he constantly searched for more novel explanations at the level of genetics, epigenesis, and ontogenesis. Haldane also thought along these lines and in 1932 formed the conception of the time of gene action to explain neoteny as the most important epigenetic phenomenon and mechanism in the origin of higher taxa (Haldane, 1932b).

In 1925, HG Wells invited Huxley to prepare a collaborative, multivolume publication on biology to serve as an encyclopedia. The co-authors included Wells's son, GP Wells, a young biologist. HG Wells heard Thomas Henry Huxley's lectures on evolutionary theory and considered himself Huxley's student. By this time, Wells was well known in Britain and the U.S.A. for his book, *An Outline of History*. Naturally, all sections on evolutionary theory, genetics, and phylogeny in the encyclopedia were written by Huxley. The book appeared in Great Britain from 1929-1930 under the name, *The Science of Life*, in three volumes, and in the United States (in 1931) in two volumes (of thicker size). Here, I cite the American volume, which I found at the library of the Zoological Institute of the Russian Academy of Science.

The first volume of *The Science of Life* contains 773 pages, 500 of which are devoted to genetics, evolutionary theory, systematics, and animal and plant phylogeny. Recall that the work was written from 1925-1928. The situation in evolutionary was complicated, but Huxley masterly navigated around all the "sunken rocks."

Genetics and natural selection

In the chapter on "Variation in Species", Huxley completely surveyed all the fundamental discoveries in genetics and in an historical manner compared the views of neo-Darwinists, supporters of ontogenesis, Lamarckism, and of creative evolution on the nature of genetic variation. Weismann's concepts, or neo-Darwinian concepts, thought that heritable variations are chance variations in the embryonic plasma. Lamarckists supposed that variations are acquired during individual development. Orthogeneticists claimed that variations move in a determined direction. According to A Bergson, variation is a "mystical force" and moves in a "creative" direction. How did Huxley organize his discussion evaluating the historically complex views on variation? He declared that he was a neo-Darwinist (supporting Weismann), and concluded that he automatically discounted the Lamarckian claim of the inheritance of acquired characteristics (somatic variation). He devoted two paragraphs to the analysis of the nature of mutations. He gave a popular outline of all contemporary achievements, including the chromosomal theory of inheritance. The readers of *The Science of Life* could not have any doubts about the depths to which Huxley's pen would reach. He constantly - literally every day - wrote surveys and short reviews of the newest genetics research, and began experiments on genetics of Crustaceans and, moreover, maintained a good "genetic" form.

Since Lamarckism was still popular among British botanists and zoologists at the beginning of the 20th century, Huxley wrote a large section in *The Science of Life* on "Are Acquired Characteristics Heritable?" (see Haldane, 1932a). He again noted the great evolutionary-biological achievements of Weismann. Huxley wrote: "We, undoubtedly, see that

the inheritance of acquired traits is not proven even in simple observations on animals, plants, and human beings” (Wells, Huxley and Wells, 1931e, p. 592).

It is interesting that Huxley analyzed melanism in butterflies, not as proof of natural selection, but as direct evidence of the possibility of the appearance of mutations in natural conditions. Only after evaluating the appearance of melanism in that way, did he take up the theme of “Selection in Evolution”. He used many examples of selection in plants and animals, which were accumulated by biometricians, geneticists, zoologists, and botanists; in order to strengthen selectionism, he underlined that “Natural selection . . . is a fact in evolution, and not a theory” (Ibid., p. 604). The sharpness of Huxley’s opinion should not make us suspicious. In those years, there were still strong arguments on the reality of natural selection. Therefore, the word “fact” only established proof.

The phenomenon of melanism offered Huxley good material on what the Darwinists subsequently called *driving, or directed*, selection; and all this became part of the scientific literature. Actually, it was important to review the evidence that proved the role of selection in the formation of species. The idea that natural selection is a conservative, of stabilizing force entered into almost every non-Darwinian concepts of evolution. And Huxley accomplished a non-standard synthesis. In *The Science of Life*, he wrote a section on “Natural Selection as a Conservative Force.” In which he instigated that: “If the environment remains stable, then natural selection will be a stabilizing force that has a conservative influence. If a species is to be well adapted to its role in life, natural selection will remove variants that are moving in another direction from the current optimum. But the environment can change and this requires a response to the changes. This revolutionizes the selectionists’s position, and natural selection in the changed environment has a radical influence” (Ibid. p. 605). The sources for the concept of conservative selection were the most varied. But it served to recall Huxley’s grandfather—the well-known Thomas Henry Huxley—who in 1862 in his essay, “The Geology of Contemporary and Persistent Types of Life”, essentially had already formulated the contemporary conception of evolutionary stasis (T Huxley, 1894). Huxley senior hardly thought about the evolutionary causes of the observed phenomena, but his grandson strove to “wrestle” with that fundamental biological mystery. Having sorted through many variants of solutions, Julian Huxley formulated it in 1958.

Didactically and uncharacteristically, Huxley literally bolstered up this hypothesis. He began the section by outlining the conservative form of selection that none disagreed with, and finished with the driving form of selection, by which he showed the delicate transitions between forms of selection. However, in order to strengthen the evidence for driving selection, he added a paragraph on “Natural selection in Changing Conditions, or the Adaptation of Species to New Conditions.” He showed that the best example of the force of selection is melanism in butterflies, and strengthen his analysis with the authority of Haldane. Huxley also conducted an analysis of the time of species change. He wrote: “If it is considered that evolution proceeds by small steps, then it will take not less than 100,000 generations for the evolution of each new species” (Wells, Huxley and Wells, 1931e, p. 606). Apparently, this was one of the first measurements of the intensity of natural selection not only on the improvement of adaptation, but also regarding the transformation of species. The connection of “conservative selection and driving selection” had great value on the plane of public perception. If the investigator or reader accepts the idea of conservative selection, then he just cannot “brush aside” the theory of driving selection. And the following discussion of Huxley’s views proves that in distinction from the neo-Darwinists, he did not believe at all that natural selection produces “all around good.”

His analysis of natural selection in *The Science of Life* concluded the section, which dealt with intraspecies selection of traits useless to the species. The title itself, if laconic, “Selection against Adaptation, or the Lowering of Adaptation” seems, at the least, strange. He began the demonstration of the selection of useless traits by comparing the presence/absence of several adaptations in closely related species living in the same conditions. For example, a butterfly is defended by a close similarity to the background, when another had not such defense. Comparing the similar adaptations Huxley used the term “intraspecies selection.” He wrote: “If you chose a term for selection, the action of which can transform all individuals of a species (or one sex inside a species) without a special advantage for the species as a whole, then this would be *intraspecies selection* (Ibid., p. 610). He placed the idea of intraspecies selection on solid ground using material, which characterized the action of sexual selection. He wrote: “Darwin showed one aspect of that process (of intraspecies selection) calling it competition between males or females. Darwin’s theory of sexual selection received more severe criticism than any of his other works” (Ibid., p.612). It is clear that in Huxley’s experiments on ethology, one must search for all specificity in the completely original concept of intraspecies selection.

In a large work on the ethology of birds in 1930, he more clearly outlined his theory of intra- and inter-species selection. He wrote the above-cited (from *The Science of Life*) and latter (from the work of the 1930s) texts at the same time, thereby extending and broadening one another quite well. He noted that: “Interspecies (or species) selection, apparently, should make possible the biological improvement of the species. Intraspecies [or individual] selection, although it might also act in an analogous way, in defined conditions favors traits which appear useless or even harmful regarding the species as a whole. For example, competition between males can promote species, as well as individual advantages, that is, everything that is related to the majority of secondary sexual traits (play in monogamous species). However, traits useless to the species can make possible the earlier appearance of the males in the breeding grounds. It is correct that after G Howard’s conclusions, all this still requires special investigation” (Huxley, 1930b, pp. 22-23). Conclusive evidence that bird ethology became the primary source for Huxley’s non-standard views on natural selection is found in the authoritative works of historians of science (see Durant, 1992, pp. 158-159; Bartley, 1995, pp. 93-94).

Huxley was perhaps the only evolutionist who evenhandedly and critically analyzed the theory of natural selection. He did not relate the action of any form of natural selection to the formation of adaptations as had done all evolutionists. Although the idea of interspecies and species selection became very popular, especially after the publication of Stanley’s book, Huxley’s idea of intraspecies selection completely failed to “fade” (Stanley, 1978). It was picked up by Haldane, who suggested that intraspecies selection can lead to the overdevelopment of traits (hypermorphosis), and demonstrated this in the growth of ancient plants. In 1947, Haldane’s idea were developed by Cirill Zavadskii, who had studied the mechanisms of natural selection in overpopulated cultures of wild and semi-wild grass plants (Zavadskii, 1947). At the same time, the idea of species selection occupied a central place in the concept of macroevolution, suggested by Gould in his last (unfortunately) book (Gould, 2002; see also Stearns, 2002). It is correct that Gould and Stearns built the species selection on the analogy of “species-individual,” which already existed in Darwin’s *Notebooks* of 1837-1839. Such a metaphor showed how individuals (and for that matter, species) work in the process of species selection. Moreover, Gould suggested that the idea of stasis and species selection allows for solving the difficult problem of defining a species in the fossil record, and also in adaptive and

neutral evolution. [In the 1970s, J Price discussed the concepts of adaptive and neutral evolution using the idea of species selection on a theoretical level.]

Geographic species formation

In *The Science of Life* there is a large section entitled “Isolation as a Species Marker.” In all of Ernst Mayr’s work, the idea existed that the contemporary concept of geographic species formation worked out by himself in 1942 (see, for example, Mayr, 1982). Many concepts of geographic species formation existed before the appearance of this book, but their status was very problematic due to the weakness of their genetic basis. Thus, the majority of the early models of geographic species formation carried a Lamarckian character (Lukin, 1940; Popov, 1997).

Huxley examined only the geographical model of species formation independently, besides the simple enumeration of the other forms of increasing the number of species. He began with the fact that many traits of subspecies in closely related species are adaptively neutral. He wrote: “Maybe, a future discovery will show that these traits are useful or directly related with useful traits” (Wells, Huxley and Wells, 1931e, p.620). Suddenly Huxley asked the question, what will happen if future investigations observe nothing in this aspect? He concluded that species formation sprang up in conditions when widely separated species through isolation disintegrated into small geographic races, which inhabit various regions. He noted that: “When there are no geographic barriers, one subspecies constantly interbreeds with another in an intermediate zone” (Ibid., p.620). And furthermore, in an already completely contemporary form, as if by Mayr, he moved to an evaluation of geographic isolation. Huxley wrote: “The effect of isolation helps to make new species, and this is an everyday fact of systematic biology. More telling is complete isolation, which exists in plants and animals that live on islands. The best example is the Galapagos mocking-birds” (Ibid). He concluded that isolation makes possible not only species formation, but enhances divergence.

Huxley absolutely and precisely turned to island biogeography for evidence of the role of isolation in evolution. What happens on the genetic level when isolation is complete? He drew on the Galapagos mockingbirds as an example of geographic species formation. The example is very successful since all of the species of Galapagos mockingbirds live on different islands and the covering of the natural habitat is not fixed. He examined the role of geographic isolation simultaneously in species formation and divergence. Huxley discussed divergence and what he latter called evolutionary trends as some type of special evolutionary paths. He also discussed within the genetics of species formation the role of hybridization and polyploidy in increasing the number of species. Why did Huxley not mention at all the genetic aspects of geographic species formation? The preconditions for it existed in the theories of Haldane and Fisher. It is correct that the main concept, especially analyzing the genetic processes in small colonies, had been published in 1931 by the American geneticist, S Wright (see Provine, 1971, 1989). Therefore Mayr was first, and yet Huxley had the possibility of forming a conclusive theory of genetic-geographic species formation even by the end of the 1920s. In 1926, the Russian geneticist, SS Chetverikov published a classic article on the population and evolutionary genetics (Chetverikov, 1926). As a systematist and geneticist, he discussed peculiarities of genetic processes that occur in small isolates during sharp drops in the number of populations. In agreement with Chetverikov, in the “valleys” of the waves of life occurs the chance fixation of alleles which serves as a cause of the formation of adaptively neutral traits at the level of

subspecies and species. It is interesting that Chetverikov's genetic-populational ideas were broadly naturalistic.

Biological and social progress; Non-Darwinian concepts of evolution; Purpose and evolution

It was completely logical that Huxley took up the problem of "big" evolution, but he did not do this in the form of a monograph or textbook, but as a critical analysis of popular non-Darwinian concepts. But the theme of "big" evolution, including progressive evolution with social consequences, had already been widely discussed by Huxley in his 1923 *Essays of a Biologist* (Huxley, 1923d), and even in the lectures he delivered in 1916 at Rice University. In one of these lectures, entitled "The Concept of Evolution and its Application to the Affairs of Man," he strongly expressed the idea that scientists and engineers should possess great political power, since thanks to their specialized knowledge, only they have the key to social control. Surprising, but again in that lecture of 1916, he listed the criteria for evolutionary progress, which he preserved in his scientific publications on biological and social planning, i.e. *control over nature* (for more information, see Swetlitz, 1995, p. 184). In 1923, he focused on the criteria, adding the phrase: "*and the growth of independence from nature*" (Huxley, 1923d, p. 52). In other words, the idea of state intervention and planning in the area of economics and broad social politics came to Huxley early on, and later, as will be shown, it only strengthened and grew.

In Huxley's archives, a 1916 manuscript entitled *Biology, the Individual and the State* is preserved, in which he insistently defends the idea of the extreme necessity of the great control over the inheritance in man by eugenic measures (see Swetlitz, 1995). In Huxley's manuscript, *Notes on Religion* (1916-1917), he openly traces the social and philosophical roots of his ideas of evolutionary progress. In the social aspect, he claimed, evolutionary progress should serve as the general ideology for asserting social order and would be the scientific key to social politics. He argued that contemporary chaotic international order by its own roots is deeply sinking into the absence of a "general theory of life." Various conflicting creeds, such as official religions, capitalism, socialism, imperialism, nationalism, and scientism, should be replaced with a new vision of life and humanity on the grounds of the hard facts of evolutionary progress. At the beginning of the 1920s both in lectures and print, Huxley often declared that the direction of evolutionary progress is the basis for social ethics: human ideals lay in that very direction, which is also the "main tendency of evolving life" (Swetlitz, 1995, p. 184).

Essentially, in 1924 Huxley introduced another criterion for evolutionary progress related to the appearance of human consciousness (Huxley, 1923d). Humans are the highest product of evolution thanks to their great intellectual development. "Consciousness" established human superiority in the cosmos and allowed humans to have choice and control over the path of their own evolution. In 1923, Huxley wrote that people: "are the trustees of evolutionary progress." These words first appeared in the preface to *Essays of a Biologist*, becoming the central idea in his views on man's place in nature and at the same time reflects the idea of planning. Actually, in the majority of his notes on trusteeship in the 1920s-1930s, he discussed eugenics; he called trusteeship the "simple, but magnificent truth that lay at the foundation of eugenics" (Huxley, 1923d, P. xii). In 1926, he wrote for the Labor Party an article on "*Control of the Birthrate*," in which he suggested passing a law limiting the possibility of reproduction in people with "weak genetics" (Huxley, 1926e).

He examined the question of progress in its objective and subjective aspects. He used graphs to express the physico-chemical and biological progress with the "critical point", Q,

representing the stage in the history of life, when humans appeared. He suggested that with their appearance, intelligent organization became biologically more important than organization of the body—material was obviously added to by a conscious factor. In the essay “*Rationalism and the Idea of God*” he openly discussed the connection between biology and the higher human values using Freudism. He asserted that the subconscious, which is supposedly a sexual instinct, can produce great science, great art, and religious ecstasy. Evolutionary biology and the new psychology, for Huxley, is a “religious system based on the scientific method.” Unlimited nature is indifferent to human values, but organic nature can form a trend in the direction of forming with high spiritual needs and hopes. *Intelligent human activity, he suggested, changed the entire path of evolution by forming new methods, which introduced values common to all of the human species and generated the complex interaction of the conscious with the subconscious.* This theme was introduced in the article “*Religion and Science: Old Wine in New Bottles*” (Huxley, 1923d, p. 255). With the appearance of humans, he wrote, a new phase in evolution began, since the mind acquired consciousness. The speeding up of the tempo of evolutionary progress will occur faster through the selection of ideas than through the old tested way of the natural selection of individuals and species. Some forms of action are higher than others, and thus the scale of moral values arises. “In the human mind science (Huxley dreamed) is connected to the general teleology of the future” (Huxley, 1923d, p. 220). He recalled, however, that Darwin examined the possibility of the appearance of purposeful structures by way of non-purposeful mechanisms, i.e. analyzing teleology. Huxley wrote: “Purpose is a term which should mean the special action of the human intellect and should be used when a psychological basis is postulated” (Huxley, 1923d, p. 41). His thoughts on the growth of the role of consciousness in evolution, when brought to its logical end in the words of the historian, John Greene, took the following form: “The triumph of evolution is the triumph of mind over matter” (Greene, 1990, p. 47).

Huxley—a scientist, moralist, philosopher, poet and defender of nature—began to advocate a new “religion”, one of scientific or evolutionary humanism.

Many paleontologists, observing clearly the expression of direction in evolution, concluded that chance mutations are incompatible with the fossil record. For Huxley, this process is explained by mutations and natural selection. His discussion was directed against the views of H Osborn on the strict directing of the evolutionary process (orthogenesis). On the example of body growth in horses during evolution, Huxley concluded that growth occurred, based on mutations and natural selection. Horses and titanotheria were Osborn’s loved groups of investigations, and from studying them he developed his “tetrakinetic theory of evolution, and later also the “theory of aristogenesis” (for more, see Zavadskii, 1973). It is curious that in criticizing Osborn, Huxley did not mention his name—apparently, due to his deep respect for the paleontologist and biologist. And still Huxley did not “abandon” the concept of orthogenesis: he constantly considered new data regarding that concept.

Huxley always wrote the forwards for his students’ monographs (Elton, Hardy, and others). In the forward to de Beer’s book *Vertebrate Zoology* (1932), he noted that: “Homology is not always based on common ancestors.” This position has been essentially modified by modern genetics. Identical, but independent mutations of genes can arise; for example, they are observed in *Drosophila*. We have come directly to orthogenesis . . . Another direct example of orthogenesis is the development of antlers in various lines of mammals. Developmental physiology and the theory of relative growth, in the strong sense of the word, do not need the application of orthogenesis. The study of the mechanism of the relative growth of parts has shown that natural selection, leading to growth in size, automatically led to the growth of antlers.

Darwin called this correlative variation. A re-evaluation of the theory of recapitulation is needed in the light of these investigations into growth and developmental genetics” (Huxley, 1932e, pp. xi-xiv). Any concept of orthogenesis is based on the views of evolutionary trend. Evolutionary trend was one of the central ideas of Huxley’s 1942 book. Of course, the interpretation was different, but it allowed him to “eliminate” the understanding of “macro- and micro-evolution” and principally “go around” Dobzhansky and Mayr, whose classic monographs concluded the analyses of species formation. Huxley’s primary intention was to place orthogenesis at the service of Darwinism.

Huxley did not even criticize Bergson’s creative evolution, but was briefly and beautifully outlined in the French manner. ‘Vital force’ by itself, for Bergson, can cause evolution. It is the same as orthogenesis, but translated into vitalistic terms. Further Huxley almost accomplished “saltations,” transferring his terminology into the channel of Darwinian paradigm. He wrote “...vital force is not a new and secret creative principle, but the elementary chemical properties of living matter, which are idealized and personified. In reality, metabolism and self-reproduction are the basic properties of living matter. From these two properties follow: super-fertility, the struggle for existence, the survival of the fittest, and the constant press of natural selection.” Bergson indicated the basic preconditions for life, but strictly ignored the consequences [For this Bergson can be forgiven since he was a superb and write and essayist]. His “creative evolution” is a magnificent poetic description, but not a scientific explanation” (Wells, Huxley and Wells, 1931e, p. 639).

Huxley devoted most of his pages to a discussion of the purposes of evolution. He constantly balanced in the framework of a dualism: the randomness of evolution and the evolutionary progress, leading to purposeful social evolution. Nevertheless before the publication of *The Science of Life*, he thought and wrote about theology and teleology. In 1926, he published a popular essay entitled, “*Evolution and Purpose*.” In it he noted that: Contemporary science created a pseudoteleology, in which evidence of creation should be sought in natural selection; therefore we cannot talk about purposes, but should talk about functions, adaptations, and mechanisms, which are useful for the possessor” (Huxley, 1926e, p. 155). Here a strong mechanistic position is clearly expressed. But it is completely explained: Huxley’s essay had a critical character and was a review of V Stopp’s book, *Argument from Creation*. With time, Huxley’s position changed as far as his interest in the idea of evolutionary progress grew, with the appearance of social processes. The complexity of his position to some extent is discernable in *The Science of Life*. His essay, “*Evolution and Purpose*,” was read by the broadest public, since it was published in the collection *Essays on Popular Science* (Huxley, 1926e, pp. 155-160).

In the section “Is there a Purpose in Evolution?” in *The Science of Life*, Huxley summed up all of his views against leading teleological concepts of evolution. He wrote: “Bergson in the company of others made purpose the key theoretical position of their evolutionary views. Moreover, they converted purpose into a method. The question of purpose in evolution is key to biology and for its contribution to general thought. It is necessary to formulate precisely a position, to decide whether or not a purpose exists in evolution”(Wells, Huxley and Wells, 1931e, p.69). Huxley suggested that in deciding the question of purpose in evolution Lamarckism should be decisively disregarded, since the direct conscious or unconscious effects of the environment are never hereditary. He also suggested that “orthogenesis is not a necessary hypothesis.” Only the theory of natural selection, he claimed, offers an adequate explanation for almost all evolutionary facts—“it can explain detailed adaptations of animals and plants and the extensive trends of specialization, the appearance of new types and the extinction of old ones. the

progress of life, regression, and degeneration” (Ibid., p. 640). It is interesting that Huxley’s closest friend, Lord Solly Zuckerman, and his son, Francis Huxley, declared in 1987 at a conference in honor of Julian Huxley at Rice University in a friendly way that the subject of the celebration was a vitalist, citing Huxley’s works of the 1930s (see Greene, 1990, p. 44). This was an entirely serious declaration. The complex historical question can be analyzed in several directions. Huxley persistently claimed that “living material is not a special succession of usual material,”; it does not possess special attributes. And chiefly, he completely recognized natural selection as the mechanism of evolution. It is correct that he loved the expression the “pressure” (or “press”) of selection, which in agreement with Greene, was a quasi-analogy to *élan vital* (Greene, 1990, P. 44). Not accepting vitalism, Huxley to some extent used language which implied the presence of purpose. For him natural selection was not simply a question of differential survival and reproduction, but a method “which begets” progress by realizing vital potentials through the competitive struggle for existence and the reproduction. “Progressive” traits were selected not because they were progressive from the point of view of humans, but because they possessed competitive advantages over other organisms. Their “progressiveness” was realized only after they were appreciated by the beings that arose along the very same path.

It is interesting that in characterizing the action of selection, Huxley accepted the role of the biotic environment in evolution. He also wanted to “finish off” Lamarckism right away, since it did not examine the role of the biotic environment in evolution and orthogenesis, since it cannot devise a purpose for adaptation to the dynamic biotic environment. Huxley wrote: “Allow us to admit that the environment of life includes not only inert nature but also biotic nature” (Wells, Huxley, Wells, 1931e, p. 640). Any contemporary evolutionary ecologist, having read Huxley’s words, would be surprised by the preciseness of the treatment of natural selection, in the action of which the biotic relationships play a powerful role. Moreover, the primacy of biotic relationships in evolution tests Lamarckism and ontogenesis with insurmountable difficulties.

The concept of purpose in evolution was extremely important for Huxley in regard to his future investigations, and, remaining in the framework of the theory of natural selection, he strove to prove it somehow. The logic of combining the non-combinable appears. The growth of adaptability is the primary result of natural selection. But in the perfection of adaptability there are limits, since the variations themselves can be limited qualitatively and quantitatively. The logic of the discussions led Huxley to the idea of purpose in evolution. Variations occur by chance, and the environment is always changing character. And this is not paradoxical, Huxley found in this only support for the idea of purpose in evolution: actually, each variation is due to chance, but selection shifts and directs it following changes in the environment. He wrote: “If we understand this, then we should promote evolution as a purposeful process. This is an obvious purpose, but obviousness is not a real purpose. It is the result of purposeless (Ibid, p. 640).

In addition, he was able to examine purposeful concepts of evolution not only from a position of selectionism, but also in the broader context. What is the source of his so constant interest in purposeful concepts of evolution? We may bravely say—in the question of man—in part in the works of his friend, the French thinker, Teilhard de Chardin, who developed the theory of “Christian evolutionism.” In the preface to the English edition of his *The Phenomenon of Man*, Huxley clearly described the purposeful aspects of evolution, combining his own views with those of the French investigator.

Before preserving the understanding of “purpose” in the scientific custom, Huxley commented upon the term itself. He wrote: “The term “purpose” has a completely definite meaning. This is a psychological term which describes the situation of our own conscious”

(Wells, Huxley, and Wells, 1931e, p. 641). Contemporary Creationists, he noted, claim that there exists a Plan and the gradual realization of a purpose. “This may be true,” continued Huxley, “but science can answer neither yes or no to such a direct question. It can only say the following. In the natural selection of random variations is the primary agent of evolution, then evolution has a scientific explanation in terms of natural forces. When we reach Humans, evolution becomes partly purposeful, since man—the first product of evolution - is able to control it itself. Human purpose is one of the achievements of evolution, and it arose as the mechanistic work of variation and selection” (Ibid., p. 642). He underlined that Darwinism in connection with genetics is able to explain the evolutionary process up to the appearance of humans. Darwinism has henceforward not withdrawn, but after the finale of biological the spiritual factor has become a powerful beginning of evolution. He proclaimed that humans are the highest product of evolution, and after their appearance, evolution became even more impressive and varied (Ibid., pp. 794-795).

In the 1934 edition of *The Science of Life*, he introduced a change in how he understood man’s place in evolution. He wrote: “Man has privileges regarding the future of evolution” (Wells, Huxley, Wells, 1931e; 1934, p. 806). Man can plan his own future (his economic and social life), and it is in this that he is unique. Widening the theme of social planning, which came up earlier, is perhaps directly related the U.S.S.R., which Huxley visited in 1931 as representative of the Union of British Scientists, a member of a delegation of English scientific workers and physicians. In his book, *A Scientist among the Soviets*, he spoke favorably of the Soviet experiment in the area of scientific planning of the economy, on the planned allocation of resources for fundamental and applied research. This book was published for mass circulation and widely read by Western society. In 1932, he actively participated in the formation of the committee on economical and political planning, which included among its ranks leading British businessmen, politicians, and intellectuals. At its meetings, the committee discussed the problems of central planning of the economy and general international cooperation with the aim of preventing world war. When the discussion turned to views on state planning, Huxley often referred to his small book *If I were Dictator* (1934f). Not long before the publication of this work, the British Broadcast Company (BBC) invited Huxley to present a series of shows on the relationship between science and society. On the basis of these broadcasts, he wrote his book *Scientific Research and Social Needs* (1934i), in which he described his belief that directions and forms of scientific activity always were, and should continue as, processes determined by social and economic demands.

Thus, in the 1920s, when there was a multitude of the most varied evolutionary concepts, Huxley took a clear position. From 1923-1929, the foundational evolutionary views developed in a popular form,, which were broadened and perfected over all scientific activities and finally directly influenced all other, including social, investigations.

Natural Selection and Evolutionary Progress: A Prelude to the Evolutionary Synthesis

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. Huxley's evolutionary ideas of the 1920s display a less simple picture.

In 1936, he presented an address at the British Association for Collaborative Science on "Natural Selection and Evolutionary Progress." The address was immediately published (Huxley, 1936a). His textual analysis leads to the simple conclusion: Huxley 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 book. Moreover, in his 1936 address, he examined the now lively topic, which includes the triad "genetics-individual development-evolution," deeper and more clearly than 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 than the old one-sided views on evolution" (Huxley, 1936a, 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 wrote: "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, 1936a, 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, 1936a, 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.

No one before or after Huxley considered the direction of evolution so broadly. The word "plurality" itself expresses his wide pluralistic position, which continued even when examining other closely related themes.

His critique of panadaptationism appeared in his comparison of the evolutionary views of field naturalists, physiologists, and systematics. If for the physiologist the problem of evolution always took the form of the origin of adaptations, the systematist, who diagnosed species and genera, usually neglected the existing adaptive traits at the species level all the way to the paleontological trends. Huxley calmly accepted that the most extreme points of view had the right to exist. Having formulated such wide a view of evolutionary paths, he again returned to an evaluation of the paleontologists' views. He saw the reign of Lamarckism and orthogenesis in their work being in "conflict" with contemporary studies of mutations.

He separated out numerous partial forms of evolution from the general directionality of the evolutionary process. And when examining that question he constantly recalled the most difficult problems of adaptive and neutral evolution. The principal direction of the evolutionary process (progress, specialization) always demonstrated compromises between adaptive and neutral evolution.

Selection in changing environments

In all the sections of the 1936 address, especially the most varied aspects, he touched on the problem of natural selection. The peculiarity of this analysis was that the author simply refused to enumerate examples of the action of natural selection, many of which had accumulated in the works of British biometricians and naturalists. It was as if Huxley had transferred the problem of natural selection into the Mendelian world. The conflict between Mendelism and evolutionism in a Darwinian manner was resolved by the appearance of population genetics.

Huxley examined the genetic basis of natural selection in the following section of the 1936 address: selection in the Mendelian world, adaptation and selection, and the rates of genes and selection. Besides that, the genetic aspect was steadily present in the analysis of species formation and large scale evolution [macroevolution in the contemporary sense—although the term was almost never used in Huxley's works].

In analyzing the properties of mutations, he focused on interaction, or "cooperative gene action" (Huxley, 1936a, p. 82). He criticized the old view of "one gene, one trait." For the evolutionary theory the important fact of genetics was that "mutations, which in one case would be pathological, in another case might be completely harmless, and might even add and advantage" (Ibid.). From there, he immediately moved to the problem of selection in changing environments. The transfer from experimental genetics to the genetics of natural populations provided a key to the mechanism of natural selection. The question of usefulness and harmfulness of mutations was resolved by the study of gene dynamics in populations and by comparative analysis of other populations of the same species, living in different conditions. He wrote: "Mendelian variation cannot be described as useful or harmful, but their selective value varies in different environments" (Ibid., p. 84).

It is interesting that as evidence of this important evolutionary conclusion, Huxley drew on examples of the varied survivability of *Drosophila* mutants and the experiments of VN Sukatshev (1927) on the struggle for existence in the common dandelion. In evaluating Sukatshev's experiments, Huxley focused on the different levels of survivability of the biotypes in the changing density of the experimental populations. He evaluated these experiments simultaneously in two ways: the survivability of mutants and the change of the vector of the action of natural selection. It is interesting that a similar evaluation of Sukatshev's experiments can be found in Haldane (1932a). The problem of selection in changing environments, sharply and deeply described by Huxley, is important and current today. In 1983, the logical neutralist,

M Kimura, suddenly declared that allozymes, which seem neutral in changed environments can have an influence on physiology and individual development. The many years of discussion on the adaptively neutral nature of protein polymorphism, according to P Cohen and J Hillbush, can be solved in the test-tube by standard methods, and by studying the problem in different environments (see Gall, 1987). The understanding of evolution as a process, which occurs in changing environments, is one of the most perspective directions in the investigations of evolutionary theory.

Selection in natural populations most often acts not on separate genes, but on gene complexes. Therefore, evolution does not have sharp individual steps. The interruption of inheritance in Mendelian genetics was not an obstacle in Huxley's ideas about the seeming continuity of the paleontological record. Independently from Chetverikov, Huxley described the mechanism of natural selection in dependence on the external and genotypic environment, fully dwelling on the phenotypic manifestation of mutations, which change the vector of selection.

Huxley asked why the selection of gene complexes is more important than the selection of single mutations. The selection of gene complexes can act as a blocker of the action of single harmful or lethal mutations. Besides, with the appearance of reverse mutations the survivability of a variant can fall. In the given case, the epistatic interactions prevent the non-helpful action of reverse single mutations.

Adaptation, preadaptation, and species formation

In his address of 1936, Huxley logically moved from the description of natural selection to an analysis of its role in species formation, the origin of adaptations, and macroevolution. First he examined the gradual transformation of species in time and the divergence of evolution in the space-time dimension. In analyzing the spatial or biogeographical aspect of species formation, he offered sterility, or reproductive isolation, and closely related forms as the criterion that provides evidence of the perfecting of the process of species formation. He showed that reproductive isolation can appear suddenly or sharply, while the subsequent divergence can occur gradually. Undoubtedly, this was already the contemporary concept of biological species, but Huxley is never mentioned as one of its founders.

The suddenness of species formation, for Huxley, lay in specific genetic mechanisms [hybridization, polyploidy]. But this was by no means the only path. He wrote: "The sudden origin of new species by way of chromosomal or genomic aberrations can take place even without hybridization" (Huxley, 1936a, p.85). And he further wrote that: "Thus species formation can be uninterrupted and linear, uninterrupted and divergent; and sharp and conservative" (Ibid.) He outlined the most difficult problem of species and species formation, which constantly hindered investigators [it is enough to recall the discussion between Simpson and Mayr]. The problem sounds like an aphorism: species in paleontology. Huxley addressed the complexity in applying the idea of reproductive isolation to an analysis of fossilized material. Many paleontologists insisted on gradual processes, which move on the scales of geological time,, but with a great amount of scepticism Huxley noted that "good" evidence is simply absent.

The problem of adaptation has its roots in the idea of entelechy, purposeful vital forces, Lamarckism, and orthogenesis. In this section of the address, Huxley discussed "Adaptation and Natural Selection." He separated out the two directions of investigations—the change of population structures and the mechanism of the formation of adaptations ["Natural selection acts by way of dissemination of mutations in populations" (Huxley, 1936a, p. 87)].

The question of adaptation in evolutionary trends is exclusively complex and literally, in Huxley's words, saturated with observations. Osborn introduced a helpful concept—adaptive radiation. Indeed, many trends demonstrate adaptability. When there exists abundant paleontological material, then adaptive radiation appears as the result of a series of evolutionary trends, each of which becomes more specialized or possesses a great adaptive effectiveness. Specialization in the higher mammals takes 10-14 million years, and then the specialized types quickly go extinct or persist. Osborn used much the same evolutionary schema as evidence for determining orthogenesis. Huxley suggested that in this schema, there is no evidence of orthogenesis. He claimed that instead of evolutionary factors, the limits of improvement were proved by purely mechanistic principles. Surprisingly it was a new idea. In essence, Huxley placed the question of biological evolution in a framework of physical limits (see Zavadskii, 1970; Moroz, 1972). Huxley's primary novelty was the idea of the wide dispersion of *potentially preadaptive mutations* in populations. This type of mutation plays an important role in macroevolution, especially in a period of harsh environmental change. Discussing preadaptation at the level of population genetics opened the possibility to bring that complex and mystical problem under strict scientific analysis. Huxley was really the first to explore the problem of preadaptation in the broad context of big evolution, and only after him did the problem begin to be discussed by other biologists adhering to the synthetic theory of evolution, for example Simpson, 1948. [The history of the concept of preadaptation is deeply investigated in AB Georgievskii's monograph, *The Problem of Preadaptation: An Historical-Critical Investigation* (in Russian; Georgievsky, 1974). At the present time, the primary founder of preadaptation—the well-known French zoologist and geneticist, Lucien Cuenot, has attracted the attention of historians (see C Gimoult, *L'évolution theorie d'un evolutionniste: Lucien Cuenot* (Ludus Vitalis, 2001), Vol. IX, No. 16., pp. 3-26).]

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. And 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. And 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 Hersch's work had appeared in 1934. Huxley suggested that the concept of correlated traits plus developmental genetics makes 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. But 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). But he elaborated on his new position, noting that the *initial uselessness* later becomes useful. He cited Hersch'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, 1936a, 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. But then, de Beer's evolutionary investigations of the 1930s-1950s were almost completely based on Huxley's ideas.

Selection as a biological "illness"

Just how far Huxley was from panadaptationism and panselectionism is clearly demonstrated by the fact that in his 1936 address he devoted only one special section to the "harmful" consequences of selection, but also significantly enriched it. The section is entitled, "The Results of Selection, Good and Bad." As an example, he used competition between males and females. He wrote: "Intraspecies selection often leads to results which are primarily, or even

completely useless to the species. . . . We can go farther and repeat Haldane's words that intraspecies selection on the whole is a biological illness" (Huxley, 1936a, p. 95).

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, really, 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* taxa acquire a high evolutionary tempo; simultaneously large gaps can form between major taxa. In this evolutionary pathway, the investigator's attempts to find intermediary forms are simply hopeless. In 1933, NK Kol'tsov published his article "*The Problem of Progressive Evolution*," in which he showed the broad dissemination of the phenomena of neoteny in the living realm, and ten years later AL Takhtajan discovered the role of neoteny in the origin of higher plants, including also flowers (Kol'tsov, 1933; Takhtajan 1943).

Huxley did not examine the problem correlating onto- and phylo-genesis independently, but as a field of investigation where it is possible to observe epigenic mechanisms, which explain the directionality of evolution. Goldschmidt, Haldane, and Huxley created physiological genetics and the genetics of individual growth, striving to solve the old, fundamental questions of evolution. Of all the founders of the evolutionary synthesis, only Huxley in his 1936 address departed from the exclusively transmissionist (Morganist) tradition in genetics, which dominated the works of Mayr, Dobzhansky, Simpson, and Stebbins, and finally it closed a path to the strictly scientific understanding of big evolution on a genetic basis. This side of Huxley's research either underwent criticism, or fell silent. But Huxley's unorthodox approach to big evolution significantly survived over time, and his evolutionary program was somewhat more interesting than the programs of those investigators who saw evolution only in the changes of a percentage of the genes in a population. The genetics of individual development and in general developmental biology [allometry, embryology] by 1936 allowed Huxley to go beyond the general discussions of micro- and macro-evolution, and to include all evolutionary questions in a single investigatory block.

Evolutionary progress

The ideas of progressive evolution were widely discussed in the 19th and early 20th centuries. Many biologists, philosophers, and sociologists had an unrestrained belief in progress. But subsequently the idea of evolutionary progress almost disappeared from the works of evolutionary biologists—it came to be seen as an anthropomorphic, inaccessible experimental examination and, subsequently, a speculative idea. The so-called opportunistic interpretation of natural selection was accepted, according to which natural selection always works for the needs of the present day, and only through the accumulation of small mutations does it relate to big evolution.

Huxley approached this question from a wide perspective, considering many non-Darwinian concepts of progress. For him it was important to show that natural selection answers not only to adaptation, but to the general improvement of organization connected to the appearance, for example, of temperature regulation or placental reproduction. Biological novelties [lungs, egg shells] open the world of land to vertebrates and only after that did specialization occur. Did the mentioned novelties of the same nature also produce such things, for example, as birds' wings? Wings helped to produce a new adaptive zone—and in that sense clear progress occurred. But birds gave nothing for future progress, and in this sense their evolution was only specialization. Natural selection would never be able to produce temperature regulation, except for in the case of fast temperature changes in nature. Here Huxley recalled his own interpretation of effectiveness of natural selection in a changing environment. He enumerated the basic discoveries “in a series of steps,” which led to the formation of new dominant types, and became completely clear how progress acts: cells gather into an many-celled organism, the evolution of the head and brain were great evolutionary steps, the development of lungs, warm-bloodedness and mainly—the growth of intellectual abilities based on speech. All these were achieved in different ways.

After describing the phenomena that served as evidence of the very phenomena of progressive evolution, he asked: what is the mechanism of progress? This question can be solved if proof is collected that the “vector” of selection is firm and remains the same primary agent in forming all evolutionary trends. For him, the theme of progress looses the stamp of anthropomorphism in this way. There is a real direction of evolution, which can scientifically be called progressive, and that direction leads to the appearance of defined properties of organisms. These properties include control of the environment as well as independence from it. More detailed things also include mechanistic and chemical effectiveness, the growth of self-regulation, a more stable internal environment, and finally the facility of knowledge and methods, related to knowledge (Huxley, 1936a, p. 96). Specialization, for him, is unilateral progress.

Natural selection, acting for the general improvement in organization, can at the same time explain evolutionary progress. Evolutionary progress, he suggested, is first and foremost the appearance of new adaptive types. He described a magisterial line of evolution from the first multi-cellular organisms to the anthropoids and called it “unlimited” progress. The height of evolutionary progress was the appearance of humans and conceptual thought. Man's uniqueness, for Huxley, was that conceptual thought, the bearer of which man had become, could arise only in him as a mammal, whose pregnancies resulted in the birth of only one child. Moreover, conceptual thought could not appear and evolve in any other phyletic line on the Earth. The powerful emphasis that Huxley placed on humans in his evolutionary doctrine, apparently, “alarmed” him. He had clearly come to understand that, immediately after the grand discussions on the majestic line of evolution, “Evolution is a series of blind alleys. If the alleys are short, they lead to new species and genera, which either remain stable or go extinct. If the alleys are longer, they become lines of adaptive radiation. If the alleys are still longer, they are lines that lead to the development and achievement of great phyla. Naturally this takes hundreds of millions of years. And only one line of the alleys is progressive, with future possibilities—this is the line of humans” (Huxley, 1936a, p. 98). There is no argument that here he succeeded in observing “evolutionary balance” and escaping the charge of anthropomorphism.

The evolutionary future

The culmination of the grand biological evolution is the appearance of humans. But this is only the beginning of psychological evolution. The arrangement looked like this. The appearance of conceptual thought was a factor and explanation for the growing of biological evolution in psychological evolution, but in many ways it differed from the usual biological evolution. The progress to humans was accomplished either by an explosion of changes, by the exploitation of new possibilities of adaptive radiation, by ecological expansion (the setting of new environments), or by way of the evolutionary mechanism itself. Through all of these, there came an impasse, making it impossible to predict today a new evolution. Fantasy, in Huxley's words, is a dangerous thing. But several events are automatically excluded. Adaptive radiation will not happen. First in evolutionary history, a great progressive step will be made by one species. In the near future in human society will grow altruistic instincts, which exist, for example, in social insects. He suggested that there are many paths for the further evolution of the mind. Expanding the old theme of purpose in evolution, he wrote that: "Purpose in life is not observed. But if we can discover purpose in evolution, then it should be evolutionary progress. And this previous direction can serve as the key for determining our purpose in the future" (Huxley, 1936a, p.100). With the appearance of reason, purpose should be defined in accordance with human values. But to define a coordinated purpose for all humanity is a task of great difficulty. He literally introduced into the discussion a Declaration of Human Rights. He wrote: "Today we have the experience of the struggle between two ideals—the subordination of individuals to associations and the innate superiority of the individual...Until that time when these great conflicts are solved, humanity will not have a great single purpose, and progress will go slowly. But let us not deny progress—the optimism of the 19th century illustrated its existence and its inevitability." The truth lies between the two extremes. Progress is a great fact of previous evolution, but it was limited to several selected lines. Progress can be continued in the future, but it is not inevitable; man must work and plan if he wants to achieve future progress for himself and for all life. This is a difficult problem. And we, zoologists, can contribute to its solution, relying primarily on evolutionary biology" (Ibid.).

Thus, in the 1936 address, Huxley with great optimism wrote about man, who holds in his hands evolutionary progress. In this Huxley did not mention Metchnikov or Severtsov, who had made a fundamental contribution to this field of investigation. It stands to reason that Huxley knew well Metchnikov's works (he had used them widely in his analysis of sexual selection). All of Severtsov's foundational works had been translated into German and should not have escaped Huxley's attention (de Beer steadily cited Severtsov's work on evolutionary embryology and morphology, and most likely, discussed them with Huxley). In the 1936 address, Huxley also completely ignored the question of evolutionary progress from the point of the view of the biosphere. But in truth a penetrating look made it clear that the appearance of man on a global scale was a catastrophe. At that time he was apparently preparing to discuss this question. It was not by accident that contemporary views on evolutionary progress were excluded after the appearance of the work of Huxley and Teilhard de Chardin (see Gascoigne, 1991; Ayala, 1994; Wuketits, 1997).

Before the section on evolutionary progress in the 1936 address, Huxley concentrated his attention on neoteny and its genetic basis. Here he developed this idea in connection with the appearance of man, although he already had briefly written about in 1927, discussing the evolutionary consequences of the rate of genes. The formation of altruism is a problem in which the concepts of neoteny and juvenile ontogenesis are actively used. We should recall that there were only a few significant thoughts in that plan. "Man is only man, when he is playing" (F

Nietzsche). “Childish qualities belong, without a doubt, to the supposition of the origin of man” (K Lorenz).

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 principal 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.

Huxley criticised the idea of evolutionary progress consistently in all his expositions. The situation changed in 1946 after *The Meaning of Evolution* appeared (Simpson, 1949). The book was based on a series of 25 lectures entitled, Lectures on ‘Religion in the Light of Science and Philosophy.’ They had been suggested by the Terry Foundation, which supported the idea of evolutionary humanism and sponsored lectures not only on scientific discoveries, but also their accumulation and interpretation in human life, especially regarding the foundation of a new religion on the achievements of science and philosophy. Thanks to the Terry Foundation, which allowed Simpson to popularize his generalize his paleontological material in that forum, the theme of progress began to become familiar to evolutionists. As is well-known, the Terry Foundation helped to promote not only the concept of evolutionary progress, but also how new concepts integrate with social life. From almost all the work, the formation of the synthetic theory of evolution served in some way or another as the framework for the evolutionary program, which Huxley had suggested at the dawn of the evolutionary synthesis. Huxley himself “leaped” from the frameworks, since he had not sought at whom to direct his work: geneticists (Dobzhansky), systematicists (Mayr), or paleontologists (Simpson). 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 on the basis of 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 could have no influence on the embryologists. These disciplines shared no elementary theme, and in fact they became the “work horses” of the evolutionary synthesis. But 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. Thus, now, when the problematics of Evo-Devo are so stormily developing, a history of science journal has been devoted to that subject (see Luchnikova, Gall, 1994; Gilbert, 1994, 2000; Gilbert, Atkinson, 1992; Burian, 2000; Burian, Thieffry, 2000; Dietrich, 2000; Fantini, 2000; Hall, 2000; Wilkins, 2002).

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. All the abovementioned complexities in the development of Huxley's evolutionary theory were successfully overcome by Takhtajan, who almost excised from the scientific lexicon the expressions "synthetic evolutionary theory" and "contemporary evolutionary synthesis" (Takhtajan, 1991; Takhtajan, 1991). Having great experience investigating evolutionary embryology and morphology, and constantly engaging the genetics literature, Takhtadjan suggested not multiplying the essences, but using the expression "contemporary evolutionary theory." In analyzing the problem of the origin of super-species taxa, he suggested that the so-called two syntheses had already transformed into a single investigatory stream. His approach to evolutionary biology allowed for hoping that Huxley's 1936 address has earned a perspective for "survival."

The New Systematics

In 1937, the Committee for Taxonomy in Great Britain organized the Association for the Study of Systematics in terms of general biology (Winsor, 1995). Prominent botanists and zoologists joined the Association, and almost unanimously chose Huxley as their representative. This choice was completely logical: after publication of the 1936 address, Huxley had become one of the leading evolutionary biologists. The Association sought to investigate the interrelationship between systematics and evolutionary theory in new historical conditions. It so actively pursued this goal that already by 1940 it had produced the collective work, *New Systematics*. Huxley was the organizer and main editor of the publication. But before preparing *New Systematics*, he completed important works on intraspecies variation, which were discussed in the literature on systematics and evolutionary theory.

Clines

His works on clines in all effect continued the line of research of the 1936 address. Huxley insisted that evolution in many species with continuous habitats and constant climatic changes, and evolution in few geographically removed species go by completely different paths. Neighboring populations will be similar in their external and internal traits, and as a rule, they will not have any abrupt changes in environmental conditions. In such areas, for example in neighboring continents or a chain of islands, each local climate steadily progresses into the next, forming a single unbroken gradient. Using the already well appropriated analytical method (the problem of relative growth), he focused on "gradations in changing traits," which take place in widely dispersed species. For gradations, he suggested the term "clines," which embraced a large number of phenomena, first and foremost geographic variation, which had been studied for over a century by the specialists of different persuasions (Huxley, 1938a; Mayr, 1947; Gall, Popov, 1998).

Huxley published a comprehensive work on clines in 1939, outlining several types of gradations and describing in great detail the paths by which traits can change when a species moves from one area to another (Huxley, 1939a). The most important was the division into continuous and broken clines. Continuous lines signify complete, freely-mixing populations. In broken lines, the geographically isolated populations can subspecies or even species. In his 1939 article, he focused on geographic clines and defined them as “geographic clines in phenotypic traits.” Research showed that geographic variation had a clinal character. Botanists claimed that clines can widen and narrow due to climatic changes. Considering species in time and paleontological trends, Huxley suggested the term “chronoclines.”

It is difficult to say whether his work on clinal variation corresponded to the general logic of his investigations or to the work produced in the Association, but in *New Systematics*, Huxley and his co-authors widely used the concept in interpreting materials on geographic variation. Here Huxley introduced new data in discussing this question (Huxley, 1940). He surveyed all cases of clinal variation in terms of natural selection and the concept of widely polytypical species. The subspecies and geographic races were at the center of his research. NV Timofeev-Resovsky used the concept of clines to explain cases of “squeezing” of a populations gene pool in periods of sharp drops in population (Timofeev-Resovsky, 1940, p. 121). Viewing the problem of clinal variation in the broadest context, he wrote that: “in many cases of intraspecies (and sometimes also interspecies) variation demonstrate the phenomenon of geographic gradients of traits, for which Huxley . . . suggested the term “clines.” Geographic clines often exhibit traits, which follow so-called “geographic rules.” Clines can be a useful field for investigating and discussing biogeography” (Ibid., p.125). Timofeev-Resovsky also analyzed different biogeographical situations, incorporating Huxley’s concept.

Every systematist faces the technical difficulty of how to separate and describe various geographical forms, when the continuous geographic variation is disturbed. Geographic clines help greatly in describing forms according to the quantity of traits and in separate populations inside continuous clines. There is an extensive conversation on the reality and mechanisms of the origin of geographic rules. Lamarckism long dominated in this field (see, for example, the work of B Rensh up to 1929). In fact, many parallel geographic lines and geographic convergences exist within the large systematic categories. The explanation of these phenomena in terms of natural selection is not an insuperable barrier, although for the time being the relationship between ecological and physiological traits in the external environment are not well-known. Geographical rules have been studied for over 100 years, and still little is known of their relationship to geographic clines. Thus many clines have no relationship to geographic rules, but are phenotypic gradients of polygenic quantitative traits around the center of their highest development, or the path of the dispersion, migration, or expansion of mutations or groups of organisms. Timofeev-Resovsky also suggested that the constriction of clinal variation is connected to the sharp “squeezing” of populations on the periphery of habitats, but in distinction from Mayr did not relate that phenomenon so directly with species formation (Timofeev-Resovsky, 1940, pp. 125-127). Probably this is related to Timofeev-Resovsky’s disregard of the question of discontinuity of any clinal variation in the case of geographic species formation; i.e. , he did not “squeeze out” their species formation possibilities from small isolates.

There are many examples of geoclines in water animals in the article of E Worthington (1940, p. 293). The philosopher J Gilmour actively participated in the Association’s work, concluding that for the formation of a new systematics especially important is the research of G Turreson, NI Vavilov, and Huxley. They all sought to discover the complexities of the structure

of species, combining the different methods of genetics, ecology, and geography (Gilmour, 1940, pp. 461-474).

Goldschmidt had 25 years of experience studying geographic variation in the gypsy moth, *Lymantria dispar*. He quickly accepted the concept of clines, but unlike Huxley he did not so categorically insist on a selectionist interpretation of clinal variation (Goldschmidt, 1940, pp. 77, 88). He conducted a beautiful analysis of clinal variation in the European and Japanese races of gypsy moths. Although between the continental and island races there were pronounced differences, he found clinal variation from the north to the south, even in the Japanese races, and observed that the direction of the clines may be different for different traits. Goldschmidt first discovered clinal variation in butterflies not only for morphological, but also ecological, behavioral traits and connected these especially with adaptation to the environment. Later, Huxley called Goldschmidt's investigations "excellent" (Huxley, 1944, p. 211).

And even more to the point, Goldschmidt was of two minds on the question of the evolutionary significance of clines. He wrote: "Species of Darwinian origin make sense only when the path leading to species variations is the continuation of the subspecies clines. Otherwise, any isolated population potentially would be an incipient species" (Goldschmidt, 1940, p. 141). The latter phrase literally depreciates all that he said about clines. It is now well known that in small isolated species, the processes of species formation progress most actively. Clines are most often found where continuous series of populations are located, for example in united continental areas. If some isolating factors appear, then a discontinuity arises in the clines. The more the formation of species requires discontinuity, the less the number of clines—this is a necessary condition of species formation. Mayr even formulated the following rule, which is opposed to Goldschmidt's thoughts: "*The more clines are observed in some area, the less actively species are formed there*" (Mayr, 1957, p. 161). Mayr tried to support his rule with examples. He noted that in continuous continental areas of the mentioned zone with numerous clines there are many less traits of the active formation of species than in tropical archipelagos or other areas with the island regions of species.

Mayr also criticised the selectionist interpretation of clines and the prognosticating side of Huxley's concept. He wrote that: "The significance of clines lies in another plane. The fact that neighboring populations subtly react to small climactic changes indicates the extreme sensitivity of the process of natural selection. The exact of significance of clines often gives systematics a thread for determining which type of geographical variation can survive in another form with a similar habitat (Mayr, 1947, p. 161).

In 1954 the collective monograph, *Evolution as Process* appeared, dedicated to the 65 year-old Huxley, in which it was noted that Mayr (in his essay, "Change in the Genetic Environment and Evolution") proposed the founder principle (Mayr, 1954). This clinal approach became an important component of evidence supporting the idea of a quick species formation in small isolated populations. Mayr noted that widely dispersed and thriving species with great reserves of genetic variation often demonstrate varied clines. The presence of clines proves the evolutionary conservatism of species. Thus, according to Mayr, wide clinal variation is evidence of the stability of species, or the "fading" of species formation. At the same time, the variation of isolated populations is not predicted and is often completely independent of such clines that are observed in continuous neighboring populations. In a fundamental report, Mayr succinctly summarized his views on clinal variation and geographic isolates. The continuity and

discontinuity of clines, for him, is the starting point for investigating the evolutionary balance between widely dispersed populations and isolates.

Clinal variation to this time was widely used by systematicists and is even found in contemporary monographs on the history of evolutionary ideas in biology. Thus, NN Vorontsov considered the concept of clines in a broad context of adaptation and neutral evolution. His evaluation of the problem is clearly directed against Mayr's opinions. Vorontsov wrote: "The clinal character of variability can be not only evidence of the adaptability of one or another trait, but also the result of the introgressive hybridization of two earlier isolated populations that acquired in the past under isolated conditions monomorphism for various alleles for one gene, and which are now integrated in the wide area with the absence of existing physical, geographic barriers. A break in the cline almost always indicates the recent rise of contact between earlier isolated populations, and the fixation of various alleles in different isolates occurred *randomly*" (Vorontsov, 1999, p. 528; authors emphasis).

Thus, it is completely apparent that the concept of clines is very useful in discussing the structure of species, intraspecies variation, and as one of the instruments in studying the first steps the species forming processes. Undoubtedly, Huxley's concrete work on the problem of species (although it is not the work of a systematist) promoted him to the ranks of British leaders in the area of forming a new systematics, demand for which was felt by many investigators, especially after the rise of population genetics.

The founder of the old, classic concept of species was K Linne. It was based on the level of morphological variation and until now was the single practical concept for all museum systematists, who described and catalogued a group. Contemporary systematics places the focus on the population structure of a species and on the study of the various biological properties of populations (the concept of polytypical species and of biological species).

In this case, it is difficult to find a single author of the new systematics. Mayr, who often credited Huxley for his work in the most difficult problem of systematics and evolutionary theory, and who completed so many monographs analyzing the most varied aspects of clinal variation, had no doubt about the exclusivity of his interest in this question, since it regarded species structure and formation, and claimed that there was little of the new systematics in the collected work *New Systematics*, edited by Huxley (Mayr, 1963; Russian trans.: Mayr, 1968, p. 290-294, 305-308, 418-419). Mayr's assessment of *New Systematics* was shared by Provine (1992, p. 162).

Huxley, Dobzhansky and Mayr, apparently, can equally be called the creators of the new systematics. In April 1936, Huxley actually outlined the concept of a biological species, since he had considered the formation of reproductive isolation as the main criteria for improving the process of species formation. Furthermore, he actively applied the methods of population genetics to the study of species structure and precisely developed the difference between the evolutionary potential of widely dispersed (polytypical) species and monomorphic species, represented by one of a small number of geographically isolated small populations. Huxley introduced theoretical population genetics in the problem of species and species formation even earlier than had Dobzhansky. Finally, the concept of clines clearly lay at the foundation of the new systematics, that, incidentally, Mayr also recognized.

Questioning Huxley's merits as editor of *New Systematics* automatically vanishes. He wrote an extensive (42 page) introductory article for this collective work entitled, "*On the Road to New Systematics*," in which he noted that the goals of the new systematics would be to carry

out a synthesis of classical taxonomy with the data from cytology, genetics, ecology, developmental physiology, and medical and agricultural entomology (Huxley, 1940, pp. 5-46). If such a synthesis could be achieved in taxonomy, Huxley thought, the latter would become the focus of biology and contemporary evolutionary theory. He laconically called new systematics “evolution in action.”

To formulate the *New Systematics*, Huxley formed a collective of 23 authors from 5 countries (Great Britain, U.S.A., New Zealand, U.S.S.R. and Germany). Among them were such authoritative scholars as NV Timofeev-Resovsky (the section on “Mutation and Geographic Variation”), C Darlington (on “Taxonomic Species and Genetic Systems”), S Wright (on “Statistical Laws of Mendelian Inheritance in Relation to Species Formation”), H Müller (on “The Significance of *Drosophila* Investigations for Systematics”), G de Beer (“Embryology and Systematics”), E Ford (“Polymorphism and Systematics”), and NI Vavilov (“New Systematics of Cultured Plants”).

The diverse authors and the varied subjects of investigation, of course, did not permit the precise formulation of the principles of new systematics. But every article of “New Systematics” was on its own original and deep. Thus, Timofeev-Resovsky covered a huge amount of material and presented his own investigations on the genetics of various sub-species and closely related species. Wright carefully surveyed the interaction of selection and genetic drift in populations of different size. Darlington showed the role of recombination processes in evolution and the evolution of genetic systems.

It is clear that for separate positions that the collective work, *New Systematics*, surpassed many works on a given subject. The advantage of the monograph, however, was that it made it possible to outline consistently and completely the final concept. In 1942, Mayr realized this potential in his book, *Systematics and the Origin of Species*. He subsequently developed the population concept of species and species formation. Thanks to work in the American Museum of Natural History in the role of curator of the Rothschild collection, Mayr possessed unique material for developing the concept of the polytypical species and geographic species formation. His arguments and factual material on geographic species formation were exceptionally thorough and convincing. After 1942, Mayr’s concept was immediately widely accepted by the most varied specialists, including Huxley. The theoretical status of all other forms of species formation, of which there were as many as there were authors, sharply dwindled—they were simply annulled for being obsolete.

And thus, participation in *New Systematics*, even more so than the 1936 address and the concept of “clines”, allowed Huxley to “sense” earlier than all the others that the new and quickly developing fields of biology were sources of the theoretical foundations for the most fundamental of biological disciplines—systematics.

Evolution: The Modern Synthesis

After publishing the 1936 address, Natural Selection and Evolutionary Progress, Huxley immediately began to write a general monograph on evolutionary theory. His reason for turning this address into a book was that: “Evolutionary theory had changed since Darwin’s time. Besides, the idea of evolutionary progress was completely disregarded by biologists. It seems to me that the valuable attempt was that, in the address, I gave a broad explanation for two concepts

and the relationships between them. The result exceeded all my expectations. So many of my colleagues showed interest in the topic and expressed a desire to see the address in a more developed form, that I decided to turn it into a book” (Huxley, 1944. p. 7). The book *Evolution: The Modern Synthesis* appeared in 1942 and was 637 pages long.

In the introduction, Huxley expressed his thanks to many scientists who had read parts of the manuscript and made valuable comments (Müller, Darlington, Fisher, Carpenter, and others). He also noted that by the time the book was being finished, other books by Dobzhansky, Waddington, Morgan, and Goldschmidt had appeared. Huxley deeply respected these books, especially the works by the schools of Morgan and Goldschmidt, which, in his opinion, “should be used in any contemporary book on evolution” (Huxley, 1944, p. 8). At the end of the introduction, Huxley briefly outlined the essence of the book’s ideas. He wrote: “The time has come for our quick advancement in the understanding of evolution. Genetics, developmental physiology, ecology, systematics, paleontology, cytology, and mathematical analysis have achieved new facts or new means of investigation. The problem, which we face now, is the demands related to the synthesis” (Ibid.). It is interesting to look at the succession of disciplines in Huxley’s synthesis. After genetics, he immediately named developmental biology. Already here we can find many peculiarities of Huxley’s *Evolution*—he almost continued the investigatory line of the 1920s-1930s. In this regard, he can be compared with Goldschmidt.

Different from the monographs of Dobzhansky, Goldschmidt, and Mayr, in *Evolution* Huxley made no strong delineation between micro- and macro-evolution. Everything is treated in a completely united manner. Genetics penetrates the entire book, and moreover not only population genetics, but the analysis of evolutionary genetic systems. Since *Evolution* was never translated into Russian, the table of contents—which is very revealing—is reproduced below.

The Table of Contents of Huxley’s Evolution. The Modern Synthesis.

Introduction.

Chapter 1. The theory of natural selection.

- 1.1. The theory of natural selection.
- 1.2. The nature of variation.
- 1.3. The eclipse of Darwinism

Chapter 2. The multiformity of evolution.

- 2.1. Heterogeneity of evolution.
- 2.2. Paleontological data.
- 2.3. The evolution in rare and abundant species.
- 2.4. Adaptations and their interpretations.
- 2.5. Adaptation and selection.
- 2.6. Three aspects of biological fact
- 2.7. Main types of the evolutionary process.

Chapter 3. Mendelism and evolution.

- 3.1. Mutation and selection.
- 3.2. Genes and characters
- 3.3. Variation and gene expression.
- 3.4. The evolution of dominance.
- 3.5. Types of mutation.
- 3.6. Special cases: melanism, polymorphism, fluctuating populations.
- 3.7. Mutation and evolution.

Chapter 4. Genetic systems and evolution.

- 4.1 Factors of evolution.
- 4.2. The early evolution of genetic systems.
- 4.3. The meiotic system and its adjustment
- 4.4. The consequences of polyploidy.
- 4.5. Hybridization and the determination of sex: conclusion.

Chapter 5. The problem of species. Geographic species formation.

- 5.1. The biological reality of species.
- 5.2. Various modes of speciation; successional species
- 5.3. Geographic substitution: the nature of subspecies.
- 5.4. Clines (character-gradients).
- 5.5. Spatial and ecological factors in geographical divergences.
- 5.6. Range-changes subsequent to geographical differentiation.
- 5.7. The principle of geographical differentiation

Chapter 6. Speciation, ecological and genetic..

- 6.1. Local differentiation compared to geographic. Ecological differentiation.
- 6.2. The overlapping species pairs
- 6.3. Biological differentiation.
- 6.4. Physiological and reproductive differentiation.
- 6.5. Special cases.
- 6.6. Divergence with low competition: ocean fauna.
- 6.7. Genetic divergence.
- 6.8. Convergent species formation.
- 6.9. The reticulation of differentiation.
- 6.10. Illustrative examples.

Chapter 7. Speciation, evolution, and taxonomy.

- 7.1. Different types of speciation and their results.
- 7.2. Species formation and evolution.
- 7.3. Forms of speciation and systematic methods.

Chapter 8. Adaptation and selection.

- 8.1. The omnipresence of adaptations.
- 8.2. Adaptation and function: types and examples of adaptation.
- 8.3. The regularities of adaptations.
- 8.4. Adaptation as a relative concept
- 8.5. Preadaptation.
- 8.6. The origin of adaptations: the inadequacy of Lamarckism.
- 8.7. The origin of adaptations: natural selection.
- 8.8. Adaptation and selection, not necessarily beneficial to the species.

Chapter 9. Evolutionary trends.

- 9.1. Trends in adaptive radiation.
- 9.2. Selective determination of adaptive trends.
- 9.3. The apparent orthogenesis of adaptive trends.
- 9.4. Non-adaptive trends and orthogenesis.
- 9.5. The restriction of variation.
- 9.6. Consequential evolution. The consequences of differential development.
- 9.7. Other consequential of evolutionary trends.

Chapter 10. The evolutionary progress

- 10.1. Is evolutionary progress a scientific concept?
- 10.2. The definition of evolutionary progress.
- 10.3. The nature and mechanism of evolutionary progress.
- 10.4. The past course of evolutionary progress.

10.5. Progress in the evolutionary future.

It shows that not one of the generalizing works on evolution in the 1940-1950s, with regard to the range of material and variety of themes, could compare with this book. Despite this, *Evolution* received direct and sharp criticism.

Evaluation of Huxley's evolutionary synthesis.

At the end of the 1970s, Mayr and Provine prepared a collective volume for a conference on the history of the evolutionary synthesis, which was published in 1980 as *The Evolutionary Synthesis*.

Perspectives on the Unification of Biology (Mayr, Provine, 1980)

It was completely natural that many authors of this volume strove to evaluate Huxley's scientific work, they considered Huxley, in particular for his 1942 publications, to be traditionally one of the primary architects of the evolutionary synthesis alongside Dobzhansky, Mayr, Simpson, Rensh, and Stebbins. This tradition is also preserved in the 1980 volume, but there also appeared "differential" evaluations.

For Mayr, Huxley's *Evolution* was valuable because it illuminated new genetic aspects in macroevolution (*The Evolutionary Synthesis*, 1980, p. 37). According to Mayr, Huxley achieved this because he had experience in the field of physiological genetics and allometry (Mayr made no mention of Huxley's work in ornithology and ethology). Two years later, in a book on the history of evolutionary theory, Mayr did not mention a single interesting moment in Huxley's evolutionary synthesis (Mayr, 1982). Moreover, on Huxley's views on the key problem of evolution Mayr wrote that: "The role of species in evolution is often underestimated. Huxley (1942) considered the majority of species forming processes as one of the sides of evolution, however large their part—is in some sense chance, biological wastefulness, which has nothing to do with the great and uninterrupted trends of the evolutionary process" (Mayr, 1982, p. 296). But in 1963, having his own point of view, Mayr wrote: "it seems to me that this very process of forming the majority of species leads to evolutionary progress" (Russian translation of Mayr, 1968, p. 491). It is correct that Mayr did not show how to move from the problem of species to evolutionary trends. In methodological and disciplinary plans, such a path still does not exist.

The historian of embryology, V Hamburger, having studied Huxley's contributions to experimental biology, placed the accent on a completely different level. He found that in *Evolution*, "it is clearly apparent that Huxley as a naturalist dominated Huxley the embryologist" (Hamburger, 1980, p. 97).

Another historian of embryology, F Churchill, in some ways solved the problem for his colleagues. He claimed that allometry, the concept of the rate of genes, experimental embryology (together with de Beer), the evaluation of population dynamics during temporal and spatial changes, and finally the concept of evolutionary progress, were the unlimited intellectual reserve which led Huxley to an evolutionary synthesis. Churchill (1980, p. 119) wrote that: "Apparently, Huxley with great ease moved from the problem of relative growth to the evolutionary synthesis". Churchill carefully observed that Huxley would not have accomplished the evolutionary synthesis had he remained in the framework of his own (although wide) experimental investigations. Therefore Huxley synthesized "his own" approach combining population genetics (mutations, recombination, gene complexes) with, mainly, natural history in the broadest sense of the word (systematics, paleontology, and biogeography). Classic genetics

and population genetics, for Churchill, allowed Huxley to discuss the question of species and species formation on new level. The genetics of individual development gave him the possibility to include in the evolutionary synthesis the problem of the correlation between onto- and phylogenesis, and also on a principally new level to discuss big evolution. It is possible to say that all of Huxley's lines of investigation in the 1920-1930s, as will be shown, led to the reorganization of factual material. He really was well disposed to the idea that the basic problems of evolution "are sitting" in the bosom of classical naturalism, and new disciplines introduce new solutions and insights to the problems.

Provine on Huxley's evolutionary synthesis

One of the leading historians of genetics and evolutionary biology, and author of two monographs on the contribution of genetics to evolutionary theory, Provine as co-editor of the collaborative volume *The Evolutionary Synthesis: Perspectives on the Unification of Biology* wrote the introduction section, which discussed the history of the synthesis in England (Provine, 1971, 1986; Ibid., *The Evolutionary Synthesis*, 1980). The goal of such an introduction is to evaluate objectively Huxley's *Evolution* (Provine, 1980, p. 329-333). Many leading British naturalists recalled Darwin even during the period of the rediscovery of Mendelism. At the Darwin jubilee in 1909, Darwin's ideas at Cambridge remained stable. But the third generation of Darwinists, including Gudrich and Poulton, had fewer in number than the second generation. The increase in scientific specializations, and Darwinian views on evolution became more fragmented. Although British biologists wrote on evolution citing Darwin, they were more specialists than synthesizers. All the different disciplines that Darwin synthesized developed further on their own. The spirit of synthesis was in the air in England, but no one knew what had to be done. Bateson, for example, suggested that in order to advance the questions of evolution, one needed to study the question of inheritance (after 1900 he devoted himself completely to this research).

The naturalist-systematists of the Darwinian doctrine in England understood poorly and used ineffectively the new science of genetics, which accentuated the importance of individual mutations. Naturalists seldom discussed similar mutations in natural populations. The biometricians, K Pearson and W Weldon, were Darwinists who carried out a bitter fight with the Mendelians, especially with Bateson (see Provine, 1971). But Darwin's gigantic synthesis had evidently broken down, most intensively and in England. By the end of the 1920s, the geneticists who supported Darwin's ideas were working primarily in the United States (Castle, East and Jenkins) and in Germany (Bauer and Goldschmidt). But in England there was no experimental geneticist who was a Darwinist, and there was no Darwinian naturalist who would combine the new science of genetics with his work. This thesis was clearly demonstrated by Provine in the work of the entomologist, and later Darwinist, Powelton (*The Evolutionary Synthesis*, 1980, Pp, 329-353). In 1908, Poulton proved that Mendelism is completely unimportant for studying evolution. Thirty years later, he published the article "*Adaptation in Insects as Proof of Evolution by way of Natural Selection*," in which he did not even refer to Fisher's works on Darwinian mimicry and on the genetic basis of natural selection including its application to man (Fisher, 1927, 1930). Neither did Powelton cite Haldane's analysis of the distribution of the gene *carbonaria* in populations of *Biston betularia*, nor Ford's work on adaptation in insects (Haldane, 1931; Ford, 1931). Powelton was very familiar with the work of these authors. For example, at the meetings of the London Entomological Society, he had actively discussed Fisher's 1927 article on mimicry. Poulton concluded his article "Adaptation in Insects . . ." with

the following words: "Our observations on insects demand a Darwinian interpretation and completely exclude Lamarck's approach. The conclusions are based on the same type of evidence that was achieved by Henry Walter Bates but only two years after the publication of *The Origin of Species* (Poulton, 1938, p. 1). In his interpretation of the evolutionary process, Powelton did not mention a single geneticist and ignored the rise of genetics.

The problem of the rise of the evolutionary synthesis in England is especially instructive. Apart from analyzing Huxley's works of the 1920-1930s, Provine also called attention to Huxley's small book *The Stream of Life* (Huxley, 1927d). Provine wrote: "In this small book Huxley viewed natural selection as the main mechanism of evolution in nature. The book of only 63 pages contained so much that was interesting for a neo-Darwinian view of evolution that much of it was widely accepted in the 1930-1940s" (Provine, 1980, p. 331). Provine regarded Huxley's role highly in the development of evolutionary theory on the whole. He stressed that over his entire life, Huxley kept in mind all directions in the development of evolutionary thought and in related sciences. All this allowed Huxley to make "the best documented contemporary synthesis, which was addressed as much to biologists as it was to the broader public" (Provine, 1980, p. 332). Provine was surprised that Huxley's *Evolution: The Modern Synthesis* was thematically the most comprehensive among the other books of the time, such as Haldane's *The Causes of Evolution* (1932), Dobzhansky's *Genetics and the Origin of Species* (1937), Mayr's *Systematics and the Origin of Species* (1942), and Simpson's *The Tempo and Mode of Evolution* (1944). The books by Haldane and Dobzhansky were written primarily for geneticists, Mayr's for systematists, and Simpson's for paleontologists. Thus, Provine claimed, it was Huxley's *Evolution* together with his 1936 Address that became the dominant force of the evolutionary synthesis (Provine, 1980, p. 332). Moreover, Provine questioned the British foundation for Huxley's evolutionary synthesis. Of course, this does not exclude an international aspect from any current scientific investigation. In the process of forming the evolutionary synthesis, Huxley widely used the more specialized investigations of English evolutionists, who, in his opinion, played a decisive role in his research. British scientists discussed Fisher's role in the evolutionary synthesis and in general his role in the development of genetics and selection. The book *The Genetic Theory of Natural Selection* (1930) and the articles (especially the 1927 publication on the evolution of mimicry), according to Ford, made Fisher a prime candidate for the role of the first generalist in Great Britain (Ford, 1980, p. 339). It is thought that Haldane's role in the development of theoretical genetics (the articles of the 1920s) and the significance of his book *The Causes of Evolution* (1932) for evolutionary theory have not their proper respect. Perhaps, Haldane's book in general was first in the development of contemporary evolutionary theory for coverage of evolutionary problems. Haldane never separated micro- and macro-evolution, always viewing them through the prism of classical genetics and developmental genetics. He moved surprisingly easily from the problem of the dynamics of mutations to the process of the extinction of ammonites. Of course, we must remember Darlington, Ford, Mather and others. Huxley was not an isolated individual, and participated in a circle of first-class specialists. Darlington's works on recombination in plants and on the evolution of genetic systems were for Huxley the authoritative texts.

In September of 1987, a conference was held celebrating Huxley at Rice University. The materials of the conference appeared in a collection of articles in 1992 entitled *Julian Huxley: Biologist and Statesman of Science*. The volume included Provine's article on "Progress in Evolution and the Significance of Life" (Provine, 1992, pp. 165-180). It was here that Provine

presented his evaluation of the evolutionary synthesis in new historical conditions and reevaluated Huxley's evolutionary synthesis.

In 1983, Gould claimed that the evolutionary synthesis had by now completed its historical role and was no longer able to produce ideas. He suggested that at the time of the synthesis natural selection was accepted as a significant, but not the only, evolutionary factor. Other agents, especially genetic drift, also played important evolutionary roles. But after the synthesis, in the 1940-1960s, all cases of genetic drift were successfully reinterpreted in terms of natural selection. The synthesis, Gould noted, literally *hardened* in these understandings. Panselectionism, adaptationism, and gradualism entered so easily into the evolutionary synthesis that it was now unable to develop further. The foundational work of the geneticists was aimed at the search for or invention of new forms of natural selection (Gould, 1983). It is interesting that Gould's co-author of the concept of punctuated equilibrium, N Eldredge, evaluated the synthesis more "leniently," and thus more precisely. He called evolutionary theory prior to the rise of punctuated equilibrium an "unfinished synthesis," and new ideas, in his opinion, completed in some ways the intellectual process that had begun in the 1920-1930s (Eldredge, 1985).

In evaluating the evolutionary synthesis, Provine went even further than Gould. Provine claimed that the quantitative synthesis of Mendelian inheritance and various factors can change the percentage of genes in a population (Fisher, Haldane, Wright, and Chetverikov). With this brilliant synthesis, Provine suggested, the possibility arose of an evolutionary synthesis directed at overcoming barriers between disciplines. But he did not call this, as he had earlier, an evolutionary synthesis, since that which many today call an 'evolutionary synthesis' does not consider new discoveries, concepts, or theories, around which one can build an all-encompassing evolutionary theory. With Darwin, Provine noted, all is in order—he built his evolutionary synthesis on the basis of natural selection. But if the evolutionary synthesis was not originally a synthesis, did not address important new discoveries or theories, and did not produce agreement among evolutionary biologists regarding the mechanisms of evolution or species formation, then what did happen?

Until the mid 1930s, the majority of evolutionary theories suggested a great variety of mechanisms for evolutionary changes. These theories had exactly the same fate as did theories of inheritance until 1900; they simply died away. Mendelism defeated the earlier theories of inheritance, and the evolutionary synthesis defeated the earlier theories of evolution, such as Lamarckism, creative evolution, and orthogenesis. The evolutionary synthesis won because Dobzhansky, Wright, Ford, and Fisher applied mathematical modeling to the analysis of natural situations. Only after that were a small number of variables within genetically successful populations applied to questions in systematics and paleontology. Biology of various specialties concluded that a few variables were the decisive combinations of factors that could explain evolution in nature. Provine called this phenomenon *evolutionary constriction*. This term helps us to understand that evolutionists could debate the effectiveness of population size, the structure of populations, genetic drift, and the rate of mutations and migrations after the 1930s; but, in spite of the divergence in views on the relative role of separate factors, all agreed that these variables were or could be important in evolution. Directed forces played no evolutionary role. Moreover, all the earlier theories of evolution were eliminated by the evolutionary synthesis.

Evolutionary constriction eliminated from evolutionary biology all directed theories. Thus, the primary effect of evolutionary constriction was a conflict between evolution and religion. But in one aspect, Darwinian natural selection was supplemented by directed mechanisms after constriction. This was Huxley's concept of evolutionary progress. In spite of

the different views of Gould and Provine, they also shared a moment of agreement. Gould insisted on an elementary pluralism of the synthesis and its further “hardening.” Provine showed historically the pluralism of evolutionary theories, which was destroyed by the founders of the synthetic theory of evolution. Thus, Gould’s synthetic hardening and Provine’s evolutionary constriction in essence estimates the very same phenomenon in different dimensions.

Provine was a specialist in the history of theoretical population genetics. It is only this fact that explains how he sharply extended the period of Mendelian synthesis, biometrics, and particular elements of naturalism to the level of populations. He called this entire process a genuine synthesis. The following events in evolutionary theory appeared on the border of the synthesis—they either entered or did not enter into other scientific concepts. There are always many such concepts, each of which is a constriction because through the fewest factors, they attempted to encompass a complex reality. This is the hypothetico-deductive method that was successfully applied by Darwin and many investigators to evolutionary theory (Ghiselin, 1971).

All the historical analyses were necessary for Provine to form the intellectual basis for evaluating Huxley’s contribution to the evolutionary synthesis. He noted that Huxley’s book *Evolution: A Modern Synthesis* was the best example of evolutionary constriction: it was based on a small number of variables; Huxley’s network of variables was significantly greater than that of Dobzhansky, Wright, Simpson, Rensh and other important figures in this period (excluding Mayr and Provine). This allows for rating of Huxley’s book higher than the books of the other authors of the synthesis. If the mentioned scientists just mentioned wrote their books for geneticists, systematists, and paleontologists, then Huxley strove to make a work was the twin of Darwin’s in the 20th century. Before Huxley, there existed many directed concepts of evolution which were all progressive. Huxley was cunning, preserving the idea of progress without an end goal. In Provine’s opinion, however, whatever criteria of progress were suggested, all of them were and remain anthropomorphic. Huxley is situated within this same framework. Thomas Huxley strove to prove that evolution in nature did not have a basis in ethics, since bloody struggle and ruthless selection ought to be transferred to human relationships. But Julian Huxley, introducing the concept of evolutionary progress, suggested seeing evolutionary ethics as part of humanism. On the one hand, in the 1950s he had a literally a mystical regard for Teilhard de Chardin’s works on man. On the other hand, Huxley did not once mention the Russian scientist and social activist, PA Kropotkin, who introduced ruthless struggle with Thomas Huxley, and the ideas of mutual aid which bridged the life of animals and social life (this became completely clear in the 1980s with the development of sociobiology, where colony animals served as a direct model and the basic understanding of many social phenomena). Thus, in spite of Provine’s open interest in the ideas of evolutionary progress, he called Huxley’s *Evolution* a compilation, and firmly believed his ideas were anthropomorphic.

And thus, in Provine’s works, we find two completely different images of Huxley. The reason for the Provine’s sharp change in his views of Huxley’s work was primarily due to the changing situation in evolutionary theory. Since the end of the 1930’s the synthetic theory of evolution (STE) dominated in the majority of evolutionary biology investigations. The Chicago meeting of 1959 was a genuine triumph for STE. This was convincingly visible in the presentations of the conference, which were published in the three volume set on *Evolution after Darwin* (1960). In addition, the presentations on evolution by Dobzhansky, Mayr, Simpson, Ford, Grant, Simpson and other scientists were steadily republished with new additions, which attest to the existence of a completed paradigm. This paradigm literally provided no room for investigators who were outside the framework of STE. The journal *Evolution* published only

neo-Darwinian biologists, who were striving to use experimental material perpetuate by the authors of the evolutionary synthesis.

It is correct that after Eldredge and Gould's article "*Punctuated equilibrium: an alternative to phyletic gradualism*" appeared, a systematic critique of STE began (Eldredge and Gould, 1972). By an irony of fate, the meeting in Chicago in 1982 under the motto "Evolutionary theory under fire" had the greatest effect. Young paleontologists (Gould, Eldredge, and Stanley) subjected STE to a destructive critique and simultaneously outlined in a more compressed form discontinuous equilibrium, or punctualism, which, thanks to the activity not only of scientists, but also broadly literate journalists, initiated an unseen expansion. The meeting in Chicago, also pondered firmly the aim of transforming the semi-scientific conference into a great showcase—"funeral" for 20th century Darwinism. The new journal *Paleobiology* became the foundational organ for the founders and propagandists of the new views on evolution. Critics claimed that STE had already fallen out of style since it looked at all of evolution only in the light of the theory of adaptation, natural selection, and gradualism. Moreover, evolution is neutrally or indifferently adaptive; the gap between the main taxa can never be filled-in, since evolution is punctuated. This is connected with specific genetic and ontogenetic mechanisms, which include mutations with large phenotypic effects (mutations in the regulatory parts of the genome or the change in activity of regulatory genes), which more often appear in small isolated populations, and neoteny (the preservation of juvenile traits in adult organisms or the dropping of the final stages of individual development). Punctualism claims that evolution is discontinuous in the sense that species formation and the appearance of new morphologies occurs over brief geological time spans, which is followed by a long period of species stability, or evolutionary stasis, and ends with either the explosion of species forming processes or the extinction of species. All the founders and supporters of STE immediately objected to the collection of new ideas of punctuated equilibrium; however, they aimed their "fire" against Huxley, who put into circulation the expression "evolutionary synthesis." Moreover, many ideas of punctuated equilibrium were contained in Huxley's works, especially in those parts that related to macroevolution. It is most surprising of all that Gould, who criticized Huxley and STE, knew Huxley's work well.

The question naturally arises of the contents and fate of Huxley's evolutionary views, which were outlined in his fundamental book on evolution. If his book was "buried" by development of evolutionary theory, then historical analysis simply records that it was formed at a particular some time, but no longer "works" on contemporary science. If his book is "living", then it would be interesting to see how it is inscribed in that stormy life. Only in such a context is it possible to evaluate "Huxley's two forms" (as proposed by Provine). At the end of the 1970s, when the evolutionary synthesis still dominated, Huxley was most highly regarded. But in 1992, Provine had already analyzed the STE and Huxley's views, strongly following Gould's article of 1983, in which the evolutionary synthesis was evaluated as a theory unable to develop further.

Now is the right time to examine the text of Huxley's *Evolution*, paying attention primarily to those aspects that had undergone a critique or did not receive their due appreciation in the history of science or evolutionary biology literature.

History of science component of Huxley's synthesis

In Huxley's *Evolution*, an historical perspective is almost always present. The historical approach was suggested in the organization of the first chapter as a study of the methodological and philosophical problems of evolutionary theory. In general, with an exceptionally precise view, Huxley was the first in the history of science to describe the conflict during the first quarter of the 20th century between Mendelism and Darwinism in Section 1.3 "The Eclipse of Darwinism." He noted that the growth of Darwinism occurred at first with the growth of neo-Mendelism (the second generation of geneticists and geneticist-mathematicians). He briefly showed the contribution of other sciences to contemporary evolutionary theory, in every possible way stressing that it has changed since the time of Darwin and his followers. He did not even use the concept of "neo-Darwinism" (that term was used by Dobzhansky and Mayr), but preferred the expression "evolutionary synthesis." The goal of the historical study the theory of natural selection is apparent—to show the progress of evolutionary theory and the striving, in Huxley's words, to unify biology. The problem was successfully resolved using models based on interrelationships of genetics and Darwinism.

Huxley's constantly used digressions in order to formulate clearly problems on a contemporaneous basis and at the same time give them a historical perspective. For example, the theme of the application of theoretical deductions to evolutionary investigations always worried Huxley, and he addressed it as a historical question, apparently to evaluate its resolution. For him it was always important to know in what ways the Mendelian world a place for the action of natural selection today. He wrote: "Deduction and mathematical generalization can only achieve valuable results with the aid of a firm foundation of fact: : the history of science abounds with examples. Indeed, the history of this particular subject is especially instructive on the point.. The biometrical school, inspired by Galton and carried on by Karl Pearson and his disciples, such as Weldon, applied mathematical methods extremely delicacy and ingenuity to the study of evolutionary problems. But the foundation on which they built was one of assumption. When these were not simply erroneous, like the assumption of blending or non-particulate inheritance, they were extremely incomplete, or partial, like the assumption of genetic regression or that of the truth of Galton's so-called Law of Ancestral Inheritance, which have validity only as statistical formulations and even at that are no more than first approximation. As a result, it is not unfair to say that on the biological side (as opposed to the mathematical, where definite progress occurred) non fundamental advances were registered through the employment of the biometric treatment.. This is in strong contrast with the rapid and steady advances which followed on discovery of the Mendelian facts of segregation and recombination. The more recent fruits of evolutionary mathematics have been of far greater value, because mathematical treatment has in this case been applied to a firm basis of fact.. But their foundation concerns the entirely simple facts of segregation and recombination, the dominance and recessiveness of their possible appearance, and the rates of gene mutations.

Undoubtedly, the conclusions deduced from these premises are extremely important, but they do not cover all areas of investigation. In higher plants, the f mutant genomes (e.g. polyploidy) play a significant role. Hybridization, the exchange of parts of chromosomes, act on the chromosome mechanism of inheritance in plants, and more contemporary investigations on *Drosophila* have shown that many of them also play an important role in animals" (Huxley, 1944, p. 151- 152). Huxley traced the principle schema of evolution, based on the selection of point mutations, but did not channel that path of evolution. He consistently thought of the role of polyploidy and duplication in evolution, which is especially widely distributed in plants. It is now known that this is the magisterial path of the evolution of the genome, since the entire

genome is duplicated (as predicted by M Kimura and S Ono; see Pennisi, 2001). Huxley clearly explained progress in the field of theoretical genetics, but also defined the limits that had been reached. In his opinion, the study of the behavior of the chromosome opened up new aspects in investigations in evolutionary biology.

Many historians of science and philosophy do not even suspect that Huxley was the first to complete a methodological and logical analysis of the structure of Darwin's theory. He noted the strong deductive element in Darwinism. He pointed out that Darwin based his theory on three observed facts and two deductions from them. The first fact is that all organisms constantly strive to increase their number in geometrical progression (Malthusian parameters). The second is that in spite of a tendency towards progressive growth, the number of any population, and the number of a given species remains more or less constant. Result 1—it can be deduced from these two facts that there is a struggle for existence, since there are more young than can survive and subsequent competition for reproduction. Darwin called the third fact variation. All organisms are varied (Huxley did not mention the amount of variation). Result 2—deduced from result 1 and three facts—is natural selection (Huxley, 1944, p. 14). Huxley completely “broke down” and very clearly commentated on the logical structure of Darwin's theory. He focused on the contemporary understanding of variation in connection with the achievements of genetics. But Huxley's commentary regarding the hypothetico-deductive method found complete understanding only many years later (Ghiselin, 1969; Mayr, 1982, 1992). It is important also, that Huxley's analysis is evidence of his outstanding philosophical and historical culture. None of the architects of the evolutionary synthesis analyzed Darwin's theory and the subsequent events in historical sequence. Through his assessment of Darwin's theory, Huxley put forward the contemporary questions of evolutionary theory and even adjusted the structure of his monograph through the Darwinian *The Origin of Species*. He wrote: “Thus it occurred that Darwin confused the problem, calling his most important book the *Origin of Species*, but really this composes only one aspect of evolution. Evolution includes many aspects (or levels—author). One of them is the origin of species, more exactly—the *origin of biologically discrete groups*. If you look more broadly, the problem appears as the origin of small systematic variations, including variants and subspecies, species, genera, and, perhaps, families. The next problem is one of extinction. In many regards, the most important problem is the origin and maintenance of great evolutionary trends” (Huxley, 1944, p. 153). Huxley noted that many enumerated problems cover one another, but they are purposefully separated.

The Plurality of Evolutionary Forms

In the second chapter (16 pages), Huxley succinctly touched on the majority of evolutionary questions in outlining his own position. He used the expression “plurality of form” to connote two issues: first, the difference in intensity of the action of evolutionary factors in different groups of organisms; and second, the hierarchy of evolutionary levels from population dynamics to evolutionary trends and evolutionary progress. [Huxley's idea on the hierarchy of evolution was accepted by Eldredge, occupying a central place in his book (Eldredge, 1985).] In fact, Huxley's first meaning of plurality is close to the ideas that Dobzhansky described in his book *Genetics and the Origin of Species* (Dobzhansky, 1937). The general mathematical theory of populations, he noted, does not suggest models of evolution in natural situations. The theory lacks specificity, i.e., it is not possible to say that it generated contemporary Darwinism. Everything must be tested in nature. On the basis of mathematical models, Dobzhansky wrote, it is possible to build different concepts of speciation and macroevolution, but they lack the relative

part of the descriptive events, i.e., it is impossible to say how often they are found in nature. Such a position is entirely debatable, since even a unique event can have catastrophic results in biology. And in not measuring the rate of the smallest events, they therefore contribute little or nothing to our understanding the global results of single geological or climatic acts. Dobzhansky wrote: "Evolution as a biogenic process; it is apparent, includes all agents of evolutionary change, and the problem of the relative importance of various agents stands on its own. Over the next several years, the problem was keenly discussed, although the outcome was notoriously unsuccessful. One of the possible reasons for the situation was that the theory in relation to the natural world hardly attainable, since the evolution of different groups, is perhaps directed by different agents" (Dobzhansky, 1937, p. 186).

In discussion the plurality of evolutionary forms, Huxley displayed the widest pluralism, not limiting himself to the framework of theoretical population genetics. He even indicated that explanatory possibilities of theoretical population genetics should have limits and showed the way to search for boundaries. The absence of boundaries, Huxley noted, in the action and in the dissemination of a theory, there was a clear trait of its maturity, which supports the idea that it is really a scientific theory, and not a metaphysical construction. He wrote: "We are beginning to understand that different groups can show different types of evolution and here it is completely reasonable to note that different groups of organisms display different properties of individual development, physiological, genetic, and group qualities" (Huxley, 1944, p. 45). He wrote: "Different evolutionary agencies differ in intensity and sometimes in kind in different sorts of organisms, partly owing to differences in the environment, partly to differences in way of life, partly to differences in genetic machinery...No one *formula* (author's emphasis) can be applied universally; but the different aspects of evolution can be studied in each group of animals and plants" (Ibid, p. 46). To generalize peculiarities of evolutionary theory in varied groups of animals and plants, Huxley introduced the term "*comparative evolution*" (Ibid, p. 128). CM Zavadskii and EI Kolchinskii developed the idea of the "evolution of evolution," which on an ideological plan is close to the views of Huxley (Zavadskii and Kolchinskii, 1977).

It is interesting that Huxley returned to this theme more than once. It worried him, being perhaps a *guiding* idea. He noted that "Writers who wrote about evolution ten to twenty years ago discussed the mechanisms which direct or limit the evolutionary process, about the way variation acted on the form of evolution of their ancestors. Higher animals cannot evolve in the same way that higher plants can, thanks to the differences in their chromosomal apparatus: extracellular or asexual organisms, such as bacteria, have their own evolutionary rules" (Huxley, 1944, p. 126). Within the concept of comparative evolution, Huxley saw also a great limitation in applicability of theoretical population genetics to natural situations.

Huxley extended the problem of the plurality of evolutionary forms in several aspects. He wrote, for example, "Not a single general organization or type of development (ontogenesis) exists without its evolutionary consequences. The meristematic growth of flowering plants permits a fuller evolutionary utilization of a rather greater variety of types of mutations, than is possible in higher plants. In animals, allometric growth has an evolutionary consequence. The simple fact that the majority of genes act on the rate of the developmental processes is reflected in the evolution of vestigial organs, recapitulation and neoteny. Thus the nature of an organism influences the form of its evolution. This is applicable at each level. Inside organisms, there is the microscopic machine of the genes and chromosomes, the form of cellular aggregation and growth of tissues. At the individual level, there is the type of reproduction, the level of behavior, and the method of development And; at the level of the group, there is the size and structure of

the group where individuals are unified and in respect to other groups. These and many other facts have their own evolutionary consequences” (Huxley, 1944, p.127). Huxley was a pluralist in the widest sense of the word. He suggested that mathematical theories of evolution should still prove their ability in concrete applications in solving not simply problems of population dynamics, but at higher levels of evolution. He introduced into the discussion the problems of individual development, physiological genetics, and allometry, that is, concisely made up of the triad of “genetics—development—evolution.” This was needed to show that the type of development had different evolutionary consequences and can be discussed in the course of general ideas of diversity of “evolutionary agents” and the “plurality of evolution.”

Huxley was the first in the history of science to build the theory of evolution on the principle of a hierarchical system. Even Darwin, in truth, did not rise higher than the level of species and the adaptation of organisms. In connection with this, SS Chetverikov wrote to AL. Takhtajan on 2nd May 1956: “Perhaps, Darwin’s greatest mistake, of which I know, is the title of his book “On the Origins of Species by way of Natural Selection.” Darwin’s extraordinary work treats not the origin of species traits and distinctions, but the purposeful adaptation of organisms to the conditions of existence surrounding them, but really these things are completely not equivalent” (Cited in: Takhtadjan, 1991, p. 501). Even reading Darwin’s book closely, one feels that it is difficult to find a concrete schema of the speciation process. Darwin only insisted on the possibility of the transformation of variants into an independent species. It is clear that solving such a cardinal question automatically eliminated creationism. Darwin offered much proof for this plan, but they were never consolidated into a decisive argument. It is thought that, in this period of the development of evolutionary theory, it was impossible to do this. Currently the scientific analysis of the problem of speciation has become possible only after Chetverikov’s classic article in 1926, and Wright’s in 1931. Before this the problem of speciation on a series of positions still remained in the bosom of natural teleology, in spite of the many speculative discussions of the most varied evolutionary senses (Gall, 1993). Regarding the problem of adaptation, Darwin conducted an entirely beautiful analysis, successfully “tearing” it out from the framework of evolutionary teleology. In addition, he easily identified that process with speciation. For Darwin, there simply were no other possibilities.

Adaptability and neutrality in evolution

In analyzing the plurality of evolutionary forms, Huxley very briefly, while addressing several aspects, discussed the problem of adaptability and neutrality. This problem existed throughout the entire text of *Evolution*, including even macroevolution. Dobzhansky in 1937 and Mayr in 1942 also tested and widely used Wright’s model of genetic drift in studying genetic polymorphism, intraspecies differentiation, and speciation. But they swept aside the problem of large evolution.

In the 1936 Address, Huxley compared the views of the physiologists and the systematists on the question of adaptive and neutral traits. He extended this theme in *Evolution*. It is important that, in analyzing the panadaptationist position of the physiologists, he recalled Darwin and his followers. Huxley wrote: “This was the orthodox post-Darwinian view up to the end of the 19th century, as it was represented by Darwin himself in his last books, in the works of Wallace, Weismann and Poullton” (Huxley, 1944, p. 30). Obviously not separating the panadaptationism and the panselectionism of his predecessors, Huxley considered similar views extreme and already outside the framework of contemporary views on natural selection and

evolutionary theory in general. In assessing the neutralism of the systematists, he also added a supplement, which later was sharply criticized by specialists in the evolution at the level of species. He wrote: "Systematists often over-emphasize on the origin of species as the key problem of evolutionary biology" (Ibid. p. 31). The position of the systematists regarding the non-adaptability of many of Huxley's diagnostic traits not only continued, but strengthened. His student, the ecologist Charles Elton (1927), developed ideas of neutrality adding to the study the dynamics of population numbers. Huxley wrote the preface for Elton's 1927 book, which he concluded noting that: "Many animals periodically undergo unlimited growth in number. When the population grows quickly beginning from a minimum point, almost each animal survives and their numbers can reach great sizes, than in conditions where populations exist in equilibrium. If a variation appears in populations of lower numbers, then afterwards it will quickly disseminate throughout the entire population. It is possible that in such a way, non-adaptive (non-differential) traits spread in a population, and we get a partial explanation of the facts of the existence in closely related animal species of many apparently non-adaptive traits" (Elton, 1927, p.187). Elton's work on the ecology of populations of vertebrate animals, and Huxley's investigations on allometry were considered by Wright when he formed his theory of "genetic drift" (Provine, 1986, pp. 297-298).

Another of Huxley's students, Ford, suggested that "the Huxley concept of allometry and the ideas of other authors* demonstrates that traits, available for systematists for the classification of related species, can be on the whole non-adaptive" (Ford, 1931, Pp. 78-79) - [*he was apparently thinking mainly of Elton]. Ford sought genetic explanation of the facts collected by Richardson and Robson on the non-adaptive nature of variations between subspecies and closely-related species (Robson, 1928; Robson and Richards, 1936; see: Gall, 1984). The first edition of Ford's widely read book *Mendelism and Evolution* appeared in 1931, and subsequently went through seven editions. In it, Ford wrote: "I will discuss the nature of traits, which will help separate local races and closely-related species. Richards and Robson have successfully shown that these traits are completely non-adaptive. It is obvious that certain genes, which at first are favorable, at the same time are able to form traits of a non-adaptive type. In other words, the chain of reactions which genes form, and the final product, which appears in the juvenile trait or at the adult stage, may not have adaptive significance" (Ford, 1931, p. 78).

Huxley widely used the data and discussions of his students. He wrote in particular: "Elton made the suggestion that periodic fluctuation in population numbers allow greater scope for chance in evolution, since if a rare mutation or gene-combination happens to me present in the much-reduced minimum population, it will be automatically reproduced in the same proportion during the period of rapid increase when the struggle for existence is light and intensity of selection low (Huxley, 1944, p. 112). The views of ecologists thus support the opinions of the geneticists. Huxley also cited the work of RL Berg, who showed that in micro-populations of *Drosophila melanogaster*, random mutations grow in number and selection pressure drops (Berg, 1941). Continuing the theme of paths of evolution of different groups of animals and plants, Huxley again noted that evolution can be adaptive, non-adaptive, gradual, and also sharp. He obviously inclined towards the idea that the processes of the formation of species are most active in small isolated populations, and in addition nothing definitive can be said about the question of the possibility of completing the process of speciation in widely dispersed species. It thus serves to document his preliminary discussion.

In section 2.3, "The evolution of rare and widely dispersed species," he attempted to synthesize theoretical population genetics with the ideas of evolution in natural populations; i.e.,

to find in population genetics an explanation for evolutionary processes in nature right through to the birth of new species. He wrote: "Rare species, on the other hand will not only possess less evolutionary adaptability, but will, as Sewell Wright (1932) has emphasized, be prone to have useless or even deleterious mutations become accidentally fixed in their constitution. When numbers are increasing after being abnormally low, a chance mutation spread through a considerable proportion of the population. Furthermore, genes which are neutral or even deleterious have a chance of becoming incorporated in a small local population-unit. Such "accidental" divergence may continue to an indefinite extent. Also, rare species will tend to become subdivided into discontinuous group, and these, once isolated, will have a greater likelihood of differentiating into separate species, partly by the accidental accumulation of mutations, as we have just seen, and partly because selection can work on them unhampered by immigration from other areas inhabited by slightly different types.

Many abundant species, on the other hand, will differentiate into subspecies in different parts of a continuous range; these will differ adaptively in accordance with the environment, but there will not be complete isolation between them (except as the result of climatic or geological changes producing a barrier) and migration will keep distributing genes from one sub-species to its " (Huxley, 1944, p. 33)). With the second case, it is more difficult to determine the possibility of a satisfactory conclusion on speciation in subspecies, which belong to widely dispersed species.

In solving the evolutionary problems of any range, Huxley attempted to use the possibility of theoretical population genetics, in particular Wright's idea of genetic drift. In *Evolution*, Wright's work is cited 37 times to his idea of genetic drift. Looking at several examples will demonstrate the many ways in which Huxley used the idea of genetic drift. Discussing the meaning of population size in evolution, he wrote: "We will merely mention the important conclusion established by Sewell Wright, that the greatest amount of evolutionary potentiality is available to large species divided into partially discontinuous groups (sub-species etc.). The partial isolation between the groups favors diversity by local adaptation and also by drift and the establishment of non-adaptive recombinations; while the fact that it is only partial implies that the variance provided by all the diversity taken together is potentially available to the species as a whole (Huxley, 1944, p. 60). " Discussing the problem of geographic speciation, Huxley many times recalled that: "When isolation is relatively complete and when, in addition the isolated populations are small, then non-adaptive divergence exceeds the adaptive; often this occurs because of the effect known as the 'Sewell Wright Effect'" (Ibid., p. 155). Of all the works on theoretical population genetics and the mathematical evolutionary theory, Huxley had the highest respect for Wright's work, thanks to which neo-Mendelism (or, for R Olby, the second theory of mutations) received factual support.

Accident and adaptation occupy an identical place in evolution. Huxley noted that the random aspect in nature always led to the confusion of early selectionists when they compared the divergence of forms on islands and continents. The fifth chapter of *Evolution*, which discusses geographic speciation, is built on the broad use of genetic drift. Huxley introduced a number of concrete examples and supplemental conceptual confirmations. He regarded Dobzhansky's *concept of micro-geographic races* very highly, which was suggested in 1937 (Gall and Konashev, 1977), and, of course, Goldschmidt's *sub-species*, which was outlined in 1940. Huxley noted examples of investigations of non-adaptive intraspecies differentiation in Uvarov's work on locusts, on Mayr's work on different species of island birds, and Hobbs' freshwater fish (Huxley, 1944, p. 202). In chapter five, Huxley also added a list of examples that

proved the role of random processes in the differentiation of species. The most obvious example, he believed, was described by Gulick (1905) as generalization, which investigated the different forms of land snails on Pacific islands (Ibid., pp. 232-233). Huxley used a personal report of the great authority on ornithology, E Shtrezeman, on the fast random differentiation of birds that live on the islands of Java and Sumatra. Shtrezeman showed that similar forms of islands of great size did not demonstrate such a level of divergence from the continental ancestors. In connection with this, Huxley wrote: "*Here the accidental type of change must be decisive, since mere size of area should not inhibit adaptive change*" (Ibid., p. 238; author's emphasis). He often returned to the finches, and also to the fauna of other islands, in order to show not simply the existence of non-adaptive variation, but the interaction and certain consistency of evolutionary variations of the adaptive and neutral plan. He wrote: "Thus while geographical divergence always depends for its initiation on spatial isolation, it may subsequently be linked in varying degrees with ecological divergence of an adaptive nature, and also, in small). In section 5.7, "The principles of geographic differentiation," among the main factors, Huxley listed natural selection and Wright's "drift."

Huxley discussed the problem of neutrality in evolution as related to an analysis of Goldschmidt's views on subspecies and speciation. Goldschmidt suggested that the formation of subspecies and species are qualitatively different processes (1940). The formation of subspecies included only quantified modifications of the organism's genome, by way of a sudden formation. Huxley did not accept the orthodox point of view, which agreed that the formation of a subspecies is always a move towards the appearance of a new species. In addition, he suggested, there are situations where the so-called subspecies becomes an independent species. Huxley sought clarification in the structure of the species and again in the specifics of small isolated populations, applying Wright's concepts. Local, low populations of subspecies will sharply diverge due to random recombinations, and the differences between them will be more random than adaptive. Huxley remarked that in 1913, Bateson had already collected many examples of different methods of divergence in widely dispersed and rare species. It is interesting that Huxley discussed Wright's Effect as the possible reason for the extinction of different forms. He noted: "In extremely small populations the Sewell Wright Effect may even fix deleterious mutations, and so result in extinction" (Ibid., P. 201). An analogous point of view was also expressed by Haldane (1932).

One proof of the theory of 'neutral' evolution, for Huxley, was the differentiation of finches from the Galapagos, most intensively studied by David Lack on an English expedition to the Galapagos in 1939-1940. Lack was convinced that "minor adaptive radiation" in numerous non-adaptive species distinctions do indeed exist, due to the Sewell Wright Effect (Lack, 1940, p. 58). Before the work on the Galapagos finches, Lack used the concept of habitat selection in discussing the process of speciation in British sparrows. The idea of genetic drift appeared in his work, probably after a discussion with Wright at the beginning of 1940, when, because of the war, the British expeditionary vessel had to dock in San Francisco. Lack's views on geographic speciation underwent a radical evolution (Gall, 1984, 1997). Huxley's position on this question was also not simple. At first he accepted the neutral interpretation of variations in finch beak size, then added that these variations can have the character of traits, which fulfill the function of reproductive isolation. Finally, the question of the neutral evolution of Galapagos finches was left open. In the introduction to a later edition of *Evolution*, however, he used Lack's research in all ways as propaganda.

Huxley used the concept of genetic drift in surveying all forms of speciation (geographic, ecological, and genetic). In the sixth chapter of *Evolution* he wrote: “Non-adaptive, or accidental differentiation may occur where isolated groups are small. This “drift”, which we have also call the Sewell Wright phenomenon, is perhaps the most important of recent taxonomic discoveries. . It was deduced mathematically from neo-Mendelian premises, and has been empirically is confirmed both in general and in detail” (Huxley, 1944, P. 260). Here, it seems he was the first to have so clearly formulated the theoretical meaning of genetic drift, namely for systematists. Systematists finally had an explanation for something (neutralism) in which they had believed for so long. Moreover, Huxley’s abovementioned words were the best answer to contemporary critics of his evolutionary synthesis. He showed a wide pluralism in the synthesis and expressed the significance of theoretical population genetics for solving difficult problems in evolution and taxonomy.

Perhaps what was most interesting is that he discussed the problem of “neutrality—adaptability” at the level of macroevolution. In *Evolution*, this is addressed in section 9.4 “Non-adaptive trends and orthogenesis.” The problem of non-adapted evolutionary variations at the level of species was discussed by Dobzhansky in 1937 and Mayr in 1942, i.e. at the same time as Huxley. Simpson’s book, *The Tempo and Mode of Evolution*, also appeared in 1944 (and in a Russian translation in 1948). It is impossible, however, to compare these books with Huxley’s *Evolution* in the framework of large evolution. Simpson in general did not discuss the problem of adaptively neutral evolution. In his book, there are twelve citations to Wright, which are mentioned in a list of other authors on the mathematical theory of evolution, but nothing definite is said about genetic drift. Thus, circumstances compel us to examine Huxley’s views “on their own”.

Having outlined a great amount of material on the adaptive radiation of various groups of animals, Huxley moved to an analysis of non-adaptive evolutionary trends. He wrote: “Besides the usual trends constituting the radiation of groups, the most of which, as we have already seen, appear clearly to be to words adaptive specialization, there are others also exist, for which no adaptive significance has as yet been found (Huxley, 1944, P. 504). He showed that the best evidence for the existence of non-adaptive trends is the parallel evolution of many lines of labyrinthodonts (a group of extinct amphibians). The lines of labyrinthodonts underwent radical changes in biology, moreover they were completely independent and synchronous. They transformed from water to terrestrial life and back to a second aquatic life. Haldane suggested that Huxley cited the example from the evolution of titanotheria as a proof of non-adaptive evolution. The extinction of ammonites for Huxley also had a non-adaptive character (Ibid., pp. 506-507). One example is the complexity of the joints in early forms and its simplification in later forms.

It is historically important to stress that Haldane and Huxley, in analyzing the titanotheres, leaned completely on the work of Osborn, who viewed the evolution of these animals as the simple proof of the non-adaptive character of evolution as the whole. In addition, and unlike Osborn and Haldane, Huxley drew on yet another proof in the form of intraspecies selection. He wrote: “Really, Haldane completely could use the evidence that the apparent development of unfavorable characters, as preludes to the extinction of a stock, can be the biologically evil effects of intraspecific selection” (Huxley, 1944, p. 508).

Huxley brought the problem of adaptively neutral traits into Darwinian ideas on correlated variations. He suggested that an adaptively useless trait can be coupled with a useful trait, but “the existence of factors of the rate of genes are related to the useless characters”

(Huxley, 1944, p. 533). In his further discussions on useless traits the idea of correlated variations dominated. He wrote: “Important examples of correlated characters are the higher mental faculties of man. It is obvious that natural selection cannot have been operative directly in bringing about evolution of intense musical mathematical ability, or indeed of many specifically human faculties” (Ibid., pp. 533-534).

Huxley viewed the problem of the adaptive uselessness of organs in connection with the numerous effects of genes. For him, organs which are under the action of direct selection will be modified by the system of the gene; but genes of a similar polygenic system will also have secondary effects on “indifferent” organs, and the majority of secondary effects will cause degeneration in size or function. He wrote: “when two polygenic systems linked are lodged in the same chromosome or chromosomes and selection is acting to alter the main character controlled by one system; while that controlled by the other is useless, the resultant recombination will “break up” the useless character; in virtue of the tendency of random change to be towards decreased efficiency, this also will promote degeneration.” (Huxley, 1944, p. 476).

Huxley again considered the problem of adaptive neutrality in the example of the titanotheria. He consolidated all his earlier arguments and as before claimed that “The development of correlated characters during evolution may stimulate orthogenesis” (Huxley, 1944, p. 534). He reproduced his allometric approach, according to which a useless trait (the horns of titanotheria) were correlated with an adaptive trait (body size). He again introduced the idea of *original uselessness*, but at the same time did not reject Goldschmidt’s view on the uselessness of many early embryonic changes, and used it in an obverse manner, apparently, to complete the format.

There is an obvious dissymmetry in Huxley’s analysis. He considered the widest problem of the adaptability and neutrality of evolution on the level of “population-species,” and in discussing large evolution, the factual material is diverse; the declared adaptationist approach was constantly “undermined” by doubts and reinterpretations of the material in different foreshortenings. Section 9.4, which discusses non-adaptive evolution, is the best proof that the problem of large evolution worried Huxley most of all and demanded a completely different solution. In addition, Wright worked out a “working” model at the level of “population-species”. At the level of large evolution itself, there was no analogous specialized system; the concept of rate of genes also offered an outlet to the problems of macroevolution, but it was impossible to directly connect it with neutralism, thus even this was not necessary. The concept of Ford-Huxley successfully and immediately served “two gods.”

Gradualism, intermittency and saltation

In the 1936 address, Huxley concisely formulated this problem in several sentences and then reproduced it in *Evolution* (Huxley, 1944, pp. 30-31). Here, and in chapters five through eight on species and speciation, he presented much proof of the existence of numerous evolutionary paths: from “pure” gradualism to typical interrupted evolution. Here he called reproductive isolation the main criterion for a species and proof for the ending of the speciation process. In *Evolution*, however, he added another criterion for species—morphological variation (Ibid., p. 165). In fact, he wanted to combine his old approach to species with the new one and did that after contemplating Dobzhansky’s views (1937), not wishing to deprive the museum systematists of a working instrument. Moreover, he distinctly understood that “In plants, polyploidy and asexual reproduction complicate the picture” (Ibid., p. 166).

Clearly accepting the concept of biological species, he noted the difficulties that conflicted with this concept. He wrote: "We cannot give any single reply such as that a species is an interbreeding group, completely isolated from breeding with similar groups: That would be an over-simplification. There are many different types of species which are differentiated to various degrees. Maybe, it would be more scientific to replace the term itself with many technical terms. But "species" is useful in practice and it serves to preserve it" (Huxley, 1944, p. 168). He expressed the idea of the unequal value of species, which he subsequently developed in his chapters on speciation. This became one of the leading ideas in analyzing the problem of intraspecies differentiation and speciation.

In section 5.2, "Different forms of speciation; successional species" he outlined his own concept of species and speciation, demonstrating a broad pluralism. He wrote: "A single species as a whole may become transformed gradually to such an extent that it comes to merit a new specific name" - at issue, probably, was the transformation of species in fossil series (author's comment). Or it may separate, also gradually, into two or more divergent lines whose divergence eventually transcends the limit of specific distinction: sometimes the separation into mutually infertile or otherwise distinct groups may occur suddenly, but the subsequent divergence may yet be gradual. Or it may hybridize with another species and their hybrid product may then, by chromosome-doubling, at one bound constitute a new species, obviously distinct from the outset: here, instead of one species diverging to form two, two converge to form one. (It is possible that such sudden origins of new species by means of chromosome or genome aberrations may also occur without hybridization, from a single instead of a dual origin.) We may thus classify the types of species-formation in various ways-whether they are gradual and continuous or sudden and abrupt; whether they are divergent or convergent; what kind of isolation has been operative; what barriers to fertility have been developed; and to what environmental factors, if any, the process of species-formation is related (Huxley, 1944, p.171). In several sentences, he outlined simultaneously his views on speciation and the entire investigatory program. This he realized in chapters five through eight in *Evolution*,

Huxley distinguished four basic types of species and corresponding forms of speciation - successionalist, geographic, ecological, and genetic. The geological model of speciation, for him, most often was gradual. Only the genetic model, perhaps, most distinctly demonstrated the suddenness of the process. He noted precisely that in the case of geographic speciation, spatial isolation is central and primary. All genetic transformations are simple successive and secondary. Paleontology provides classic examples of gradual speciation. Moreover, speciation can be part of an adaptive trend, as for example in horses or elephants. Although he considered speciation an independent problem, as stated by Darwin, Huxley in every way possible wanted to include it in the trends of large evolution and thus to show its subordinate significance in regards to large evolution. But even in analyzing adaptive trends in connection with speciation he strongly insisted on adaptationism. He wrote: "Our analysis shows that the great trends are adaptive. Thus, the main agency in producing successional speciation is selection, although it is possible that *orthogenesis* may in several cases be at work" (author's emphasis; see Huxley, 1944, p. 173). He did not relate divergence of forms, or, as is now said, the splitting of phyletic lines, with the creation of large evolutionary trends. Only successionalist speciation, he suggested, "represents steps in an evolutionary trend, and not simply a divergence related to the peculiarities of a local environment or genetic structure" (Ibid.) Successional speciation, for him was in essence equal to a species in paleontology. This also leads, correspondingly, to the peculiarities of the species-forming processes. But even in analyzing this aspect of evolution, where gradualism and

orthogenesis are primary, Huxley admitted also intermittency, and open saltationism. He wrote: "Successional speciation often proceeds, partly or wholly, by discontinuous changes of small or moderate extent. These are usually called "Waagen's mutations", after the paleontologist who first drew attention to them" (Ibid., p. 174). Through the analysis species forming processes in fossil species, Huxley suggested, that we can escape from the problem of large evolution. Although the amount of knowledge here is less than in the analysis of recent species, the evolutionary possibilities are somewhat greater. The evolutionary situations in rare and numerous contemporary species and correspondingly in fossil species take a similar form. He wrote: "We, probably, are correct to think that the successionist transformation in populous species, which are represented by fossilized series, is always a gradual and unbroken process" (Ibid.).

NN Vorontsov, analyzing the situation in contemporary evolutionary theory, very capaciously and precisely defined the characteristics of the evolutionary process. He wrote: "Discreteness and continuity, integrity and mosaic patterns, adaptability and neutralism, determinism and stochastic processes are inseparably connected with one another in the evolutionary process. The question of "either/or" is a false opposition which should be called "and/and" (Vorontsov, 1999, p. 533).

Most of the evidence for neutral and random processes in evolution Huxley borrowed from the fifth chapter of *Evolution*, which addressed geographic speciation. This evidence had a direct relationship to the problem of "gradualism—intermittency." Small isolates evolve not only in an adaptively neutral way, but always intermittently. This intermittency is in no way connected with macromutations, but is simply making gradualness vanish in the common action of natural selection by the accumulation of small mutations. Intermittency arises as the result of the effect of the colonization of islands or of sharp fluctuations in population number. Therefore, it seems, the connection "gradualism-intermittency" is successfully demonstrated in the framework of canonical speciation. At the same time, supporters of the concept of intermittent equilibrium, in all cases, in the initial variant, propagandized for the idea of intermittency, placing the accent not on macromutations, but on the Wright Effect and the principle founded by Mayr (1988, pp. 457-488).

In chapter six of *Evolution (speciation ecological and genetic)*, Huxley introduced a huge amount of factual material on the formation of hybrid forms and polyploids. Not knowing how these forms ranged, he carefully called them simply forms. It is correct that he precisely analyzed the geographic and adaptationist advantages of polyploids. These forms are able to penetrate the borders of the areas of the common species and are more viable than their relatives and ancestors. Polyploidy gives a species the possibility to survive in conditions of average stress. He wrote: "The most interesting evolutionary fact related to auto-polyploids, which is that the various members of the line can have difference geographic dispersals. In general, the tetraploid forms are better adapted to difficult environmental conditions. Many of them are more adapted to the cold than their diploid brothers. Correspondingly, we find many tetraploid forms in the north and in mountainous regions. Almost all grasses of Spitzbergen are polyploids" (Huxley, 1944, p.337). Furthermore, as if in a contemporary cytogenetic aspect, Huxley continued: "Crossbreeding sometimes takes place between members of a series, forming new polyploidy types, which then can be pre-adapted to other conditions. Polyploidy, however, reduces perspective plasticity" (Ibid., p. 338).

It is interesting that many contemporary plant cytogeneticists have shown a connection between polyploidy and their dispersal (the percentage of polyploids growing from the south to the north) and interpreted this data as the result of the great adaptability of polyploids to extreme ecological conditions (a survey of the data for the problem was conducted by the great Austrian botanist, F Erendorfer). The cytogeneticists noted that polyploidy increases the adaptability to stressful situations, but at the same time decreases ecological plasticity. Plasticity is paid for by stress-tolerance.

Analyzing the role of inversions, Huxley questioned the role of macromutations in evolution, which are suddenly able to form reproductive isolation. He wrote: "Darlington was the first who found an application for the facts of inversions, which related to their properties (the main one being that inversions "lock" crossing-over, author's comment), and similar "chromosomal isolation" is just as important as other more obvious types of isolation, such as geographic isolation" (Huxley, 1944, p. 332-333). As a first class evolutionist, Huxley, added to Darlington's words the following: inversions acquire important evolutionary significance if there is decrease in fertility of the heterozygote. He indicated the mechanism, which starts up the species-forming process on the basis of inversions, and, thus, avoided the problem, which is the Achilles heel of all theories of chromosomal speciation. The fact of the matter is that if chromosomal restructuring forms heterozygotes which surpass the fertility of both homozygotes, then the process can lead to the formation of chromosomal polymorphism, but can never lead to speciation (White, 1978, Chapter 6).

In 1936, Kurt Stern considered speciation on the basis of inversions. He discussed the following model. Single inversions in chromosomes can decrease hybrid fertility between forms. Fertility will further decrease due to inversions in other chromosomes, when two or more inversions in each of the two chromosomes produce significant sterility (Stern, 1980). Summing up the work of Darlington and Stern, Huxley wrote: "Large inversions might be the method or way for the splitting of a species into two non-interbreeding groups" (Huxley, 1944, P. 332). The question of the role of inversions in evolution was investigated in detail by the Dobzhansky school (Dobzhansky, 1970) and the group of colleagues led by NP Dubinnin (Dubinnin and Tiniankov, 1946; Borisov, 1969). In studying inversions, only VN Stegnyi was able to get to the level of speciation and macroevolution (Stegnyi, 1993, 2002). It is curious, that in the 1920s, when inversions were widely investigated by the Morgan school, Goldschmidt advanced the idea of "hopeful monsters."

Sudden speciation occurs on the basis of orthogenesis and apomixis. With regard to parthenogenesis, the arising complexes can survive or be eliminated. After a phase of rapid appearances of the surviving complexes, there follows a phase of slow divergence by way of small mutations (Huxley, 1944, p. 334). The discovery of parthenogenesis in many species of vertebrate animals, especially in lizards, led to the idea of the mass character of speciation on islands and parthenogenesis, and polyploidy (Borkin and Darevskii, 1980). Russian plant cytogeneticists with great mastery uncovered the structure of apomictic complexes, which possess principal significance for fast and diverse speciation. (Rubtsova, 1989).

In *Evolution*, Huxley analyzed the action of natural selection in two different situations. He showed that in situations when a trait appears sharply and intermittently, natural selection has no influence on the divergence of the trait, but acts on the species as a whole, testing its success in competition. Interspecies selection decides the fate of species in so-called saltationist speciation (Huxley, 1944, p. 384). Huxley placed all forms of speciation in a table, which shows which role in evolution led to intermittent speciation and its interaction with gradual forms. In all

forms of so-called genetic speciation is present an intermittent component (asexual isolation, the exchange of chromosome parts, polyploidy, allopolyploidy, autopolyploidy). Convergent speciation always occurs intermittently. Reticular evolution ends sharply and suddenly (Ibid., p. 386). Huxley's table of forms of speciation impressed, of course, the great departure from gradualist orthodoxy and the accentuation of genetic isolation. In 1942, however, Mayr's book *Systematics and the Origin of Species* appeared, in which the main precondition for speciation was also geographic isolation. Huxley was familiar with Mayr's ideas and even in the process of typesetting *Evolution* wrote: "I should reference his important conclusion that especially in higher animals the main factor, which allows group divergence, is geographic isolation; neither ecological, nor genetic isolation are primary. I am bound to say that Mayr has convinced me on this point (Ibid., p.381).

This is another extreme point of view. But was Mayr so strongly influenced by Huxley? And if so, why did Huxley, under this influence, change nothing in the text of *Evolution* in its subsequent editions? It is interesting that M. White in his book, *Modes of Speciation* (1978), practically followed Huxley's approach and parapatric (for Huxley, ecological) speciation in phytophages a common phenomenon (White, 1978). It is necessary to say something more about the possibility of sympatric speciation in phytophages through the assimilation of new trophic niches. This example has been discussed for many years. The most detailed investigation was completed on fruit flies—colored-winged flies from the family, *Tephritidae*, in particular on several polymorphous species of the genus *Rhagoletis*, which live in North America (Bush, 1966, 1975). The fast formation in colored-winged flies of apple and cherry races is considered direct proof of sympatric speciation. Moreover, it was shown that two species of colored-winged flies from the genus *Prececidochara*, being sympatric species in Texas, differ in several gene loci that control their ability to live in various types of *Compositae*.

Huxley analyzed this material (of course, without cytogenetics) in *Evolution* and came to the conclusion that the issue concerned the formation of "biological races," which should be viewed by evolutionary biologists as separate species (Huxley, 1944, pp. 296-297). Mayr, citing the investigations of entomologists and cytogeneticists, recognized in a series of cases the possibility of sympatric speciation (Mayr, 1977). In reviewing a book by M White, however, Mayr weakened his own position and began to think that a small level of spatial isolation should exist even in cases of the formation of biological races in phytophages (Mayr, 1978, p. 479). In spite of Mayr's active stance in defending the concept of geographic speciation, G. Shaposhnikov, professor of the Institute of Zoology at the Russian Academy of Sciences, using evidence from experimental and systematic materials persistently proved that the reality, and also the wide dispersion of sympatric speciation in insects (Shaposhnikov, 1974, 1978).

Thus, from all the above, it is clear that Huxley was not an orthodox gradualist, but accepted numerous paths of speciation. As to how much his views are located in the framework of the evolutionary synthesis, the question naturally arises as to what extent they seem to be in comparison to heresy.

Huxley and Goldschmidt: views on speciation and large evolution

The choice of this pair is not accidental. Gould in the 1970-80s constantly claimed that from the synthesis came other views on orthogenesis and its evolutionary significance, leaving out developmental genetics and in general the entire question of the relationship between onto- and phylogenetics. Gould knew well, and constantly cited, Huxley's work on allometry, the rate of

genes, and embryology (Gould, 1977), but considered them to be orthodox evolutionary models. For a model to integrate views on individual development, genetics, and evolution, Gould always drew on Goldschmidt's book, *The Material Basis for Evolution* (Goldschmidt, 1940)--its appearance as much as said that the evolutionary synthesis is not indeed a synthesis. Moreover, in 1982, Gould republished Goldschmidt's book, writing a long preface entitled "On the Usefulness of Heresy" (Gould, 1982).

Goldschmidt's *The Material Basis for Evolution* appeared in 1940 when Huxley had almost finished the work on *Evolution*. Huxley, however, succeeded in making a series of notes and references to Goldschmidt, and also in section 8.5 on pre-adaptation outlined the concepts, which passed for evolutionary heresy. Huxley wrote: "Goldschmidt repeatedly claimed that pre-adaptation can produce an influence through large mutations, or "hopeful monsters," which as a result can serve as starting point for completely new evolutionary trends. However, Goldschmidt goes even further. In his last book (1940), he introduces a fundamental difference between micro- and macroevolution. Microevolution depends on gene mutations and recombination and can lead to subspecies and other diversifications within the species, but cannot produce new species, or, *a fortiori*, higher taxa. The latter are formed due to macroevolutionary changes, which, Goldschmidt suggested, demand radical changes in all chromosome patterns or a reactionary system. Similar changes in the reactionary system, he called a *systemic mutation*, which, not exclusively, can arise in several successive steps. Selection does not act on the new system as a whole. I do not propose to discuss these revolutionary views, for, in general, I do not agree with them. Gene mutations together with chromosomal restructuring can have relatively large effects. Goldschmidt insisted on the importance for evolution of mutations with consequences for the processes of development, but in Waddington's work there is proof of the importance of gene mutations. However, if we are not in agreement with Goldschmidt's general views, then the pre-adaptation of various kinds have clearly played a significant role in evolution (Huxley, 1944, p. 456-457).

All the same, in the views of Huxley and Goldschmidt on pre-adaptation, there was much in common. It is a matter of taste to interpret the phenomenon of pre-adaptation as systemic mutations or as a mutation with numerous phenotypical effects. For Huxley as an evolutionist indifferent to the question of size of mutations at the genome level, he was most interested in which phenotypic effect causes a given mutation. He wrote, for example, that reproductive isolation often appears sharply, suddenly, but he was certainly not thinking of specific systemic mutations. Regarding the theme of "ontogenesis—evolution," it was always at the center of attention for both Goldschmidt and Huxley, but it is not clear why Huxley referred to the work of Waddington in the cited quote.

And so between Huxley and Goldschmidt alongside the abovementioned themes (the rate of genes, allometry, and embryology), there are many common and, in arrangement, general biological questions of the synthesis of evolutionary theory. Thus, Huxley and Goldschmidt suggested that fast speciation can end, not only on the basis of neutral mutations, but also as macromutations. Huxley wrote: "The intermittent formation, *per saltum*, of new plant species . . . is known in several groups of flowering plants, and small number of cytologists and geneticists insist that it is more common" (Huxley, 1944, p. 34).

In discussions of explosive speciation on islands and a series of lake populations in Africa, Huxley and Goldschmidt were principally separated. A series of biologists have observed that in conditions of isolation on islands and in lakes, numerous endemic species and genera

appear. This especially concerns the fauna of volcanic islands in the Pacific of comparatively recent origin (the Galapagos and Hawaiian Islands). Huxley and Goldschmidt independently cited the description of the majority of endemic species of finches from the family *Geospizidae* (Galapagos) and the Hawaiian honeycreeper family *Drepanididae* for the strikingly varied forms of beaks and methods of obtaining food. Since Huxley was the first to discuss this theme, it is helpful to see how Goldschmidt evaluated Huxley's thoughts. Considering the diversification of Galapagos finches in beak size, Goldschmidt came to the conclusion that: "a small number of systemic mutations is entirely enough in small populations" (Goldschmidt, 1940, p. 208). This example makes more difficulties for neo-Darwinian concepts, and Goldschmidt cited Huxley who attempted to clarify the variation in forms on islands with the theory of natural selection, which acts in conditions of the weakened pressure of predators and a lowered level of competition. Goldschmidt wrote: "Huxley admits selection and thinks that terrestrial finches demonstrate a special form of evolution - diversification without speciation. He suggests the term reticular evolution in the opposite branch for this type of evolutionary change. I agree with the general appraisal of the case from standpoint of taxonomy and evolution, but prefer an explanation that is free from neo-Darwinian bias" (Ibid., p. 209).

How was this phenomenon of the fast diversification of groups subsequently explained? The concept of macromutations was completely denied, and thus Goldschmidt's interpretation did not undergo analysis. Huxley's views are close to contemporary understanding, but they had to be supplemented and reformed. The classic model of speciation, as mentioned above, was suggested by Lack; therefore it follows that we should return to his views (Lack, 1947; Gall, 1984, 1997).

Lack noted that the formation of endemic groups of Galapagos finches, primarily, began with the colonization of one of the islands of the archipelago by several individuals, the relatives of continental finches. Then the finches of the population-founders spread to the other islands, where they formed new colonies and due to spatial isolation evolutionary variation began. These variations, suggested Lack, were not great because of the evolutionary similarity of the islands. At the next stage, the newly formed closely related groups inhabited new islands, which led to secondary contacts with the original populations. If the formerly isolated populations differed from one another, then the hybrids from their breeding which possessed intermediary morphological and physiological traits would die, since they were inferior to the parental populations in competition for food. The majority of morphological changes affected the size and form of the beak and body, and moreover, there was a strong connection between morphological variations and displacements in ecological niches. If the area of dispersion of two or even three closely related species overlapped, then the difference in morphology, physiology, and behavior increased according to competition, namely in these overlapping zones (later this phenomenon was called the mixing of traits). Lack claimed also that displacement in ecological niches was conditioned by the presence or absence of competitors: a species occupies a more varied place of residence in the presence of a few competitors; the more species competing for food, the stronger their specialization in food finding and the sharper their morphological variation. On the basis of his investigations, Lack offered a two-step model for speciation, in distinction from one-step, or purely geographical, models. The process of speciation, for Lack, is the geographic isolation of a few individuals of a certain species by way of genetic drift and partly natural selection; after a secondary contact and the strengthening of isolating mechanisms (selection against hybrids) niches differentiate due to competition and natural selection. Thus, Lack claimed that the formation of reproduction isolation and new ecological niches is a united process, which occurs

under the action of these same factors. It is noteworthy that Lack steadily corresponded with Huxley and even sent him a manuscript of his book in order to receive critical remarks. It is believed that the concept of niches and Gause's Law appeared in Lack's work almost without the influence of Huxley. Goldschmidt's concept of macromutations in the given case was abandoned. But Huxley's views also underwent significant reform, although they were closer to the truth. The newest investigations of the evolution of island ornithology and fauna shows that the role of random drift often increases, and the role of natural selection drops (Clegg et al, 2002).

Huxley and Goldschmidt cited the broad multiyear investigations of flora on the islands of Ceylon, South India, and New Zealand, which were carried out by the English botanist, Willis. Willis wrote two books: *Age and Area*, with the subtitle *The study of geographic distribution and the origin of species* (Willis, 1922), and *The Course of Evolution* with the subtitle, *Sooner differentiation and divergent mutation than natural selection* (Willis, 1940; Golubovskii, 2000, Pp. 59-63). Willis developed two original approaches: 1) the quantitative survey of the number of species in a genus related to the character of the chance of meeting on continents and islands, 2) the comparison of received distribution in various areas. Thus, in the flora of Ceylon among 2089 species of seed-covered plants 809 were endemic for that island. Moreover, the area of distribution of almost 200 endemic species was limited by a group of mountains or even separate mountains. The majority of genera were monotypic, represented by one species. The genera rich in species were older and usually continental. Willis found that the speed of appearance and distribution of new species is independent of their organization for all species.

Goldschmidt cited Willis's 1922 claim that for speciation "one large and vital mutation found on a portion of land of several square yards and, possibly, once in fifteen years, apparently, will be enough. The chances of noting such a mutation is practically nil" (Goldschmidt, 1940, p. 211). Willis noted the absence of transitions between the studied species and repeated acquiring of similar traits by species of the same genera. His book, *Age and Area*, included articles by other authors, including the sympathetic article by the founder of the mutation theory and the mutational concept of speciation, Hugo de Vries. Undoubtedly, all these works and their interpretation correspond to Goldschmidt's concept of macroevolution.

Huxley, citing the work of Willis and other botanists and zoologists, generalized a large amount of material showing that geographic variation did not always have an adaptive character. In addition, Huxley criticized Willis' conclusions, justly claiming that they should be made only on the basis of cytogenetic and ecological analysis. Huxley wrote: "If such an analysis was done, then many of his [Willis's] endemic species, undoubtedly, would seem not new, complete species, but new half-species, the result of drift" (Huxley, 1944, p. 204). To this can be added that Wright's model of balanced evolution (1940), in his own words, discusses the possibility of securing in a population macromutations through the mechanism of genetic drift (Wright, 1982). But his biographer, Provine, expressed doubt that Wright was able to understand neutralism at such a high level as species, genera, etc. (Provine, 1986, pp. 412-413). Provine documented his point of view using Wright's review of the books of Willis and Goldschmidt. Here Wright suggested that the authors refrain from ideas of macromutations and accept the concept of genetic drift in a broad naturalistic interpretation.

The objections of Huxley and Wright to Willis' conclusions were justified at the beginning of the 1940s, however, they were largely cancelled out by subsequent cytological investigations of explosive speciation in plants, which Grant called quantum (1980), and Lewis', speciation by saltations (Lewis, 1968). Lewis had observed sharp transitions between closely

related species of the annual genus *Clarkia*, at times in an area of a square mile. The species differed in structure by plural chromosomal restructuring such that hybrids formed easily but were sterile. In conditions of spatial isolation, species could arise from separate individuals that had been changed in saltations. Grant noted that, although Goldschmidt's views were received sceptically by evolutionary zoologists, they were supported by a series of investigators, who studied plant speciation (Grant, 1984, p. 169).

The most conclusive evidence, however, of the truthfulness of Willis's conclusions were the speciation investigations of H Carson. On the basis of morphological and cytogenetic variations, Carson and his colleagues observed in Hawaii more than 500 endemic species of *Drosophila*. The scientists were able to trace the sequence of appearance and distribution of new endemic species on the younger islands of the Hawaiian archipelago due to migration from the older islands. In a number of cases, reverse migration was also shown. Carson concluded that that speciation and adaptation are separated in time and constitute two aspects of evolution. He wrote: "The speciation phase precedes the adaptive phase. An episode of speciation is connected with the subsequent colonization of an unoccupied ecological niche by one of a founding female" (Carson, 1970, p. 1417).

Commentating on these data, Dobzhansky (1972, P. 688) noted that they are "a radical deviation from the orthodox point of view". The orthodox point of view was that speciation is the result of adaptive divergence, which is a long and steady process. But Huxley had just widely analyzed non-traditional methods of speciation that occur sharply and intermittently (chromosomal restructuring, polyploidy, hybridization and others). Even on the question of speciation, Huxley never agreed with orthodoxy. It is curious that Carson's conclusions were repeated almost verbatim in Willis' conclusions in studying island fauna; over these Huxley and Goldschmidt had disagreed during the 1940s.

For proof of the role of macromutations in the processes of speciation and the origin of higher taxa, Goldschmidt returned to the investigations of Willis, Gould and other authors on the formation of the families of Hawaiian honeycreepers (*Drepanididae*). He noted that the group formed quickly by diversification in size and shape of beak, which is connected with various types of feeding. Moreover, fast speciation begins with the invasion of one species that becomes the founder of the entire family. Goldschmidt considered the different points of view on the question of the reasons for the origin of the families of Hawaiian honeycreepers and formed his own views. At first denying Darwinism, he wrote: "Since the geneticist is unable to accept a Lamarckian point of view, then there remains only a single solution—origin by large steps, our systemic mutations, which lead immediately to a new type; large evolution takes place in the short or even very short period of time required for forming a subspecies" (Goldschmidt, 1940, p. 216).

We will now consider Huxley's orthodoxy on the question in hand. It is simple: he suggested that the very fact of the fast diversification of groups with precise understanding of growth and patterns is of exclusive interest for evolutionary theory. He wrote: "Perhaps, the most notable example of oceanic adaptive radiation is the example of the honeycreepers of the Hawaiian archipelago *Drepanididae*—the singing finches, which, according to Gulick (1932), came from the American tropical honeycreepers, but according to Mordvilko (1937) came from a finch related to the golden finch (*Carduelis*). On the Hawaii and Laysan islands, many types appeared, including at least eighteen genera. No other family of birds has demonstrated such adaptive radiation" (Huxley, 1944, pp. 324-325). The surprisingly fast or even explosive evolution of a group was the result of the interaction of natural selection and genetic drift,

geographic isolation and population size. But Huxley added the following: “A high level of differentiation in the given case, undoubtedly, is the result of the small size of island populations, which allows “drift” and non-adaptive divergence” (Ibid., P. 184.) It is interesting that Huxley, as an ornithologist, did not respond to Goldschmidt's interpretation either of Hawaiian honeycreepers or of Galapagos finches.

In 1970, W Bock created an evolutionary model for the Hawaiian honeycreepers, which by that time had separated into the two subfamilies, the *Drepanidinae* and *Psittirostrinae*, by D Amadon (1950). Bock worked on the second subfamily, which was richer in species (Bock, 1970). Bock's model was extended by J Valentine, and Bock and Valentine vividly showed the similarity of the processes of the fast evolution of Galapagos finches and Hawaiian honeycreepers. Thus, in the section '*Adaptive trans-speciation of evolution*' of their collaborative work, Valentine (1977, p. 251) wrote: “The appearance of different genera (and actually subfamilies) went through gradual evolutionary processes, suggested by Simpson's model. If one considers that the Hawaiian islands are less than ten million years old, then the Hawaiian honeycreepers also differentiated in that time-frame, and perhaps, a significantly shorter period.” Huxley's logic and evolutionary interpretations were close to the clear analysis of Bock and Valentine. It is interesting that the rich ornithological material, which Goldschmidt used widely in his 1940 book was absent in his later theoretical constructions. It is possible that it was for this reason that Goldschmidt's investigation of the problems of “development—evolution” disappeared from the works of the founders of the evolutionary synthesis (Gould, 1982).

It was, however, shown above that Huxley and Goldschmidt worked much in a one direction. Moreover, between the two evolutionists there was a great interaction and understanding. They thought that the change in path of ontogenesis in early embryological development was important for the processes of large evolution. The genetic aspect of similar processes was connected with the change in the speed of the rate of genes or special mutations, which influence the absolute and relative rate of growth, or the amount of special morphogenetic matter (first and foremost hormones and molecular-morphogenes). Huxley and Goldschmidt placed special significance on the integrity of ontogenesis and ontogenetic aberrations (Takhtajan, 1991, pp. 4-5). They often saw the process of large evolution as sharply interrupted, connected with the falling out of entire stages of individual development and leading to the formation of new taxa, and to changes in the very tempo of evolution. Huxley called neoteny a principle of wonderful importance (Huxley, 1944, p. 532). Later he strengthened his own interpretation of the role of juvenile ontogenetic variations in evolution. He wrote: “One way of escaping from blind alleys may be that which has been given the rather formidable name of *paedomorphosis* – *prolonging an early developmental stage into adult life and going on from there*” (Huxley, 1954, p.125). Goldschmidt demonstrated the role of neoteny in macroevolution primarily in the Mexican salamanders, which Huxley studied. Goldschmidt (1940, pp. 273-275) suggested that macroevolutionary events in amphibians occurred due to the change in status of the hormonal system, and, apparently, without macromutations.

The following is telling of the similarity of the positions of Huxley and Goldschmidt. In the ninth chapter of *Evolution*, “Evolutionary trends,” Huxley discussed two areas of evolutionary consequences in changes of individual development. In the book, *The Material Basis of Evolution*, Goldschmidt also devoted significant attention to the problem of “the evolutionary consequences of individual development,” and in particular the theme “evolution and the potential for development.” Huxley noted that in the 1920s, Goldschmidt had already recognized that “changes in inheritance can take place only within the limits of possibilities and

limitations, which are dictated by the normal processes of development,” and illustrated this position with long examples. In the 1940 work, Goldschmidt, again declared even more energetically: “that which is called the general way of the mechanics of development, will decide the direction of possible evolutionary changes. In many cases there will be only one direction. This is orthogenesis without Lamarckism and mysticism, and without selection adult conditions” (Goldschmidt, 1940, p. 322). On Goldschmidt’s embryological approaches regarding the concept of evolution, Huxley wrote: “Goldschmidt completely agreed that the demonstration of the gradients of growth and the area of growth explain many examples of non-adaptive variation and the numerous correlated changes in proportions, which take place as the result of the action of single mutations on the shape of the gradient of growth.” Furthermore, in unison with Goldschmidt, Huxley noted: “It seems clear, however, that the endocrine system constitutes a “chemical skeleton” whose existence and nature prescribes certain favored modes of evolutionary change in its possessors” (Huxley, 1944, p. 553).

The ninth chapter of *Evolution*, in which evolutionary trends are discussed, Huxley based his arguments on the broad synthesis of experimental embryology, the allometry of growth, and developmental genetics. Most likely, he was one of the very first to appreciate that experimental embryology will make an important contribution to evolutionary theory. Meanwhile, many great evolutionary embryologists and morphologists have suggested that experimental embryology offers nothing new and is principally unable to give anything to evolutionary theory (Adams, 1980, pp. 193-225; Gilbert, 1994, p. 197). Throughout the entire ninth chapter, the Huxley-de Beer idea of embryological synthesis is presented as an evolutionary approach. In constantly citing Goldschmidt’s work, Huxley had a deeply creative and cultured dialogue. A thorough analysis of the text *Evolution* shows that many of Goldschmidt’s embryological themes were developed in the framework of a broader approach. But naturalism hardly added embryology for Huxley. Experimental embryology with developmental genetics literally burst into science with the appearance of *evolution* and formed an island of understanding in the overall problem of large evolution.

As has already been mentioned, Mayr noted that Huxley introduced new genetic aspects into the problem of macroevolution. On various aspects Huxley discussed the influence of genes on development and the subsequent evolutionary consequences. This is especially visible in discussions of the problems related to onto- and phylo-genesis. Of course, the genetics approaches of Huxley and Goldschmidt to large evolution differed in several principles. For Huxley small variations in the rate of genes led to large phenotypic effects, but Goldschmidt often simply fixed great morphological variations and called them macromutations. In the snail, *Cepaea*, Huxley showed how expression of mutations in the rates of genes change the pigmentation and the growth rate. But in other conditions these comparatively small genetic changes led to sharp influences on metamorphosis, improvements in sexual maturity or in general the rate of growth and development, the result of which has long term consequences (Huxley, 1944, p. 532). The genetics of allometry and the phenomenon itself so interested Huxley that he insisted on adding to the already written *Evolution* the conclusions of F Weidenreich, who had worked on the evolutionary trends of mammalian skulls in relation to brain growth. He noted that in the early embryological life of the majority of mammals, the rate of brain growth is high, but later it drops noticeably, leading to the sharp allometry of the parts of the face. In domesticated and small wild species, facial allometry is strongly limited. Man is not a “dwarf” species, but demonstrates a “dwarf” type of skull with a huge brain. Unlike Bolk’s examples, in Weidenreich’s examples there is no delay in the development of mature traits, but

in the latter stages there remains the original high growth rate of the brain. Weidenreich (1941) was attentive to the main difference between man and the man-like apes—not so much a larger brain as a different type of growth, which is connected not only with a larger brain, but also with a special structure of skull. He came to the conclusion that, if the curve of allometric growth was identical in man and man-like apes, humans would be ape-like. For Huxley there was no longer the possibility to comment on Weidenreich's investigations, but he did not, as a dogmatically inclined scientist consider it necessary to apply his point of view to such an important question. Undoubtedly, the allometric approach was broader than that of neoteny, since neoteny itself appears as the consequence of allometry or heterochrony (Gould, 1977; McKinney, 1998; Takhtajan, 1991; Takhtajan, 2001).

Goldschmidt had a high regard for Huxley's investigations on the evolutionary consequences of variations in early embryological development and the roles of the rate of genes in these processes (Goldschmidt, 1940, p. 311). For himself, in leading up to the results of the ninth chapter of *Evolution* on evolutionary trends, Huxley wrote: "The examples we have been considering in these sections show how the fact that most genes affect the rate, the time of onset, the duration, and the type of developmental processes will provide the raw material for trends involving progressive alteration in one or other of these factors of development. Since the raw material is so abundant, consequential trends of this sort will be frequent. This theme is partly discussed by Gall (1932), and more completely presented not only by Goldschmidt (1940), but also Haldane in his article (1932), de Beer (1940), and from the standpoint of physiological genetics by Waddington (1941). The course of Darwinian evolution is thus seen as determined (in varying degrees and in different forms) not only by the type of selection, not only by the frequency of mutation, not only by the past history of the species, but by the nature of the developmental effects of genes and of the ontogenetic process in general (Huxley, 1944, p. 555). Huxley and Goldschmidt were the main figures in the formation and development of the triad "genetics—development—evolution." However, their general evolutionary conclusions were quite contrary. Huxley built the triad in order to develop a construction viewing evolution as an integral process without the extrapolations of ideas and facts, obtained in the study of microevolution, in the course of large evolution, as Dobzhansky and Mayr had done, and leaning primarily on population genetics and micro-systematics. The one and same mutations and the action of the one and same genes correspond to the entire course of evolution, but phenotypic and developmental effects are completely different. The ideas of globalism, which Huxley throughout his entire life developed in both humanitarian and public spheres, were subsequently built by him into the scientific concept of the global unity of the evolutionary process. Goldschmidt's triad literally broke the evolutionary process, which brought to reality the dream of Filipchenko. It is difficult to judge who is right and who is wrong. Now it is apparent that the power of population genetics in studying evolution has fallen. Many phenomena of the dynamics of genes in populations, which were interpreted as evolution, are in fact homeostatic processes aimed at the survival of the species through internal diversification. In this sense, Goldschmidt was the true prophet, but IM Lerner constructed a well organized concept of genetic homeostasis.

The development of contemporary evolutionary theory demonstrates convergence. In the framework of the evolutionary synthesis, great results were obtained, but not all supporters of the synthetic theory of evolution were twin-brothers. Yes, the ontogenetic theory was best of all presented in Huxley's works. He suggested the name "contemporary synthesis" and when the synthetic theory of evolution is spoken of, Huxley's name is remembered first and foremost. Historically, in the work of the next generation of evolutionists, Huxley the synthesizer and

Goldschmidt the heretic were brought together, and in first place what came out was their extraordinary intuition and understanding of the future paths of development, no longer synthetic or heretical, but simply contemporary evolutionary theory.

The hardening of the synthesis

Huxley's *Evolution* was written from the position of broadest pluralism. The "hardening" of the synthesis, however, continued until 1963, when *Evolution* was republished with a new general introduction, which included an evaluation of the evolutionary events beginning with the first edition. Of course, to simply judge from the introduction whether Huxley changed his position in 1963, as had influential biologists (for example, Dobzhansky, Ford, and, in part, Mayr). But the very fact that Huxley did not edit or rewrite the text of the 1942 edition probably shows that his views underwent no major changes. Evidence of this also comes from his evaluation of Ford's book, *Ecological Genetics* (1963). Huxley wrote to Ford that that clearly reevaluated the role of natural selection in the differentiation of populations of the snails, *Cepaea*, and depreciated the role of genetic drift (Beatty, 1992, p. 187). In the introduction to the 1963 edition of *Evolution*, Huxley expressed himself more calmly. He claimed that Ford used many examples in his book of the action of natural selection and strove to show the inadequacy of genetic drift (Huxley, 1963, pp. xxii-xxiii). Here, in the introduction to the new edition of *Evolution*, Huxley highly evaluated Mayr's founder principle, which was advanced in its final form in 1954, and showed its ideological kinship with the concept of genetic drift suggested by Wright in 1931. Huxley showed that Mayr's 1963 book, *Animal Species and Evolution*, largely recalled Ford's hardened synthesis. Mayr reconsidered his neutralism of 1942 from the position of natural selection and adaptation (right up to the coadaptation of genes). In his review of Mayr's book, Huxley wrote: "Mayr evaluated drift as a secondary factor" (Huxley, 1963). In the introduction to the 1963 of *Evolution*, Huxley also noted the Dobzhansky's change in views from 1937 to 1953, and Gould's reaction to them. Huxley stressed that, in the 1930s, Dobzhansky most often interpreted chromosomal polymorphism in the manner of Wright, and later placed the main accent on natural selection. From Dobzhansky's adaptationism, in essence, there grew a balanced model of the genetic structure of populations. Gould published the first edition of Dobzhansky's book, *Genetics and the Origin of Species* (1937), noting its novel and even revolutionary character. Thus, Huxley showed that in evolutionary theory in the 1940-1960s, great changes occurred in the question of the role of random processes and natural selection in evolution. However, Huxley himself retained his own opinion.

Provine has suggested that Huxley's *Evolution* is unsupported in at least two aspects. The first is that Huxley's synthesis was entirely built upon variables, which were proposed by theoretical population genetics. The second aspect comes to the fact that the evolutionary synthesis eliminated a great number of interesting, primarily purposeful, evolutionary theories, which existed until the 1930s. Thus, opinions immediately fell into two positions.

It follows that Huxley was, perhaps, the only evolutionary biologist who outlined his ideas in a more or less historical form. All the most important concepts of evolution, which were popular, he analyzed in his articles and monographs, advanced the contrary arguments, or looked over in correlation with contemporary situations in science. Huxley's constructivism speaks of the fact that in *Evolution*, he broadly discussed orthogenesis. The final doctrine of preadaptationism had been turned by Huxley into a real problem of the role of preadaptation in evolution in 1936, when neo-Darwinists were struggling to discuss it (Georgievskii, 1974; Gall,

1999). He used the ideas of Lamarck, propagandizing the concept of organic selection, the “Baldwin effect” (Baldwin, 1896). Through analyzing the Baldwin effect, Huxley found a way for a conjunction of genetics and developmental biology. The work of Gause and Waddington (Gause, 1947; Luchnikova and Gall, 1994) went in the same direction. No one subsequently has investigated this interesting creative search, except perhaps MA Shishkin (1984) and AS Severtsov. In this way, one can speak of the rebirth of not only Darwinism, but also Lamarckism, with Huxley’s idea of the important role of non-inherited variations in evolution, and thus of the widening of Darwin’s theory of natural selection on a “Lamarckian” basis.

Progressionism was an important component or even Omega point of all purposeful evolutionary concepts. Huxley organized an unprecedented connection: natural selection—evolutionary progress. Many purposeful evolutionary concepts continued the line of K Bear, which is that within them carries on the analogy between evolution and development. Huxley included the huge question of the genetics of development, embryology, and in general developmental biology, in the evolutionary synthesis. None of the representatives of the evolutionary synthesis took such an interesting path. Is it possible to call Huxley’s *Evolution* an example of judgement, or in the broadness of theme and scope of unbounded material does it surpass Darwin’s *The Origin of Species*?

Evolutionary progress and the end of biological evolution

In VI Nazarov’s book, *Finalism in Contemporary Evolutionary Study* (1984), the broad spectrum of scientists who maintain non-orthodox views is demonstrated. Such names as L Cuenot, A Lvov, O Shindewolf, A Vandell amongst many others, speak eloquently on the force and power of various forms of finalism. “Struggling” with such a company is no joking matter. In Huxley’s work, the idea of evolutionary finality appeared in one connection with the idea of progress. He discussed the idea of progress in the tenth and partly in the ninth chapters of *Evolution*. Here his position is almost transitional between the two ideas outlined in the 1936 Address, and the concepts published at the beginning of the 1950s.

In 1936, he did not really discuss the question of the role of neoteny and pedomorphosis in unlimited progress. In 1942, finally, he used the fundamental principles of the concept of neoteny and pedomorphosis to explain the appearance of man. In *Evolution*, he outlined the concepts of de Beer and Garstang on the role of pedomorphosis “an escape from specialization” and called them “ideas of primary importance” (Huxley, 1944, p. 532). At the same time, Huxley evaluated as “highly speculative” Garstang’s ideas on the origin of higher types from embryonic organization, (Ibid., pp. 562-563).

It is believed that Huxley’s caution in evaluating neoteny and pedomorphosis was not accidental. All the coauthors of the evolutionary synthesis thought that the very idea of the correlation of onto- and phylogenesis is highly speculative, and did not discuss it seriously. De Beer, however, published two works, in which he showed that pedomorphosis is one of the main mechanisms of large evolution (de Beer, 1940a; 1940b). For de Beer (1948), it is impossible to claim that large evolution has already ended, and thus it is impossible to speak of a unique status of man. In the article, “*Embryology and the Evolution of Man*,” he does not even mention Huxley’s views on the role of neoteny in the origin of man. The idea of the end of biological evolution, which Huxley propagated, was naturally unacceptable to de Beer, who claimed that any specialized taxa could “discard” *adult* (for de Beer, “gerontological”) traits and open for itself new evolutionary possibilities. For previous evolution, Huxley did not deny this, but with the appearance of man for any higher taxa large evolution had closed or had come to an end.

Man completely destroyed all paths of “juvenile” evolution; it was as if neoteny and pedomorphosis exhausted themselves.

Huxley invariably and automatically accepted Cope’s law of non-specialized forms, which simultaneously served as proof of the evolutionary dead-ends of specialized forms. Moreover, Huxley suggested that specialization is the common path to extinction. At the beginning of the 1940s, the views on specialization and Cope’s law underwent critique, as did the concept of the finale of evolution. Thus, Mayr wrote: “In agreement with Cope’s principle, any phylogenetic series goes from non-specialized “primitive” forms to more and more specialized forms, that in the end leads to high specialization and extinction. This principle also is correct only in a limited way. Mammals, like reptiles and birds, possess specialized structures and functions, but they achieved new adaptive positions and became the ancestors of higher taxa” (Mayr, 1942, p. 294; cited in Mayr, 1947).

In 1949, the idea of an end of evolution, with the exclusion of the evolution of man, was criticized by Simpson. He pointed out the main source of ideas, which are contained in the finalistic and metaphysical theories of evolution of the South African paleontologist, Robert Broom. He wrote: “Some authors, actually, have claimed that great evolutionary changes stop at a defined point. Finalists strongly believe that evolution has a single goal, such as the creation of man, and after that achievement, the evolutionary process stops. But evolution is not finalistic, and it will continue as long as there is life” (Simpson, 1949, p. 325). And in the notes to the general discussion, Simpson added: “I do not know any serious investigators who would support Broom’s general theory, except Julian Huxley, who, however, made an exception for man. He expressed the opinion that future evolution would take place *only* in man” (Ibid.).

Simpson noted the connection of the ideas of Broom and Huxley. Was this connection logical and historically thematic? What other sources influenced Huxley’s extraordinary position? In *Evolution*, Huxley mentioned Broom only once, sharply criticizing his views on the importance of “spiritual agents” in all of biological evolution (Huxley, 1944, p. 568). Thus this source did not throw any light on the history of the problem.

Huxley’s old friend, Conklin, an embryologist and broad evolutionist from Princeton University, published an article in 1919 “*Does Progressive Evolution come to an End?*,” and in 1921 the book entitled *The Direction of the Evolution of Man*, in which he presents completely different views on progress than that of Huxley (Conklin, 1919; 1921). After meeting in Napoli in 1910, Huxley and Conklin corresponded for over twenty years. Progress, for Conklin, meant the growth of complexity connected with the growth of specialization and the coordination of parts of an organism and the general activity of organisms. Progress takes place inside large taxa, since evolution moves from unspecialized ancestors to divergently specialized offspring. Conklin suggested that progressive evolution in every line has an end. He wrote: “The complexity of body, social organization and intellectual ability, progressive evolution comes to an end among organisms lower than humans” (Conklin, 1921, p. 24). In the evolution of man, the complexity of body and intellectual ability also reach their own limits. Further progress of man can take place only through growth of specialization and coordination inside a social system. Conklin was an active defender of Cope’s principle of non-specialized forms—a principle, which exhausted itself at the same time as evolution.

Conklin’s ideas, judging by the available literature, were seldom discussed. Although several historians of science claim that, Teilhard de Chardin, in an unpublished essay in the 1920s (“*Notes on Progress*”) discussed ideas similar to Conklin’s (Swetlitz, 1995, p. 190). de Beer in “*Embryology and Evolution*” (1930) cited Conklin’s claims on the finale of biological

evolution and called it obsolete for the investigation of problems related to onto- and phylogenesis, as well as absurd and dismal. Such a claim seems to arise almost automatically when large evolution is discussed on the basis of gerontomorphosis. For de Beer (1930, pp. 88-101), it was necessary to change the premises, considering that pedomorphosis continues to play an important evolutionary role. If evolution occurs only through the modification of adult stages of ontogenesis, then the organism can evolve into more complex and specialized forms. These specialized forms impose strong limitations on the direction of future evolution. They cannot be the ancestors of new higher taxa, since only generalized (non-specialized) organisms possess sufficient potential. By studying only adult forms, it is impossible to observe ancestors but impossible to establish future evolutionary potential. Moreover, if evolution occurred only through gerontomorphosis, then it would come to an end and the origin of new higher taxa would be impossible. De Beer was absolutely convinced that his theory of pedomorphosis allowed one to avoid the absurd conclusion that, in agreement with that theory, original juvenile traits are maintained by adult offspring, making new specialized adult forms that possess the plasticity necessary for the evolution of new higher taxa.

Huxley's familiarity with the works of Conklin and de Beer is in itself understandable. But how was it with Broom? In 1933, Huxley began to write a work called "*Man's Place in the Cosmos*," but did not complete it. This work was partly reproduced by the historian, Swetlitz, according to whom Huxley, having repeated a series of standard evidence for on evolutionary progress and having raised the question of progress in the future, cited Broom as claiming that future progress among the higher taxa of animals has already stopped (Swetlitz, 1995, pp. 192-193). Moreover, this was Huxley's first citation of Broom, who was a world expert on early mammals and fossil reptiles. At a meeting of the British Association for the Assistance of Science in London in 1931, and in the monographs of 1932 and 1933, Broom developed the idea of the finale of evolution. He accepted Cope's law of non-specialized forms and completely denied the possibility of pedomorphosis in "big evolution". Broom offered two kinds of evidence to show that big evolution had ended. The evidence itself was not new, but he systematized it and presented them in a more detailed form than had his predecessors. First, he showed that non-specialized types, from which the higher taxa came, existed for a short period of time and that all the now living species are highly specialized. For example, fish, from which came the amphibians, possess extremely specialized and degenerated fins and skulls. Second, Broom, largely taking Conklin's path, noted that the latest higher taxa that appeared last on a macroevolutionary level no longer evolved: reptiles have not evolved since the Triassic period, mammals and birds for the last 40 million years. Of course, Broom became incensed, since it is well known that the sparrows of the islands of the Pacific Ocean have experienced a powerful adaptive radiation for the past five million years, with no less than three new families appearing. These data were known in the 1930s, especially after the intensive Rothschild expeditions and those of The Royal Society of London (Gall, 2002).

Broom made few appearances in London, however, and in 1933 he gave the Presidential Address at The Royal Society of South Africa. The address contained only one thought—evolution has come to its end. The famous British paleontologist, Arthur Keats immediately responded: "There exist no facts which would make us believe that today nature is less fertile than earlier" (Swetlitz, 1995, p. 193). But Broom persisted, claiming that he had interrogated leading zoologists and paleontologists asking them to name some mammal that had initiated a new group, and noted that not a single one of them had given an intelligible answer. It stands to

reason, that it would be possible to expect only such a result. The appearance of a new species, even by saltation, is always a long, or gradual, process.

Simpson, as has already been mentioned, showed a sharp negative regard for Broom's work on evolution due to his devotion to extreme metaphysics, which manifested itself in the control of evolution by "spiritual forces." Swetlitz also established that many scientists associated Broom's ideas on the end of evolution with his metaphysics (Swetlitz, 1995, p. 193). But the matter went somewhat differently. Broom himself connected these ideas when he claimed that a spiritual force existed, which planned and directed evolution towards a final goal - to the human species. Simpson (1944) was the first to bring attention to this single aspect of Broom's views. But few have noted that Broom later offered a "lighter" interpretation. He thought that the material evolutionary process and the action of spiritual forces coincide or operated in parallel. Non-specialized types exist only until the appearance of primates, then a "decline" in the evolution of the higher taxa occurred, and after the appearance of man large evolution ended completely (Broom, 1932a; 1932b; 1933).

In spite of massive critique by the scientific community of Broom's ideas on the finale of biological evolution, Huxley wrote to Broom in the summer of 1933: "I often think of your idea of the finale of evolution and, although I cannot agree with several of your philosophical arguments, I am increasingly leaning towards your idea that this fact is of great importance" (op. cit., Swetlitz, 1995, p. 194). Thus, Huxley quickly separated Broom's metaphysics from the evolutionary ideas, which underlay the discussion of scientific methods (for a full analysis of Broom's views, see Bowler, 1986).

At this time Huxley was preparing a new edition of *The Science of Life*. He made several additions without essentially altering the text. In particular, he introduced the phrase that evolution comes to an end, not citing Broom. To the ideas of Broom and Conklin, Huxley added in entirety a half-page. Huxley wrote: "All existing groups are specialized along their own actual lines, even the most primitive contemporary types are specialized in various details. Thanks to his unique intellect, only man has avoided the evolutionary limitations which are imposed by specialization" (Wells, Huxley and Wells, 1931e; Ibid., 1934, 9. 806). Huxley showed that in morphology, *Homo sapiens* contains a large number of primitive traits, which have been lost in many other mammals. At the same time in the evolution of man specialized traits, also appeared primarily related to the brain. This particular type of specialization, however, did not render a limited influence on future evolution. The brain due to the physical basis of speech and conceptual thought allows its possessor to achieve a high level of control over nature, securing progress in the future.

It is interesting that a similar point of view on human beings was shared by many zoologists and paleontologists in the first two decades of the 20th century. de Beer also readily accepted it. In 1934, Huxley introduced an innovation, highlighting that only human beings were able to avoid the evolutionary limitations of specialization (therefore he so "raged" about evaluating the evolutionary roles of neoteny and pedomorphosis). Thus, with the origin of man, neoteny and pedomorphosis became almost exhausted or extinguished at the level of the origin of the higher taxa. Huxley broadly applied the concept of neoteny and pedomorphosis in *Evolution* for explaining "small" morphological evolution. He noted that the process, which de Beer called *clandestine evolution*, acts on a small scale in neotenic beetles and amphibians (Huxley, 1944, p. 532). But how was it possible to bring together the ideas of Garstang, Bolk, and de Beer with the ideas of the end of large evolution?

Unlike de Beer, Huxley did not consider the end of large evolution as an obsolete absurd and dismal conclusion, which demanded a revision of its assumptions. He introduced only the earlier mentioned assumption of the guardianship of the evolutionary process. These inadequate words had far reaching consequences. Huxley noted man's special place in the Cosmos—thanks to consciousness he forever would monopolize the ability to control events. From this directly flows the idea of the uniqueness of man, to which Huxley dedicated many scientific and popular essays. In 1941, at the height of the Second World War, he contributed 300 pages of essays to the book, *The Uniqueness of Man*. But the amount of pages is not important; Huxley connected the views on the evolution of man with his own on the eugenics, and, having literally “destroyed” the idea of race hygiene, defended the disputable eugenics as a genuine science. A deep knowledge of genetics allowed him to propose the central problem of eugenics as the improvement of the human species through the interaction of genetics and the social sciences. The main mistake of the “environmentalists” and geneticists, he claimed, was that they “turned the difference between *nature and nurture* into antithesis. This was natural and, perhaps, unavoidable. This was not scientific, nor sufficient” (Huxley, 1941b, p. 39). At an early stage, Huxley criticised the concept of race as a whole and the idea of the advantage of one race over another. In connection with this, he embarked on a complete destruction of the anti-Semitic component of the ideas of race hygiene and successfully dealt with the purveyed questions. Thus, Huxley, during the period of the “blossoming” of fascist ideology, used many different methods to destroy the “fascist intellect.”

During the war Huxley thought about the post-war organization of the world and, as a member of the preparatory committee for forming the future international organization in the areas of culture and science, wrote a brochure in which he outlined his views on the evolutionary fate of humanity. He declared: “The irrefutable fact is that man's guardianship over evolutionary progress can be achieved in the future and defines his true fate” (Huxley, 1948, p.12). The protracted stability of the world can be achieved, he claimed, if all nations will have access to the scientific and cultural resources necessary for social progress.

Huxley's line of thought on the unique evolutionary role of man appeared in its final form in his interpretation of the same evolutionary progress. It is difficult to date exactly the origin of his new views—the investigations extended over decades. He introduced a new understanding of progress, based on the conclusion that large evolution comes to an end due to wide-spread specializations, excluding man. In the 1920s, he defined evolutionary progress as the growth of control over nature and independence from nature and constantly preserved that definition. At the beginning of the 1930s, he used such phrases as “progress to the fullest extent” or “unlimited progress.” The new words or definitions designated an evolutionary path, which leads to man—a single line that avoided specializations which limited future progress (Huxley, 1941, p. 486).

In 1942, it was as if Huxley was caught between his old and new views. Thus, in *Evolution*, he wrote that the evolution of birds and insects is only “protracted specialization.” Wings led birds to an evolutionary end. The excessive capacity of insects for innate reflexes to “all events of life” is an analogous evolutionary end. Huxley (1944, pp. 563-564) proposed three terms: “specialization” for the evolution inside the higher taxa, “limited progress” for almost all cases of the origin of the higher taxa, and “unlimited progress” for selected lines of the higher taxa, which lead to man. In the Romanes Lecture, 1943, he reformulated the problem of evolution as an all-round achievement, which did not close the path to subsequent achievements. Proceeding from this, Huxley very simply moved the evolution of birds and insects to the

category of specialization. It now became completely clear that he deduced this understanding of progress from the fact that large evolution ends due to wide-spread specialization in all lines (Huxley, 1943, pp. 36-37).

Huxley throughout his investigatory life was in search of criteria interpretations of evolutionary progress. *Evolution* very naturally concluded with a chapter on evolutionary progress, the concept of which allowed Huxley to reveal all the significance of evolutionary theory, not only for biology, but also as the theoretical, or scientific, basis for understanding the origin of man and his attributes, and also morals, religion, literature, and art. All progressionists before Huxley considered the problem of progress in the framework of either the social sciences, or teleological views of evolution. In any case, in *Evolution*, Huxley was the first to “stretch” evolutionary theory on the basis of natural selection to such a high hierarchical level, at which one finds only Lamarck and Spencer.

After the publication of *Evolution*, Huxley continued to think intensely about the problem of evolutionary progress, widening its social applications. After the war, the concept of evolutionary progress provided the theoretical platform for his views on the activities of UNESCO. In 1946, he published the article “*Redefinition of Progress*,” which in 1957 was republished in the collection, *New Bottles for New Wine*. He again repeated that the majority of evolutionary trends, including also those for horses, are only specializations (Huxley, 1957e, p. 25). He wrote: “We again should make general remarks on specialization. Specialization is the unilateral adaptation to a particular form of life and unavoidable leads to evolutionary death, or end. The majority of lines show something inverse to progress or limited progress” (Ibid., p. 27). He precisely outlined the essence of the concept of evolutionary progress and its relationship to the problem of specialization, which are central to evolutionary theory. Between specialization and progress there is a principle difference: specialization is always unilateral and limited, progress is thorough and unlimited achievement. Thus we have proof that the concept of unlimited progress was retained by Huxley also in 1946. He continued this propaganda in practically all his works on evolutionary theory and sociobiology.

Evolution in Action

In 1951, Huxley taught a short lecture course on evolutionary theory at Indiana University in the United States, which became the foundation for his 1953 popular booklet on *Evolution in Action* (Huxley, 1953). The ideas outlined in this booklet served as a start for the development of his future concepts.

Evolution in Action contains the six following chapters: “The Process of Evolution,” “How does Natural Selection Work?”, Biological Improvement,” The Development of Mental Activity”, The Path of Biological Progress” and “The Human Phase.”

Depicting the entire process of evolution from inorganic nature to the formation of humans and their social future, Huxley came to the conclusion that, for a more exact description of evolutionary progress, the practice of classifying at the macro-level and characterizing types of evolutionary progress necessarily leads to an understanding of biological improvement.

The concept of biological improvement solved numerous semantic problems. All forms of so-called particular and limited progress were liquidated. There only remained a form of unlimited progress, which is characterized as *all-round improvements, which do not stand in the*

way of future improvements. It is thought that the concept of biological improvement is a successful gnosiological and simultaneously ontological find of Huxley. It was not accidental that it was widely used by Rensh, Dobzhansky, Ayala, and others. The understanding of "improvement" itself is found in Huxley's earlier works, in particular in those from 1954 and 1957, which formed the core of his ideas on evolutionary progress (Huxley, 1954a; 1957a). But previously, Huxley had not built this understanding into a theoretical construction.

It is natural that in connection with this new position, Huxley had to discuss the question of the criteria of evolutionary progress in its broader historical context, and not simply in its semantic relationships. Among historians of science, the idea was current that Huxley's views were rooted in Darwin's *Origin of Species* (Gascoigne, 1991, p. 443). Huxley himself did not deny the ideological connections with Darwin. In the third edition of *The Origin of Species*, which appeared in 1861, Darwin added to the fourth chapter (on natural selection) a new section of five pages called "The extent to which there is the tendency achieve organization." He wrote:

"The final result [of natural selection] is expressed in that each being displays the tendency to become more and more improved in relationship to the conditions surrounding it. This improvement unavoidably leads to the gradual rise in the organization of a large part of the living beings on the entire world. But here we enter the area of a very complex question, since naturalists until now have not offered a definition acceptable to all of what the rising of organization means. In vertebrates, taken into consideration is the level of intellectual abilities and nearness to the structure of man" (Darwin, 2001, pp. 110-111). Continuing this theme, Darwin indicated that the natural selection did not necessarily lead to improvement.

By the middle of the 20th century (possibly even earlier) Darwin's concepts of improvement were not only almost completely denied, but many similar idea could hardly become respectable in evolutionary theory. In the context of Darwin's views, Huxley's creative resolution is clearly visible. In *Evolution in Action* Huxley wrote: "'Improvement' is not yet a generally recognized technical term in biology. In fact, I should imagine that many of my biological colleagues would jib at its use. Some would shy away from it because it sounded teleological, while others would say that it implied a judgement of value, and that value-judgement were not scientific, or at least were outside the purview of science. However, living things are improved during evolution, and we need a term to denote that fact, and to crystallize our ideas about it. Darwin was not afraid to use the word for the results of natural selection in general, and I cannot think of anything more suitable" (Huxley, 1953, p. 65). From an evolutionary point of view "improvement" can be redefined, for Huxley, as any carefully made or constructed structure of function, which grows due to random survival.

In his earlier works, Huxley noted that the word "progress" in the works of sociologists and political economists had a purely descriptive meaning and retained an axiological approach to objective events. Teleologists strove to add "progress" and extra-scientific and extra-rational sense, which in various modifications migrated into evolutionary theory (Huxley, 1936a; 1941b; 1942; 1957a). All scientific searches in this direction concluded in the search for objective criteria or, for Huxley, a biological basis for evolutionary progress. When Huxley introduced the idea of "improvement" and began actively to make propaganda for it, he changed the accent from human values to the biological value of survival. Thus, "improvement," clearly having an evaluative sense with a great technological nuance, simply became a *biologically* evaluative word. Huxley insisted that "improvement" as the result of natural selection was a part of Darwin's theory. It follows here to mention that not only in the fourth, but also the eleventh chapter of *The Origin of Species*, Darwin discussed the concept of improvement in connection

with the ideas of “the advancement of organization.” Darwin wrote, in particular: “We have already seen in chapter four, that the level of differentiation and specialization of parts of organic beings, achieved in maturity, is, one can suggest, the most significant level of its perfection or height. Equally, we have seen that the specialization of parts serves the advantage for each being; therefore natural selection has the inclination to make the organization of each being more specialized and perfect and in that sense higher” (Darwin, 2001, p. 307). Here it is entirely clear that Darwin is the direct predecessor of the concept of “anagenesis.” More exactly, contemporary evolutionists (Rensh, Huxley) strongly followed Darwin’s reasoning.

Huxley wrote that the concept of biological improvement is a clear analogy to technological improvement. Organisms can be represented as machines for the business of life and reproduction, and idea of improvement is applicable to the growth of the effectiveness of living machines. But Huxley never used biological or technological improvement as evidence of explanation. He suggested that biological improvement has different levels, from the high adaptation in several traits of the organism to the advancement of a great scale in anatomical and physiological organization. A significant improvement of the machines is at first preceded by limited steps, each of which is followed by a phase of stability. The stable phase can serve as the starting point for the next changes, but most often remain unchanged or become extinct. Thus, biological improvement is too far from universal: often lower organisms survive, and, as in Protozoa and bacteria, their evolutionary time simply comes to a halt. Huxley, having identified with Darwin, wrote that improvement is always connected with “the conditions of life.” Subsequently, degeneration can be considered a type of improvement from the point of view of a parasitological form of life. Huxley called small improvements “special adaptations,” but the uninterrupted improvement of a line in regards to a particular form of life is “specialization” (for an example, Huxley used the protracted improvement of the horse family). Improvements on a large scale (or advances), for Huxley, can produce an advancement in the general organization or in the action of some, for example, nervous systems.

Having considered all the available definitions of “biological improvement” Huxley moved to the definition of progress. He wrote: “Most improvement is specialization – it is improvement merely on relation to some restricted to a form of life or habitat. Some improvements are advancements. But in attaining higher or more integrated organization, the effectiveness of the large functions of life grows, and the biological machine undergoes a radical evolution. All this evolutionary advancement comes to a stop, but random improvements can continue. From the above we can define progress as an improvement, which permits or facilitates further improvement, or if you please, a series of advances, which do not stand in the way of future advances” (Huxley, 1953, p. 84). In characterizing the biological properties of improvement, in particular specialization, Huxley, as has already been mentioned, stopped at the properties of stabilization, which is usually described as the limit of changes in an organ or biological group. In *Evolution in Action*, he only twice used the term “stabilization.” Both times he cited Thomas Henry Huxley’s lecture and work of 1862, in which the idea of “persistence” is discussed, that is, the protracted stagnation of a group at the scale of geological time, or the survival of “living fossils,” for example *Lingula*. In Julian Huxley’s earlier works, he often returned to the idea of persistence, but these were fragmented discussions, which were not written into the general plan of large evolution. In *Evolution in Action*, he considered this idea at the level of phyletic lines and immediately applied the theory of natural selection for explaining the “great ideas” of the famous biologist. He showed also the entire mechanism and direction of the action of persistence in the example of the evolution of finches: during the invasion of the

Galapagos islands, this bird produced a new family of finches, while at the same time the original small species of finches on the continent remained unchanged. Thus, he demonstrated the connection between stability and adaptive radiation in evolution.

Progress for Huxley was a rather rare phenomenon, at the same time as improvement figured as a common phenomenon. His definition of evolutionary progress had an extremely abstract character, and it will later be shown that it was an entirely valuable theoretical key in solving the cardinal problems of evolutionary theory and the theory of classification. Around his concept of progress, he formed a broad series of theoretical innovations.

In 1953, he maintained his ideas on the end of biological evolution, although he had to endure solid barrage of criticism (especially from Simpson). Huxley wrote: "Pure biological progress has actually come to an end, but human progress is only just beginning" (Huxley, 1953, p. 137). These words can be understood also within the context of an old common view: characterizing the finale of biological evolution; Huxley changed the broad term "evolution" to the narrower term "progress." But the main point, perhaps, is the attempt to reveal the objective scientific values of the biological concept of progress for understanding man. In other words, with the help of contemporary biology he wanted to "eliminate" the dogma of academic philosophy. According to him, the weakness of classical philosophy was its ignorance of the principles of evolution and theory of progress. In the framework of contemporary Western philosophy in interpreting the problem of man, there existed a gap between man and the animal world. This gap, Huxley claimed, would always be an obstacle to forming scientific premises in the field of the interpretation of the nature of man. The attempt to remove the evolutionary gap was accomplished by Huxley and Spencer, each in their own way.

In philosophy, Huxley noted, there is a more fundamental question about the relationship between matter and consciousness. It is stated falsely, without considering the ideas of evolutionary progress. The relationship between matter and consciousness does not exist in a static state: the growth of intellection activity in all living matter should unavoidably engender human consciousness, and then consciousness becomes the primary creative force of human evolution. The primacy of consciousness over matter is such a principle of evolutionary theory and evolutionary progress that serves as the best example of the reality of the process of evolution itself. Huxley more actively criticized the crude materialism of a Marxist sense. He wrote: "for the modern biologist, the dialectical materialism, which provides the philosophical foundation for Marxist communism, is a rude mistake. In order for this philosophy to survive, we must understand the principles of evolution, which in the days of its origin simply did not exist" (Huxley, 1953, p. 93).

In several aspects, Huxley broadened and elaborated the evolutionary role of neoteny and pedomorphosis. In *Evolution in Action*, he continued to discuss the evolutionary and social roles of extending the period of "childhood" in man and his close ancestors. Huxley wrote: "Our life arose from a foundation of conceptual thought. And this was the last step in biological progress—the attainment of true speech and conceptual thinking" (Huxley, 1953, p. 131). The best estimate of the role of neoteny in human development was made by Haldane in 1932. He noted that numerous descendents quickly grew and developed; a single child born at full term develops slowly and requires prolonged training—this is how animals with reason arose. But it is not possible to claim that Huxley offered a broader interpretation of neoteny and pedomorphosis (on this question, there most varied interpretations arise). Huxley wrote, for example: "One of the ways to avoid blind alleys [having in mind specialization] would be to accept the term pedomorphosis —the prolongation and longer development of the early stage prior to achieving

the adult form. I have already mentioned the importance of this mechanism for insects. Garstang categorically insisted that vertebrates descended from free-swimming larvae of echinoderms through pedomorphosis. *This is highly speculative and, maybe, never provable position, but it has value in regards to reason as a possibility*” [author’s emphasis] (Ibid., p. 131). These last words are simple evidence that Huxley never doubted the huge role played by neoteny and pedomorphosis in the origin of man and in the creation of human traits, but unlike de Beer, he “pulled together” neoteny from the other taxa in the line of hominids, from which man arose.

It is interesting that in citing de Beer’s book, *Embryos and Ancestors*, Huxley outlined his experiments on the transformation of Mexican salamanders. On this same material, it was entirely possible to discuss the role of neoteny in large evolution, however, an evolutionary discussion never followed. Right after the experimental material, Huxley turned to a completely different problem—evolution in geological time.

In connection with introducing the understanding of “improvement” Huxley somewhat changed the meaning of specialization (this was already discussed when subordination between categories characterized by evolutionary trends was explained). Huxley wrote: “All specializations lead to the improvement of the individual forms of life. This is the one-sided development of traits and often includes the loss or degeneration of several traits, for example the side toes in the horses” (Huxley, 1953, p. 78). In this excerpt, there is no indication of extinction as the final stage of a specialized path of development. One word “improvement” immediately changed the sense of the interpretation of the phenomenon. It is correct that an indication of the particular form of life simultaneous says that although improvements are possible, they do not result in large evolution. In order to clarify the interpretation of “specialization” it is worth examining Huxley’s article “The Evolutionary Process” from the collection *Evolution as a Process*, published when he was 65 years old (Huxley, 1954). In this article, improvement, specialization, and progress appear in a single group. He wrote: “Unilateral specializations are always limited. In general a unilateral specialization demonstrates an improvement in a particular form of life or even in prolonged geological existence. After a period of “life” at a given attained level of improvement the line either goes extinct or is forced out by competitors. *Thus, the result of a specialized improvement is the limitation of the paths for future improvements.* (Ibid., pp. 8-9). Since Huxley constantly thought of the problem of stability in evolution, in *Evolution in Action* he addressed this theme in his discussion of biological specialization. In 1954, using factual material, he wanted to prove the broad applicability of Thomas Henry Huxley’s concept of persistence, and used ornithological material, which was completely new (in any case, in comparison with the evidence of his grandfather). Huxley enumerated the “gifts” of the great taxonomic groups, whose ancestors started prior to the Devonian and yielded genuine evolutionary progress. This list appears as a consecutive outline of groups in a zoology textbook, with the difference that Huxley collected improvements from the fragments and evaluated their prospects. He conducted a strict reduction of the concept of progress. He wrote: “There exist many attempts to define biological progress, or advance in organization. The most satisfactory definition is the following: biological progress consists of biological improvements, which allow future improvements. Such an *unlimited improvement* forms a special and exclusively important category of evolutionary process and permits selecting for it the short name of “progress” or not” (Ibid., p. 11)

The collection for Huxley’s 65th year, *Evolution as Progress*, included a long article by A Hardy called “Escape from Specialization” (Hardy, 1954, pp. 122-142). Commentating in the introductory article of the collection, the celebrated [that is, Huxley] also addressed Hardy’s

essay. At first, Huxley repeated his entire thoughts on the genetic control of individual development and the role of these processes in the appearance of new traits and their disappearance. But the essence of the matter was also the genetic basis of neoteny. Noting further that pedomorphosis played a significant role in our own evolution, Huxley stressed that “one could never explain all types of traits, which we possess, as an escape from anthropoid specialization” (Huxley, 1954, p. 20). With the utmost breadth (unlike in earlier times) he evaluated the possibility of pedomorphosis and its role in the escape from specialization or the processes of de-specialization. Huxley wrote: “The possibility to escape the blind alleys of specialization and enter a new period of plasticity and adaptive radiation brings the idea of pedomorphosis to the highest level of applicability to evolutionary theory. Both possibilities and their limitations require the most attentive investigations” (Ibid.) Huxley outlined the ideas of Garstang and de Beer in the most general sense, independent of the applicability to the size of taxa and level of its advancement. At the same time, he articulated the problem of the origin of man and “human” traits. Of course, in the introductory article to the celebratory collection, Huxley did not mention, as he had in 1942, the speculative nature of the idea of pedomorphosis and the special role of ontogenetic processes in the origin of man. And by and large, it was these issues that Huxley discussed in the collection, clarifying his “light” position in regard to the idea of pedomorphosis in the form developed by de Beer and presented by Hardy.

In the concluding chapter of *Evolution in Action*, Huxley strove to show the objective value of the idea of unlimited progress. At its center was the development of biological evolution into psycho-social evolution. Huxley wrote: “Psycho-social evolution is the short human history, which acts through cultural-social transmissions from one generation to the next, and its units are societies, which are based on various types of culture. I am not an anthropologist or sociologist, and the reader can not expect from me a definition of such ideas as *culture* and *society*. I am a biologist, and see human history as a recent and very special outgrowth of biological evolution” (Huxley, 1953, pp.141-142).

Huxley set the task of applying the principles of biological evolution to evolution, which he labeled the human phase. Genetic inheritance, he suggested, lies at the foundation of all evolution, and cultural transmission appears as the analogue to the genetic transmission of traits. In other words, the entire arsenal of genetics and evolution should be used in characterizing human development. In general, the appearance of this theme is connected with Huxley’s participation in the creation of UNESCO. In part this, perhaps, is so, although he had already vigorously developed his evolutionary social ideas in the 1920s. Also the roots lie even deeper. Primarily, at stake was the special British style of theorizing in the field of global problems, which ascended to natural theology and to the topic, which in Great Britain received the moniker “problems of mankind.”

Huxley’s position was that all the main achievements of mankind in every sphere were directly related to the development of scientific knowledge. Science is the steady enemy of political absolutism. The concept of biological evolution leads to the primacy of human personality over everything else. As Ghiselin (1971) later wrote, individualism stands at the core of the Darwinian revolution. Although theologians, sociologists and anthropologists did not write about this question, this remains a hard fact of biological evolution.

However, from the principle that biological evolution always leads to the realization of new possibilities, and from the principle of individuality, a new trend arises through which significantly greater possibilities develop—the integration or cooperation of free personalities. The interaction of individuality and sociality at different levels leads to “the achievement of

internal harmony and the formation of personality, and this is as important as the development of self-regulating machines in the evolution of the animal body” (Huxley, 1953, p. 153).

From these principles, Huxley introduced a moral that made the connections between people, God and society.

The most unique achievement in the human phase of evolution, however, emerged from the achievements of biological evolution—from the appearance of conceptual thought, without which no scientific method could arise. Huxley persistently repeated these ideas. He noted that the scientific method in physics and chemistry bore great fruit. Scientists, however, for some reason had been “cautious” too long in applying the scientific method to the study of man. The development of sociology and ethology clearly showed Huxley the intrinsic mistakenness or even perniciousness of absolutism. In the West, it was generally considered that political absolutism—totalitarian government—is a poor legacy. Huxley with the utmost precision in several sentences characterized totalitarianism, and as the most conclusive model of the totalitarian organization of state life looked to Nazi Germany and life in the Soviet Union over the last twenty years. He connected Lysenkoism itself with the state organization of the U.S.S.R.

He always worried about the global demographic problems. He wrote: “A useful approach in the direction of contemporary demography was developed by the Royal Commission on Populations and the *English Church* [author’s emphasis]. Here he spoke out critically against all religion confessions that do not understand the threats, and which stand before mankind as a whole.

Huxley developed the concern for people’s welfare and fate into a scientific human ideology, which he called the newest religion—the religion of *Evolutionary Humanism*. He wrote: “The word ‘religion’ is often used in a limited way, only as belief in gods; but I use it not in that sense. I do not want to see a person with a highly raised head in the position of God, as has happened with many people in the past and still occurs to our day. I use evolutionary humanism in broad sense, with the goal of designating the relationship between a person and his fate, including his deepest feelings. Personally, evolutionary humanism is the germ of a new religion, not necessarily connected with existing beliefs. The main sense of the idea is to use scientific methodology to discover man’s possibilities, which should be mobilized for the realization of noble goals” (Huxley, 1953, p. 158).

Tightly connected with Huxley’s concepts of humanism were his ideas of genetics. In *Evolution in Action*, he noted that the most difficult problem was the absence of proof for the improvement of genetics since the time of cavemen. While not naming Müller, Huxley literally outlined his concept of genetic load. He wrote: “Actually, more probable in all, is that man’s genetic nature has degenerated and still continues to change in that direction. Here we are speaking of the accumulation of numerous harmful mutations, and this makes many problems for the human species on the whole.”

There are persuasive facts of another type. Contemporary industrial civilization favors a decrease in the number of genes related to intelligence. This is easy to see in the example of Communist Russia and the majority of capitalist countries, where people with high intellectual potential on average have fewer children than people with low intellect. These differences are genetically predetermined. But the weak differences grow in speed and can have large effects. If this process is continued the results will be extremely sad. Society should accumulate more and more intellectual people for accomplishing difficult intellectual work, and we should definitely reverse the above trend.

Eugenics should not simply stop the damage, however; it should help secure an improved future. The methods of artificial selection has given results in the plant and animal worlds, but difficulties arise when it is applied to man, primarily with the evolutionary biological order. One must think simultaneously in several directions. The main thing is that the human species does not disintegrate into separate specialized lines—all of his genes form a single freely-mixing pool, and man cannot escape from that genetic continuity. But this does not prevent the possibility of genetic improvement. Eugenics does not have to be a tool of some kind of State or similar Authority with a high level of coercion. It ought to preserve the good, normal qualities of man and, naturally, remove from human populations undesirable qualities. The geneticist knows how to do this. This is a long-term project over a series of generations, and it is important to have a broad education in the area of eugenic ideas, since man is the carrier of all future evolution.

“Human history and fate is part of a large process. And this process has two natures: self-transformation and continuity, an understanding of which gives man hope to precisely clarify his unique place in the process of advancing into the future” (Huxley, 1953, pp. 160-161).

Thus, in *Evolution in Action*, Huxley simply and elegantly outlined the entire gamut of ideas which he had developed over his life. It is also important that in this work, he expressed himself simultaneously as a scientist and a popularizer of science. It is a pity that *Evolution in Action* was not translated into Russian since it might have played an extraordinarily important role in the propaganda of evolutionary theory and in the scholastic process at any level.

Huxley and Simpson: Evolutionary Progress and Social Consequences

In Simpson's classic 1944 book, *The Tempo and Mode of Evolution*, the problems of evolutionary progress are not discussed. But, as has already been mentioned, the lectures at Yale University required him to state broadly this complex problem. In his 1949 book, *The Meaning of Evolution*, which was published six years later after Huxley's well-known work, one of the concluding chapters is called “The Concept of Progress in Evolution” (Simpson, 1949, pp. 240-262). [Simpson's biographer, the historian Leo Laporte (2000), does not even mention his 1949 book.] The Foundation also required Simpson to discuss the problems of the relationships between science and religion. The entire third part of his book treats this theme: “Evolution, Humanity, and Ethics” (Ibid., pp. 280-337). According to the title, this part covers completely Huxley's interests.

Simpson played a great role in the founding of the synthetic theory of evolution, mobilizing to the maximum extent the paleontological resources. He actively and even sharply spoke out against vitalistic and finalistic interpretations of the fossil record. In the polemics with the paleontologists, Simpson considered his main project to be the establishment of “pure materialism.” He considered evolutionism as the objective basis for morals, and the origin of reason itself is able to solve all human difficulties. As a historian of science, he strove to accomplish the synthesis not only of ideas, but also people, uniting all the best of Darwin, Lamarck, the founders of genetics, and even of the Lamarckists, eliminating that which he considered scientific mistakes. In many ways, Simpson followed in Huxley's footsteps, since he discovered morals and the spiritual key for humanity in the “work” of the evolutionary process. If you compare the Simpson's foundational books, the 1949 publication was possibly for him the most difficult—in it he had to survey simultaneously the work of paleontological and religious academics, including also transcendentalism. But Simpson, following a sequence, strongly

insisted that science only deals with causal analysis of material phenomena, as it is presented in the synthetic theory of evolution.

As a true scientist, it was important for him to show that the fossil record does not provide evidence that the evolutionary process has a directed tendency, as had been claimed by his teachers, Cope and Osborn. Through the analysis of the directionality of evolution, however, Simpson came directly to the problem of progress. Although Simpson never mentions Huxley's name in his plan of critique, essentially his critique was quite different. Simpson did not accept Huxley's line of dominant types, which lead to humans, nor his criteria of progress, which were based on the independence in control over nature. Simpson wrote: "We do not see successive domination: bony fish, birds, mammals. All these three types are dominant at one and the same time. Taking the animal kingdom as a whole, it is completely clear that it is necessary to add insects, mollusks, and also the "lower" Protozoa as groups that are currently dominant. The most dominant are the insects, but, inarguably all these groups are completely dominant, since each is in a different sphere" (Simpson, 1949, pp. 246-247).

How would it be with the criteria of "the independence of control over nature?" Simpson suggested that numerous different natures would exist and there would not be an independence from nature on the whole. Therefore he surveyed the numerous different criteria that had been suggested by biologists and paleontologists: successive invasions, mixing inside an adaptive zone, improvement in adaptation, potential for future progress, increased complexity of structure, growth in general energy, growth in reaction to natural stimuli, etc. However, he suggested that not one of the enumerated criteria could form the basis for describing the evolutionary process as a whole. He wrote: "Evolution is not accompanied by progress, and progress itself is not a necessary characteristic for evolution. Progress takes place inside evolution, but it is not its essence. Besides a great tendency for the expansion of life, there is nothing more to say about evolution as *progress*. In the limits of the evolutionary history of life, there is no single type, but there exist many different sorts of progress. Each sort is not connected with one of the lines or even one of the central lines, but is connected in the process of evolution with branching lines, instead of being isolated from many other lines. These phenomena are entirely explained by the materialist theories of evolution. They are definitely incompatible with supernatural absolute principles, with the concept of a goal in evolution, or with the control of evolution by autonomous factors of vital principles, which are common to all forms of life" (Simpson, 1949, pp. 261-262).

The basic property of evolution, he suggested, is the entry into newly available niches, and the formation of new niches for occupation and evolution. Evolution is not distinguished but by blind "opportunism." It is interesting that not one of the criteria of 'progress' characterize evolution as a whole; nevertheless Simpson made not attempt to secure for man a place as the most progressive animal in the process of evolution. He wrote: "Among the many lines, which demonstrate progress, one line possesses the highest level of development—the line that leads to humans. Man is the result of an aimless and materialist process. He is not planned" (Ibid., pp. 343-344; see also p. 284).

Thus, Simpson reached the paradoxical conclusion that the evolutionary process that formed man is free from goals or any kind of progressive inheritable tendency, but man has goals and deserves to be viewed as the "most progressive product of evolution." Simpson even re-evaluated the diagnostic traits of man—reason, flexibility, individuality, and socialization. These were the traits that made man different from the other animals. But why did Simpson call these traits progressive? From a biological point of view, the revalued traits "grow and improve by the

perception of the environment, especially through integration, coordination, and flexibility to that perception. In other words, their growth allows the survival of the species. Speaking in the language of biology, survival is always better than extinction, but is it an adequate criterion for progress? Simpson added that progress should be defined “not simply as action, but as action in the direction from worse to better, from lower to higher or less complete to more complete” (Simpson, 1949, p. 241). It is not clear, however, how a biologist could define worse or better, higher or lower. It was not by chance that Provine (1992) expressed the analogous claims.

Finally, Simpson united progress with survival or the potential for survival. He was not able to answer that question, and paraphrasing Laplace’s words, declared that he did not need that hypothesis. But Simpson did not do so by evading the requirements of the lecture course, which he gave at Yale University. In such a situation, he actually followed the path of Huxley, who, by the way, also fell into a similar state. Using metaphorical language, Simpson suggested that the “vital substance” is able to create innovation and successive types of organizations, of the animal and man, is able to evolve a principally new type—through thought, and not reproduction. He agreed with Thomas Huxley that ethics could not arise from pre-human evolution. Simpson wrote: “The best human standard is always relative since it relates to that same person, and it has to be sought in new evolution, and not in the old, which is characteristic for all organisms. Old evolution, in essence, was amoral. New evolution includes knowledge, i.e. knowledge of good” (Simpson, 1949, pp. 310-311).

The essential characteristic for new evolution for Simpson and Huxley is “knowledge, its dissemination and inheritance.” Simpson wrote: “From evolutionary ethics comes the most important situation, that knowledge in its essence is good. Science is the most successful and systematic method for acquiring knowledge at the present time, which is really new in regards to man” (Simpson, 1949, p. 311). Here is the great concurrence of the debate between TH Huxley, Julian Huxley, and Simpson. TH Huxley, in the essay “On the Advisability of Improving Natural Knowledge,” wrote directly that science generates intellectual ethics. But Simpson recognized that scientific knowledge might be used for goals both evil and good. Science is the fundamental ethics of *responsibility*. To these words Simpson added that human responsibility is not ethics, but *fact*, a fundamental and specific trait of the human species, formed in the process of evolution and, obviously, having cosmic significance.

What is human responsibility and how did it arise? How could blind forces create beings with responsibility? What is this “new evolution,” where man is the “fundamental agent?” How can we recognize a being, which is the product of an unplanned and aimless evolution? Having asked such pointed questions, Simpson wrote: “The first basis lesson, which comes from evolution, is the unity of nature. One of the greatest achievements of early Christianity and several other religions were the recognition of the brotherhood of people. The intuitive conclusion of representatives of the different Christian branches and other teleologists only confirm the truth, established by evolutionary theory, that their doctrine—is simply scientific fact. Not only are all people brothers, but everything living is related in the most real materialistic sense; everything arose from one source and developed as one divergent process” (Simpson, 1949, p. 281).

Thus, although Simpson declared ethics the result of human evolution, like Huxley he locked everything into a common evolutionary process—the “fact,” on the basis of which were built and interpreted the ideals of the human spirit. But if man and animals come from common ancestors and they are all brothers, then the concepts of morals is justified, although in evolution

random mutations, struggle for existence, and the elimination of non-adapted individuals, races, and species also occur.

When you read Huxley and Simpson attentively on the problem of evolutionary progress and its social consequences, a sort of strange logic emerges. It seems as if in biological evolution they are searching for the objective foundations of the ideals of Western culture. An incomprehensible optimism overcame Huxley and Simpson on the question of the role of science in the life of society and the organization of the State. The ideas of the two scientists on man's place in the cosmos, and on global cosmic evolution with the advancement of human values were in complete agreement. Thus, Simpson wrote: "We must know more about ourselves, about our society, our life, and our earth and cosmos. We must better balance our knowledge in the fields of physics, biology, and the social sciences, so that the social sciences can become primary, and the physical sciences last. We must also recognize the special importance of the knowledge of organic and social evolution. Such knowledge significantly clarifies the picture of our place in the cosmos and key to controlling the future evolution of humanity" (Ibid., pp. 336-337). Here this all agrees with Huxley's views that man is both the guardian and manager of evolution. Simpson, analogously to Huxley, interpreted eugenics as the protection of the future progress of through the improvement of man's intellectual qualities. At that time, Simpson noted, scientists do not know how to make mutations, which are desired or necessary, but when this occurs, then "evolution will fall under the full control of man." Like Huxley, Simpson unreservedly believed in scientific knowledge and the inherent goodness of man. Man, Simpson suggested it "is definitely not the goal of evolution, since the latter, obviously, has no goal." But it is the "final most organized matter, which has appeared on the earth, and we have no grounds to suggest that there exists more highly organized matter in the cosmos."

Huxley and Simpson also held similar views on the problems of individuality, the organization of society and state. They suggested that individuality and common brotherhood are the best medicine against totalitarianism and any violence. These were principally new things, since Sedgwick, Bueckland, and Silliman in solving these human questions attempted to demonstrate the existence of God with all of his attributes (Greene, 1981)

In understanding the evolutionary process, Huxley introduced many new theoretical innovations and on that basis took an objective view of human evolution and social life. Like H. Spencer, Huxley succeeded in including in evolutionary science, cosmic, organic, and cultural evolution. This allowed Huxley to see human history in the light of the history of the cosmos as a whole. Simpson followed the same road. It is correct, as has already been shown, that he interpreted somewhat differently evolutionary progress and its criteria. Huxley's key understanding of "advancement," "improvement," "independence," and "control over nature" underwent Simpson's critique. Simpson for himself demonstrated and evaluated the evolutionary events, but his general views on the evolutionary origin and fate of man coincided with Huxley's conclusions. This is excellent evidence that in the framework of the evolutionary synthesis, an objective analysis of the evolutionary process had been completed, and that the applications for man that came from it also had an objective character.

The work of Huxley and Simpson was taken up and continued in the works of Dobzhansky, Rensh, Mayr, Haldane, Fisher, Wright and other scientists. There were also scientists who, although they belonged to the above-mentioned group, thought differently. Neither Huxley nor Simpson used Darwin's theory of natural selection as the main factor that has acted through human history. One of the leaders of evolutionary theory was the British cytologist and geneticist, Cyril Darlington, who wrote a 753-page book called *The Evolution of*

Man and Society (Darlington, 1971). He claimed that humanity cannot imagine how much natural selection provides in the progress of civilization. Acting on the brain, natural selection determines the general appearance of human society. The perfection of the human hands, which have manufactured weapons, occurred due to the constant pressure of selection on the brain. Building his evidence on Darwin's *The Origin of Species*, Darlington (1971, P. 25) wrote: "Each improvement to the brain directs the work of the hands, which make weapons, making the way for their use; all of this ultimately serves to improve the individual. The differences in these improvements even today are secured selectively. These lines undergo hybridization, which leads to the formation of heterozygotes with even more varied genetic combinations and growth of different abilities"

The effects of mutations, hybridization, and natural selection of the most active form have occurred in the Near and Middle-(?)Far East, according to Darlington, forming the best human qualities. If hunting and gathering limited the hybridization and genetic recombination of people on the periphery of the earth, then they have limited also their inventiveness and natural gifts. The "new man" of Europe and Asia, Darlington suggested, steadily disseminated across the entire earth, because his abilities in the process of using weapons grew in the most varied ways. The general result was the advancement in the intellectual improvement of humanity during a prolonged selective process. All these innovations, he noted, promoted the survival and growth in population of the "new man." The result was entirely clear—"a step forward in the prolonged selection process of the intellectual improvement of humanity." With the intellectual improvement arose art, magic, religion, and myths. In the third millennium before the birth of Christ, different processes of hybridization occurred between the Judaic people and the Phoenicians, forming the hybrid spirituality of the Jews. The highly talented Jewish priests devoted their intellectual forces to "successful study of social behavior, its biological basis and consequences." Darlington (1971, p.178) wrote: "The religion they brought forth was the main method of survival because the religion kept the people together. The clergy considered the history of the people and the religion to be the main instruments, which should be used in their important works". In addition, these scientist socio-priests, Darlington thought, were the Judaic prophets "people, genetically rejecting the nature in which they lived, and constructing a new nature." Their prophetic intolerance, literally the dramatic polarity "between the transient interests of the political State and individual belief, social integration." simultaneously embodied a practical politics, and also a deep spiritual doctrine. The prophets claimed that achievements of the Jews were the result of the genetic differences among the settlers of Israel—the differences being connected with their form of life." He (Ibid., p.190) wrote: "Each conflict between the tribes caused the selection and differential reproduction of one line, or tribe, and the extinction of the others. In the language of the prophets this is the process of *winnowing*, a process, which they and their people well understood. The first were Isaiah and Ezekiel, who precisely formulated the doctrine of the "survival of remnants." This is the doctrine, which is similar to the biological principle of the survival of the fittest."

Thus, the Jewish religious literature, for Darlington, is one of the highest points of human achievement—and was itself the result of genetic variations. He noted that Huxley Senior, in discussing the problem of the origin of ethics, constantly returned to the ancient religious literature of the Jews. But such constant departures into history, with the articulation of the genetic aspects, according to Darlington, was not originally from TH Huxley or Julian Huxley. The first was undoubtedly Darwin. It was Darwin who showed that "man can and should be studied as an animal, using all scientific methods, which could be applied to any other animal.

This means that the physical, social, and racial traits, in illnesses and speech, in behavior and beliefs man should become the subject of experimental investigation; and in all these aspects of evolution, man underwent the principles of natural selection in all their specialized forms—sexual selection, artificial selection, and unconscious selection” (Darlington, 1971, p. 671). It is interesting that Darlington interpreted history as the result of the change in social systems, which regulate inbreeding and free-crosses. As a geneticist, he analyzed the merit and weakness of various forms of breeding. For example, he showed that free-crossing formed not only creative individuals, who strongly influenced their times, but also produced people with criminal intent.

It seems completely absurd to reduce everything to a biological interpretation of history. Moreover, without the genetic component which the prophets knew well, it would be difficult to understand historical progress, achievements, and improvement of the human intellect.

Huxley, Simpson, and Darlington suggested the complementary concepts of evolutionary progress and of human evolution. Their concepts of the evolutionary synthesis arose in the framework of the so-called organismic biology. From them came the views, which were based on the achievements of molecular biology. Perhaps, the broadest synthesis, which was based on the achievements of evolutionary biology, was the new “social physics” and theory of general systems, suggested by Takhtajan. His book (2001) is the direct application of the theoretical generalizations to contemporary social life, connected with the fall of totalitarian, imperial States and with the rise of many ethnic wars. And he has indicated a road by which man might travel in this difficult situation.

In Search of New Principles of Evolutionary Theory: Stasigenesis, Grades, and Clades

The public perception of Huxley’s evolutionary synthesis

After 1949, Huxley and Simpson had a similar interpretation of the consequences of evolutionary progress. However, they still differed in regards to other key problems of evolution. The correspondence between Huxley and Simpson was the subject of an investigation by the historian of science, Swetlitz. In these letters, he noticed interesting moments, which “slipped away” in a reading of their basic works (Swetlitz, 1995). After the publication of his *Evolution: The Modern Synthesis*, Huxley underwent sharp criticism by his colleagues on the problem of evolutionary progress. They criticized him for his dogmatic perception of Cope’s Law and for his views on biological specialization. Simpson, who had interpreted the horse family, also actively engaged the discussion on that key evolutionary paleontological problem. .

Huxley and Simpson first met in London in 1927, when Simpson was investigating fossil mammals in the British Museum of Natural History (Simpson, 1978, p. 112). Subsequently, they periodically corresponded until 1950 when they began to communicate with one another steadily. It is interesting that in the first letter, Huxley was sorry for Simpson for the many zoologists who did not agree with his views on the future of progressive evolution, which was limited by man, although such an ending was “entirely obvious” (Swetlitz, 1995, p. 203). Huxley clearly expected Simpson’s support, in spite of the fact that Huxley had already read Simpson’s *The Meaning of Evolution*, and was familiar with his views on evolutionary progress. Simpson simultaneously took a shot at Broom and Huxley. His thought that organic life and nature were always in a condition of fluctuation and would never reach a steady equilibrium; however, ignoring man, it was impossible to predict what new kinds of life might appear. Simpson

suggested a thought experiment during the reign of the dinosaurs. He wrote: "Evolution possesses all possibilities, and all existing forms were specialized, and at the same time there arose a new important adaptive radiation" (Simpson, 1949, p. 326). Simpson, like Mayr and Yang, conducted a sharp critique of Cope's principle of non-specialization. His critique of Cope's views in the 1940s simply was popular. Mayr, Simpson, Amadon, and Romer put forward a cascade of arguments claiming that specialization would not lead to the origin of the higher taxa. Also the terms "specialization" and "non-specialization" themselves by nature have two meanings and are usually applied after confirming a fact in the light of an understanding of the historical fate of organisms or lines (Mayr, 1947; Simpson, 1948; Romer, 1946). The embryological arguments, however, promoted by de Beer, were absent from the work of paleontologists and systematists. Huxley found unexpected support of from the German morphologist and behaviorist, Rensh, in evaluating Cope's Law. Rensh proved that "any taxon steadily loses its evolutionary intensity" (Rensh, 1948, pp. 111, 127, 289, 309).

In September 1950, Huxley at the invitation of the Genetics Society of the United States visited New York, where he met Simpson. During their two long conversations they did not vacillate, however, they sharply changed a subsequent topic, which they discussed in their letters and published writings. At the core of the shared interests of these two evolutionists was the problem of the stabilization of morphological variation. As a paleontologist, Simpson ideas were extraordinarily useful to Huxley in his later work on fossil materials, in order to develop new ideas in evolutionary theory. Huxley wrote a letter to Simpson about the end of evolution in which he asked him to conduct an experiment on fossil reptiles, birds, and mammals.

In the letters, Simpson openly wrote about his skepticism of Huxley's views on large evolution. However, in attempting to support his colleague he noted: "There exists strong evidence that physical, structural, and functional differences become less and less radical" (Swetlitz, 1995, p. 205). Simpson returned to an analysis of the origin and disappearance of higher taxa, which, in his words, "interestingly and clearly" illustrate the phenomenon. He suggested a series of systematic conclusions regarding phyla, classes, and orders of vertebrates, noting that contemporary evolutionary variations produce only new families of mammals. Simpson could have completely supported Huxley, but he claimed that, although in recent times only one evolutionary novelty arose (man) evolution had not lost its possibilities. Further, Simpson made a frontal attack, trying to estimate the height of morphological stabilization inside order and families of mammals. For each order and family, he selected a period of appearance, a period, as he thought, of the stabilization of the morphology and, finally, a period of the extinction of the taxon. Simpson was convinced that morphological variations in the majority of taxa finally became stabilized. He did not think, however, that all would be stabilized to such an extent that the further progression of evolution would become impossible. But collecting detailed evidence, Simpson wrote: "*Marsupialia*, *Insectivora*, *Primates*, *Rodentia*, *Carnivora*, and *Artiodactyla* each contain groups that are more evolutionary progressive or completely able to progress, if the environment allows it" These most interesting thoughts from a letter to Huxley were used in a manuscript entitled, "*The Total Tendency of Evolution*" (Ibid., see also p. 206). Thus, for Simpson, the stabilization of morphology during a prolonged geological period does not have an absolute character. He suggested that several groups began to change after an extended period of stabilization. For example, fish were a highly stabilized group but demonstrated a great progressive evolution in the Mesozoic. In the well-known 1953 book, *The Major Features Evolution*, he outlined his explanation of stabilization. More precisely, he wrote about the "adaptive" or "ecological" limits, which are formed by the equilibrium between the

organism and environment, i.e. by an equilibrium that can be destroyed by extinctions or other changes in the conditions of life. He also suggested that stabilization sometimes follows from “inherited” or “mechanistic” limits, such as the reduction of toes in the evolution of horses (Simpson, 1953, pp. 255-258).

From Simpson, Huxley received valuable information on the fossil record, and even so his faith in the end of large evolution did not waver. He began intensive consultations with many paleontologists and morphologists on the problem of morphological stabilization in evolution. The majority of experts, however, including Simpson and Westoll, were extremely wary, citing the fact that it would take so much time and effort, and that it was an unrealistic question (Clark, 1968). Without such doubts, at the beginning of the 1950s, Huxley was in a state of active creative rush, but the opinions of the experts had their effect—the problem of stabilization practically was untouched in *Evolution in Action*. At the same time, Huxley presented the standard evidence on the finale of large evolution—he remained firm on this question. It is correct, that one piece of evidence was completely new and obtained from a field in which Huxley did not work.

The Evolution of Horses

There was a vast literature on this topic, and the historian of the Huxley family, R Clark, noted that Huxley followed it closely (Gould, 1983). Gould wrote that beginning in the 1870s, the material on the evolution of horses was constantly cited in scientific literature. Clark studied Huxley’s 1951 lecture, in which he declared that the evolution of horses (*Equidae*) is direct evidence that the evolution of all higher taxa, although including in it partial improvement, in reality comes to an end. The evolution of horses illustrates that evolution on the whole—it is a final process in which each evolutionary line, excluding the line that leads to man, automatically comes to an end (Huxley, 1953, p.26). He dredged up his fundamental data from Simpson’s manuscript, “Horses,” which was published in 1951 (Simpson, 1951). In *Evolution in Action*, Huxley used a diagram of the morphological variations for five traits: size, molarization, direction of teeth, weight of (teeth), and leg mechanism. He further described how each trait steadily evolved to the point where the speed of change approached zero; the trait then remained stable until the time when the group began to die off (Huxley, 1953, pp. 55-62).

In *Major Features of Evolution*, Simpson presented his diagram, on the basis of which he analyzed the same traits on the scale of millimeters, but for different trajectory (Simpson, 1953, Pp. 262-265). Nowhere did Simpson indicate that his diagram was a response to Huxley’s diagram; however, the time of its creation and its structure allows this to be proved. For a series of positions, the diagrams “struck at one another,” especially regarding body size. Huxley was closer to an orthogenetic interpretation, when Simpson suggested a branching, indicating that a growth in size fluctuates and never reaches a stable maximum, the size of which has grown smaller since the end of the Pleistocene. Grouping all the trends in the change of teeth together, Simpson insisted on their “agreement,” i.e. that the evolution of traits in horses demonstrates three (in any case, not one) of the different paths, and he actively maintained this position throughout the 1950s. In opposition to Simpson, Huxley constructed one path for all traits—gradual change leads to a stabilized limit. It is completely clear that the diagram with the picture of the evolution of horses was necessary for Huxley to demonstrate concretely the most important idea of the striving of evolution to a limit.

The end of evolution and stasigenensis

So Huxley himself retained the idea of a finale of big evolution. Support came suddenly. In the book, *The Phenomenon of Man*, Teilhard de Chardin declared that evolution, with the exclusion of man, has ended. The interpretation of the limitation of evolutionary specialization itself, apparently, could lead to the idea of a biological finale. In the introduction to the English edition of de Chardin's book, Huxley did not mention his own agreement with such a key question, but then noted that progress leads to the triumph of reason of matter without the help of final causes (Huxley, 1959, pp. 18-28). The most varied sources are evidence that during the 1950s and early 1960s, Huxley steadily continued to claim that evolution on a large scale came to an end and only man has the ability for further progressive evolution (Huxley, 1957a; 1957b; 1958a; 1962a; 1964). Thus, in *New Bottles for Old Wine*, he noted that humanity has become "directed by the director of the entire evolutionary business" (Huxley, 1957b, p. 13). As has already been noted, Huxley began to change his view on De Beer's concept of pedomorphosis in 1954. But in 1958 he received a letter from Mayr, which acted as a "blow." Mayr had shown that Huxley's ideas on new evolutionary lines always coming from relatively unspecialized lines were "not always correct." For example, groups of reptiles, from which came the mammals and birds, were highly specialized lines in comparison with other contemporary reptiles. In response, Mayr received an invitation to organize a conference on the problem of stabilization in evolution. Mayr's ideas on the formation of epistatic interacting genotypes, which were resistant to the pressure of the resultant evolutionary changes in selection, were independently developed by Lerner and Mather. These ideas were close to Huxley's views, since they stressed the role of stabilizing processes in evolution at the species level, unlike Simpson's ideas, which divided the stability of forms at the family level the higher taxa.

After becoming familiar with the publications of the aforementioned scientists and the correspondence of Simpson and Mayr, Huxley decided to put forward the thesis that in the evolutionary process there is broad stability at each taxonomic level. He published an article in *Nature* during 1957 in which he introduced the term "stasigenesis," by which he meant the evolutionary processes that lead to "stabilization and the persistence of types and patterns of organization from the species to phyla" (Huxley, 1957a, pp. 1653-1654).

By the middle of the 1950s, many scientists supported Simpson's terms "phyletic evolution" and "splitting" (Simpson, 1953, pp. 384-385). Rensh's terms, "cladogenesis" (the formation of clades, i.e. branches) and anagenesis (formations that move apart or up) were also widely dispersed in the literature. Rensh indicated that the main character of anagenesis is growth in complexity—it is an objective criterion (Rensh, 1959, from the German edition, 1954, Chapter 7).

In the 1957 article, Huxley entirely approved of Rensh's concept of cladogenesis, but significantly broadened his concept of anagenesis, including all level of improvement, from detailed adaptation to general organizational advancements [Rensh had limited anagenesis to only the main advancements]. Afterwards, Huxley claimed that a third process acts in evolution, which is almost completely ignored by evolutionists, even though there is a common phenomenon—the process of *stasigenesis*.

Finally, the process of the stabilization of forms and the path of evolution, on which Huxley worked for many years, received a clear formulation as a theoretical construction. The main cause of stabilization for him was natural selection. A short definition of the phenomenon seems to be: *when the environment remains relatively steady for an extended period, the organisms already well adapted to it will remain unchanged through the action of natural selection, which cuts off all variations from the norm.* The well-known cases of "living fossils"

are “preserved” due to stasigenesis. Persistence is a significant phenomenon in evolution, with small changes of *groups* of organisms on taxonomic levels. Such a prolonged persistence of groups, for Huxley, are evolutionarily successful groups, and their success depends on the maintenance of an integrated plan of organization, variations, which do not depart from the plan of organization, and all this together is maintained by stasigenesis.

For a convincing example, Huxley cited the cases from his book on ants, which belong to most highly organized and most successful group of insects (Huxley, 1930c). He also mentioned the well-known case of adapted radiation - Huxley preferred the term “deployment” - of groups with a high level of improvement, or anagenesis, but in these cases the group becomes progressively limited. A good example is the evolution of birds, which achieved a high evolutionary advantage 20 million years ago, but then there appeared a powerful evolutionary conservatism. Tracheal respiration was a huge problem in insects which limited size, as well as the development of intellectual ability.

Further, Huxley introduced a definition of anagenesis and cladogenesis. Anagenesis is the achievement of a general organization or the improvement of a general function. This term relates to all kinds of biological improvements, from detailed adaptations to a general organizational achievement. Cladogenesis is the branching phyletic lines from subspecies through adaptive radiation to divergence of phyla and kingdoms. It is important that in defining anagenesis and stasigenesis, Huxley accentuated the action of natural selection, and in analyzing the branching of phyletic lines he noted especially the interaction of natural selection, isolation, and genetic drift. It is apparent that he tightly connected branching to the processes of speciation. Exactly as Simpson had done, he introduced the idea of species into paleontology.

The Huxley used the terminology to characterize grades. He noted that the majority of taxa are recognized as grades, and as clades. The principle criterion of the limit of a grade, however, would be its stasigenetic persistence (here Huxley united his terminology with that of Thomas Huxley).

The *Nature* publication was marked by maximum brevity in presenting the material. Huxley, however, was extremely interested in developing the new terminology, injecting it into the scientific community. And he planned a conference on stasigenesis. In the beginning of 1958, he consulted with Mayr, Simpson, and Waddington, and later with Rensh and Lerner. The Royal Society of London should have been the sponsor of the conference on stabilization in evolution. Many of the invited participants of the conference received the offer positively, but the author of genetic assimilation and canalized selection, Waddington, wanted to extend the theme of the conference to discuss the problem of reverse cybernetic connections in the system. In his opinion, it was necessary to clarify the phenotypic stability, which creates epigenetic canalization. Inarguably, his discourse far anticipated the time with its originality and broad approach. Huxley, however, was completely unprepared for the idea of this “unit” thinker and was categorically opposed to the topic he suggested. There were participants of the planning committee who, in general, doubted the reality of the problem of the universal action of stabilization in the process of large evolution (Swetlitz, 1995, p. 214). Finally, despite Huxley’s incredible organizing skills, the conference never occurred.

Only in the 1970s did the problem of stabilization in evolution become widely discussed by paleontologists, geneticists, and embryologists. But one should not forget that stasis was an important component of Huxley’s biology and he developed the idea of stasigenesis in connection with the ideas of evolutionary progress. Therefore investigators who have analyzed the ideas of progress and stasigenesis should be discussed together. And still Huxley’s concept of

stasigenesis can hardly be interpreted as the most likely cause of punctualism. At the center of attention of broken equilibrium was the claim that stasis is “the usual fate of the majority of species, and this was not predicted by Darwinism” (Gould, 1983, p. 137). At the same time as Huxley and the participants of the discussion looked at stasis as a typical phenomenon, which encompassed all taxonomic levels. This last approach was characteristic of Huxley’s evolutionism.

Grades and clades: evolutionary macro-systematics

Despite all the difficulties that tested Huxley in organizing the conference on stabilization, he persisted in developing his concepts. In 1957, a symposium in Uppsala was dedicated to the 250th birthday of Carl Linné (Linnaeus). For Huxley it was especially important to invite Rensh to the symposium for his work on anagenesis and cladogenesis. The theme of the symposium was broad—the general problems of systematics. Huxley presented a report that in general can be called “Evolutionary Processes and Taxonomy” (Huxley, 1958a). On many points, this report is an extension of his 1957 *Nature* article. Therefore, one can think of them as complementary.

It is helpful to consider fully Huxley’s Uppsala report, since its fundamental ideas were later widely discussed and entered evolutionary theory and the classification of taxa, which are the primary adversaries of Henning’s so-called phylogenetic system. Leading biologist-evolutionists in the most varies aspects showed that the Rensh-Huxley approach best of all provides a basis for super-species classification in correspondence with the course of the evolutionary process (Dobzhansky, Ayala, Stebbins and Valentine, 1977; Severtsov, 1987; Tatarinov, 1984; 1987; Takhtajan, 1991; Vorontsov, 1999). One should not forget that the basic ideas of the concept of progress were worked out by AN Severtsov. But it had already been accepted that many of his developments are “ascribed” to Rensh. Through Rensh’s terminology, Severtsov’s ideas entered the world literature.

Returning to Huxley’s Uppsala report, he began with definitions of the three main types of the evolutionary process: improvement, diversification, and persistence. He noted that all three types were distinguished by Darwin, but the concept of persistence in a final form appeared in 1862 on TH Huxley’s suggestion. Here Julian Huxley touched on the concept of orthogenesis and, of course, the examples of the parallel growth of horns in various lines of mammals. With vacillating, he took a strict Darwinian position. Natural selection, which acts on the growth of body size, automatically leads to the growth of horns. Huxley again repeated that all these allometric consequences are the result of correlative variation for Darwin. Since there was a large literature on the problem of recapitulation, Huxley suggested that one should verify literally all ideas in the light of the achievements of genetics and developmental biology.

Meanwhile, Huxley took up this topic and studied the problems of classification. He began with a critique of phyletic classification. He argued that phyletic groups do not explain their own evolutionary trends; subsequently there are no recognized stages within similar groups through which they pass in geological time. Huxley wrote: “Purely phylogenetic systems produce cladogenesis, but ignore anagenesis. In order to explain both processes we need a system of two dimensions. One network of the dimensions should explain anagenetic advancement, and the other network—the cladogenetic divergence of monophyletic units” (Huxley, 1958a, p.26). It is impossible to state it more clearly and precisely. This most important theoretical conclusion, or thesis, Huxley used widely in solving the problem of classifying vertebrates (Dobzhansky, 1977).

Huxley drew heavily on Rensh's concept of anagenesis, raising the value of the ideas of improvement and progress. Animals are classified in *clades*, that is, on the basis of morphological divergence. However, this is insufficient. They are also dispersed in *grades*, on the basis of the extent of biological improvement, and this is the same kind of fact as the reality of morphological divergence.

A particular improvement is the formation of a detailed adaptation to a limited niche; specialization is adaptation to particular form of life, the growth of the effectiveness of a given structure and function, the greater differentiation of functions, the improvement of the structural and physiological plan (general organization) — the fundamental collection of significant biological improvements. Huxley suggested that this is how to put together a precise description of a hierarchical evolutionary system. But it is not strange that in defining the evolutionary progress, he used the term “advance.” The reason may be that he demonstrated progress in a diagram that depicted phylogenesis from *Cyclostomata* to humans, i.e. the general path of progress in the evolution of vertebrates. He defined progress in terms of “advances” and at the same time in the framework of the ideas of the evolutionary finale. But it is also important that in the 1957 article, where Huxley considered the diagram and came to a definition of unlimited progress, he used the term “improvement.” He suggested that the final step of progress almost entirely was connected with improvements in the brain and its abilities.

Huxley sought examples for the direct application of the idea of progress to classification. He chose the example of human classification, since he had no doubts of the progressive character of evolution in this direction. He conducted an analysis in the frameworks of a double classification system. In terms of the phylogenetic classifications, hominids were “simply one phylogenetic clade” (the hominid family), which was higher than primates and anthropoids. Anagenetically they are classified as different clades, and he described *Psychozoa* as a radically new and successfully dominate group, which had evolved quickly by the method of cultural transformation. In his words, the hominids were so successful and unique that they should be equivalent to the entire animal kingdom. At the Uppsala symposium, he noted that: “they make up an entirely new Sector of the evolutionary process, which is called the psychosocial” (Huxley, 1958a, p. 36).

The concept of grades for the English evolutionary biologist really was quite important, since it introduced into the practice of classification the idea of his entire life—the idea of evolutionary progress. Huxley wrote: “Taxonomy will build its systems simultaneously in two directions, and classification itself will be founded on the facts of biological improvement and persistence, and also on phylogenetic divergence. A similar system should recognize that many taxa simultaneously are clades and grades. To solve the new problems, new terminology will probably be needed” (Huxley, 1957a, p. 455).

At the Uppsala symposium, Huxley and Rensh had a short discussion; judging by its content, Mayr also took part in it. Rensh asked Huxley to explain more thoroughly the problem of persistence and its connection with the problem of classification, especially anagenetic individuals and clades. Huxley noted: “I consider stasigenetic persistence as a fact, which mainly depends on Mayr's observation: a new successful species (or another taxon) will always possess an integrated genetic and phylogenetic plan, well coordinated inside and out. Such an architectonic demonstrates evolutionary homeostasis. A persistent taxon of any size depends on the evolution of adaptive organizational plans to an adaptive zone of varied breadth. Here is why the majority of taxa at one and the same time are both phylogenetic groups and anagenetic grades” (Huxley, 1958a, p. 38).

The concept of grades and clades entered into contemporary evolutionary theory, and was widely used to explain super-species evolution, ranging, and the weighing of taxa (Ayala and Valentine, 1979, p. 266). The main trait of grades is the origin of descendants, with new traits in comparison to their ancestors. The evolution from one grade to the next requires pure evolutionary progress. Reptiles are cold-blooded, mammals evolved from reptiles and became warm-blooded; they developed new functional abilities that reached new levels. Birds are also advanced to the warm-blooded grade, but completely independently from mammals, although they had a cold-blooded ancestor. Therefore a grade can be polyphyletic and have different ancestors.

In contrast to grades, a clade is a unitary branch of the tree of life and, subsequently, should be monophyletic; it can have many branches as a result of cladogenetic phenomena. All the members of a clade, however, should have a founder, i.e. a common ancestor. Such an approach to classification today reflects the evolutionary history of all genera, families, orders, classes, and phyla, which are represented by clades (Ayala and Valentine, 1979, p. 256). In the 1970s-1990s, the role of regulatory and structural genes in the origin of the higher taxa and new types of organization were widely discussed (Gould, 1977). The formation of new grades is connected with the higher activity of regulatory genes, and the origin of clades is connected with the less active role of the last part of the genome. Eldredge (1985, pp. 101-103) discussed the problem of grades and clades in a broad evolutionary context, drawing entirely on Huxley's ideas.

On Huxley's concept of evolutionary progress it can be argued, even though it is self-sufficient, that thanks to the formation of the conceptual apparatus of evolutionary systematics, the concept in almost a "pure" form entered into contemporary systematics and evolutionary theory. Contemporary evolutionary systematists offers the possibility to simply evaluate the significance of the concept of progress—an achievement not only for Huxley, but also other great evolutionary biologists.

Progressive evolutionism was expressed also in Huxley's views on eugenics, ethics, and evolutionary humanism.

Eugenics in an Evolutionary Perspective

Factors influencing Huxley's eugenic position

In 1936, at the Galton Lecture, Huxley claimed that the most complete application of evolutionary biology is found in eugenics, which unavoidably is becoming part of the religion of future—scientific, or evolutionary, humanism. In 1962, at the end of the second Galton Lecture, Huxley declared that best role of man is the directing the evolutionary processes on the planet, to the most complete realization of genetic possibilities.

To speak of eugenics in 1962 was blasphemy. Even more morbid was the memory of the experience of the German Nazi race hygiene. Authoritarian regimes flourished. The entire civilized world was frightened of the word "eugenics." It was not by accident that the American Eugenics Society in 1972 changed its name to the Society for the Study of Social Biology. The London Eugenics Society miraculously preserved its name, but its meetings were conducted at an extremely low level, and the journal, *Eugenics Review*, published weak works (Hubback, 1989).

As has been shown above, Huxley was an extremely broad-minded scientist, for whom there existed no border between sciences, even between the natural and humanitarian areas of activity. This broadness of interests and views defined his approach to eugenics. He was able to ask and answer eugenics problems simply, clearly, and in a form accessible to mass audiences. Among popularizers of science, he undoubtedly was number one.

The well-known historian, Allen, has shown that Huxley's interest in eugenics began in the 1930s-1940s. The greatest inspiration was the ideas of his grandfather, TH Huxley, who saw all phenomena in an evolutionary light. Therefore, Allen claims, evolutionary theory and the popular ideas that emanated from it can be considered the first and most important factor to influence Julian Huxley's position on eugenics (Allen, 1992).

The second factor, according to Allen, was Julian Huxley's striving to overcome the idea that eugenics is unavoidably connected with Nazism, and a desire to find a more scientific and more balanced approach to eugenic ideals.

The third factor, which influenced Huxley's position on eugenics, was related to changes in the social and economic environment. As a young scientist, Huxley entered the scientific and social scene before and especially after the first World War. This was a period of the collapse of the free market economy. In intellectual and governmental circles, there occurred a complete ferment of ideas. Huxley was steadily interested in the experiments on planned economics, which were occurring in the Soviet Union. The socialist ideas suggest that depression occurs from the great and long-term actively planned and realized social and economic control of organizations, and that free economics leads to worsening quality of man and only scientific planning can direct the process, and also that the birth-rate does not have to be random and uncontrolled.

The fourth factor, which, according to Allen, influenced Huxley's eugenics position, was the philosophy of scientific humanism, which later had become the philosophy of evolutionary humanism. From these positions, the practice of eugenics should have been formulated by the uniqueness of man. One might even say that Huxley's eugenics followed from the ideas of evolutionary progress and evolutionary humanism. Mendelian genetics, which was applied to personality and intelligence, was an erroneous science. All that is unique in man is not his genetics. It is correct that man, like other animals, is subject to Mendel's laws, but the existence of reason gives him two different, but equally strong forms of inheritance: the biological and cultural. The problem of eugenics is to understand the interaction of these two forms of inheritance, but neither one of them is the primary determinant of the conditions of man. A further aspect of evolutionary humanism was the negation of traditional religion as a source for ethics, human values, or the control of social politics. Man has the key to evolution in his own hands (Huxley wrote about this as early as 1942). The hands of man can be applied to rational and scientific methods, or not be used by them. But to ignore *science* leads to the degeneration of the classes, nations, to the rise of conflicts, from which extinction will follow.

The fifth factor that led to Huxley's eugenic position was the overcoming of the prejudices of the old eugenicists. Huxley for a long time was friends with JBS Haldane - a member of the Communist party in Great Britain - and Needham and Müller, who were supporters of radical social reforms, after which should follow eugenic investigations and measures. They all suggested that effective social reforms can (must?) lead to effective eugenic measures. Huxley completely discarded such views in the 1930s due to real dangers of eugenic measures, about which much propaganda emerged from Fascist Germany.

And finally, in any eugenics thought there is a difficult psychological dichotomy between the past and present, inheritance and nature, ancestors and descendants. From Allen's deep analysis of these factors, however, something important has emerged. In 1913, Huxley worked at Rice University together with the well-known geneticist Müller, who at the very beginning of his career thought about the relationship between genetics and evolutionary theory. In the future, Müller studied human genetics and in 1950 formulated the concept of genetic load. The concept was called "Our mutation load," that is it was formulated as a concept of human genetics (Müller, 1950). A survey of Huxley's publications on eugenics reveals how attentively he followed Müller's work and how willingly he cited them.

The old and the new genetics

It is difficult to draw a clear distinction between the two eugenicists. Historians of eugenics and genetics, however, consider such a division correct and suitable in most scientific and historical investigations (Kevles, 1985; Allen, 1986; Hubback, 1987). In the United States and Great Britain a change from the old to new eugenics occurred steadily from around the end of the 1930s, and finally after the Second World War, the movement transformed into the most varied social movements and institutes aimed at solving the problem of controlling the birthrate. This is now the number one problem that humanity faces, and the term no longer carries any significance. Huxley chose eugenics; that was his prerogative. But in order to "deflect" the squall of unnecessary and ignorant criticism, he published many ideas on the fate of humanity under demographic terms.

The "old style" of eugenics in Great Britain was practiced by the contemporaries, Carl Pearson (1857-1936) and Leonard Darwin (1850-1943), in the United States by Charles Davenport (1866-1944) and Madison Grant (1865-1943). In their works, they accentuated inheritance and practically excluded nature. Eugenics was considered the scientific method of conservative politicians. The old generation of eugenicists wrote dogmatically of the "pure" inheritance of personality traits, such as intellect, alcoholism, sexual deviation, criminality, etc. Almost all eugenicists were Darwinian evolutionists. After World War I, many eugenicists and their students "re-qualified" as geneticists, and primarily as theoretical geneticists. Perhaps, the rise of the Nazi theory of race hygiene after 1933 is connected with the fall and loss of influence of old eugenics (Allen, 1992, p. 199).

At the same time, a new, or reformed, eugenics was born in these same countries. The leaders were a group of young people: Huxley, Haldane (1892-1964), Müller (1890-1967), Osborn (1889-1981), and Waddington. The new eugenics accentuated nature or the interaction of inheritance and nature in determining the intellectual traits of man. It was more liberal. The reform character of the new eugenics, perhaps, was formulated best of all by Huxley in his works on the social plan.

In 1939, twenty-two leading biologists from Great Britain and the United States (Huxley, Haldane, Müller, Needham, Waddington and others) wrote *Biology and Population Improvement*. According to this manifesto, the most important genetic striving from a social point of view is the improvement of those genetic traits with regard to health, to the complex called the intellect, and to the complex of temperamental qualities, which favor the senses and social behavior. All this makes personal "success" in the contemporary sense of the word. In correspondence with the manifesto, a broader understanding of biological principles will lead sooner to a decrease, than to the spread of defects at the level of human populations (*Nature*, 1939). Furthermore, there is a long discussion in the manifesto of the possibility to improve

many through genetic methods in a short period of time. Nothing is said of the interaction of the genotype and the environment. The current opinion that the manifesto is practically consistent with old eugenics was promoted by Müller, and especially by Needham.

The Eugenics Society

After World War I, Huxley's work at Oxford and at King's College of London significantly broadened his scientific interests and circle of close friends. In the 1920s, the Eugenics Society organized a large meeting, at which there were discussions between naturalists, sociologists, economists, and reformers. In other words, the society was a typical English institute. It gathered famous, and some less famous, people from many professions in order to discuss how to apply human genetics to social problems. The society actively considered the problems of controlling the birthrate, artificial fertilization, and sterilization. The society members debated this latter problem openly and officially, in all its conceivable and inconceivable variants.

Haldane, Webb, Hogben and Glass were members of the Eugenics Society. A group of educated women entered the society as social reformers, and their participation was completely equal. Huxley became an active member of the society in the period when Darwin's fourth son, Leonard, was president (1911-1928).

Huxley's rating at the Eugenics Society was extremely high—he literally invested all his enthusiasm for romantic ideas into the possibility of improving the life of humanity. Eugenics, Huxley suggested, should play the most important role, offering man a practical method of controlling his own evolution.

The Galton lecture of 1936: a eugenicist credo

Huxley suggested that a series, if not the majority, of intellectual and other traits in man are widely heritable. In this regard, he was not an exception—this idea was part of both the old and new eugenics. In the 1936 Galton lecture, Huxley noted that there are genuine genetic differences between human groups, classes, and races when discussing the main direction eugenics. Not diminishing or heightening these differences, he claimed: "Only the visualization of genetic variations in physical traits (such as the difference between yellow, black, white, and brown human beings) makes them the primary variations, meanwhile differences in intellect and temperament, probably, are just as important. For example, I suggest that black people have a weaker intellect than white or yellow" (Huxley, 1936e, pp. 52-53).

It is interesting that even in a note of 1930 in *Nature*, Huxley had expressed a similar view. He wrote: "The majority of intellectual defects are the result of the inherited constitution and often act as a recessive trait, that is, it can be masked by a normal partner. In completely normal partners, if they appear to be the carriers of a factor or factors of intellectual backwardness, some of the children will be defective" (Huxley, 1930f, p. 504). In this same note, Huxley wrote: "Some people are born talented, others weak-minded, some inherit a healthy constitution, others an inclination to illness. Great Britain is such a place where the average level of intellectually rich people equals the number of the most ignorant and make up ten percent of the general population. The most talented people also make up ten percent" (Ibid.) Such claims by Huxley were not far from the views of the old generation of eugenicists. Elitism was expressed in Huxley as a main genetic marker. Thus he wrote to Wells in 1930 in the forward to the first Galton lecture: "I suggest that all social classes should be unprotected. You are all the time claiming the absence of differences between them, but I can agree with such passages. Undoubtedly, there exist positive differences between them, but allow me to point out the

problem. All the harm of slum life seems the result of the slums; but how does one define the type of people who inevitably fall into evil and live there without any attempts to avoid such an existence or at least strive to move higher? (Huxley, 1970, pp. 168-169).

In the 1936 Galton lecture, Huxley made an important addition. He noted that “In the future, we will have to evaluate the professional classes as reservoirs of the germ plasma. On the average, a high level has been noted regarding the intelligentsia, therefore it should serve as the basis for experiments in positive genetics” (Huxley, 1936e, p. 70).

In all the excerpts mentioned above, Huxley appears like a typical classical eugenicist with a concept of elitism. But really he possessed a broad understanding of contemporary genetics, evolutionary theory, and systematics. The question naturally arises whether Huxley’s deep knowledge was “thrown overboard.”

Eugenics and an evolutionary approach

Huxley’s achievement in reforming eugenics was that he made it a problem in the framework of evolutionary theory, in opposition to a purely genetic approach, which was cultivated by his predecessors.

. . . He began “*Eugenics and Society*” with the idea that eugenicists and evolutionists should ask and solve the same questions, when they are trying to understand how selection acts to preserve or eliminate defined certain traits. Of course, Huxley understood eugenics as a future religion, to be his own concept of evolutionary humanism. But the question arises as to, what problem Huxley attributed to an evolutionary approach and how he translated it into a task for eugenics.

There are questions that right away receive a clear answer. For the evolutionary geneticist the main question is always how traits are determined genetically, and which fall under the control of nature. This question, precisely in this form, is also current in contemporary eugenics. Huxley proclaimed an interactive approach, or, as he now termed it, the interaction between “genotype—environment.” Granting that many traits, for example, the color of eyes or flowers are independent from nature, he simultaneously highlighted that to a certain extent each phenotypic trait is the result of the interaction of genes with the external as well as internal environment. Eugenics should constantly and precisely follow the geneticists’ experiments on the breeding of animals and plants. Huxley wrote: “We are disentangling ourselves from the influence of nature and the influence of upbringing, when we follow the genetic and controlling environment . . . We should therefore conceptualize the creation of a single equal environment” (Huxley, 1936e, p. 69).

In a letter to his friend, Blaker, one of the first students at Oxford, Huxley made general comments on eugenics work. Huxley wrote: “We will never organize a large practical work in eugenics, if all classes and groups do not have more or less equal environmental possibilities” (Kevles, 1985, p. 174).

What do we know about the interaction of “genotype—environment” and its subsequent eugenics applications? It is impossible, Huxley thought, to predict man’s environment. It depends entirely on the type of “genotype—environment” interaction, and this interaction is present in every trait. The best example of the manifestation of this interaction is formation of phenocopies, which are formed in animals and plants and were first described by Goldschmidt. Plant geneticists observed that in the primrose (*Primula*) in normal temperatures mutations form red flowers, but at high temperatures, white flowers. The phenotypic variation depends on the expression of genes within its environmental conditions, although the path of realizing the genotype is unpredictable. Further, Huxley asked a typical question for geneticists. If a law-like

truth is established for flower color, then would it be true for traits of intelligence? Solving this question required in some way combining the concept of environmental uniformity (such as social justice) and the difficult concept of genetic variation. Huxley turned to a deeper analysis of developmental genetics. The transformation of phenocopies was not a persuasive argument to show that identical environments necessarily form identical phenotypes. Applying this idea, one could not predict results, and subsequently, not evaluate the experiment. Huxley hesitated and achieved no results.

In 1950, he immediately accepted Müller's concept of genetic load, simultaneously considering the idea that equalizing the environment leads to a more similar or clear expression of the genetic material. He began to widen his approach and located the eugenics problem in the question of the future evolution of man, which had constantly troubled him since the 1920s-1930s. The evolution of the human species depended, for Huxley, on such eugenic factors as: 1) the elimination of unfavorable genetic mutability (genetic diseases, intellectual retardation, etc), although undesirable eugenic measurements can be linked with the selection of desired variations through positive eugenics; and 2) the maintenance of genetic variation in populations as the basis for future evolutionary advancement, and here it becomes clear that equalizing the environment has social and moral value. Huxley did not claim that creating phenotypic and genotypic diversity is the main approach of the new genetics. He masterly combined the classical and balanced concept of the genetic structure of populations. He was neither a Müller, nor a Dobzhansky. He was always the same the great Huxley. His eugenics is undoubtedly a synthesis or, at least the combination of two fundamental concepts, in population genetics.

Huxley valued the achievements of Dobzhansky's school for accumulating wide material for the study of genetic mutability in natural populations. At the end of the 1930s-1940s, Dobzhansky's views on evolution as the change in the genetic structure of populations were widely accepted by scientists. For eugenicists Dobzhansky's ideas of population geneticists were, one can say, revolutionary, but Huxley actively disseminated them, especially in 1936 (it would be more precise, perhaps, to say not Dobzhansky's views, but those of Chetverikov's Russian school of genetics). Moreover, the investigations of bird behavior had not played its final role in forming Huxley's eugenics views. The estimation of variation in nature provides, apparently, more than the study of mutation in a standard environment, which is aimed at the study of purely genetic effects. But Huxley was both a naturalistic and experimental geneticist, therefore the information of two sharply divided scientific specializations can be evaluated in full.

The counter-version "environment—genetic variation" was the center of many of Huxley's lines of investigation. The application of these principles in eugenics led to the conclusion that it is necessary to create equitable educational possibilities for all classes, in spite of the difference in achievements among social groups. Huxley's conclusion stood in complete opposition to the eugenicists of the new generation. Thus, Carr-Sanders for ten years before Huxley's 1936 lecture had insisted that children from poor families study poorly at school, since they were genetically weaker in intellect. The conclusions about sharply different environments of the social classes or among races and ethnic groups on an intellectual level is founded on the lack of equivalent environments.

It was noted above that Huxley was completely sure that the difference in educational results or in general in personality types serve only as genetic differences. But later he came not only to doubt the arguments of the eugenicists, but also to call it a great, and genuine, warning, not supported by biological fact. He wrote: "Moreover, black people only on average have lower

intellectual abilities than white or yellow people”, as quoted just above. He also added that “Neither that fact, nor other significant eugenic claims about the racial differences are proved completely on a scientific plan” Huxley, 1936e, pp. 52-53). It is correct that Huxley suddenly began a game without concrete results. He wrote: “My declaration cannot be strictly proved, and it also cannot be called scientific. But differences between ethnic groups, difference in languages and cultures, the effects of the cultural environment are so strong that they suppress and mask genetic effects” (Ibid., p. 49). Huxley actually sought the truth, and this clearly stood out in his evaluation of Nazi race hygiene as not having any basis either in biology or in genetics in particular. He wrote: “Nazi race theory represents a rationalization of German nationalism and anti-Semitism. The German nation consists of Mendelian recombinations between Alpine, Scandinavian, and representatives of Mediterranean Sea basin. The theory of Nordic superiority is completely untrue even for the actual population: this is a myth, like all other myths, on the basis of which fascists base pseudo-religious nationalism” (Ibid., p. 50).

Undoubtedly, the evaluation of fascist ideology was an important direction in Huxley’s investigations, simultaneously demonstrating the path for reforming eugenics. Another way he demonstrated the new eugenics was his evaluation of intelligence tests. He sought strong evidence against the use of such tests as the means for measuring the natural intellectual differences among groups. The tests measure the level of education, social and intellectual achievements, but have no relationship to natural abilities. They made for the unequal social environment. In heterogenic environments, the tests measure the possibilities of an individual that he possesses in that given environment. No one can show the intellectual differences among groups using such tests. Huxley wrote: “The results of the intelligence tests are applied to different ethnic groups (or lines) and for that same reason make no sense or have no great meaning. But intelligence tests acquire great effects when they are conducted among groups with a similar social environment. And again, we stress the importance of an equal environment, which provides the best educational possibilities. Only when satisfied that we are in such an environment, can we evaluate genetic differences ” (Huxley, 1936e, p. 51).

In complete contradiction with the main line of the American eugenicists, Huxley denied the test-index IQ as adequately reflecting any genetic components. Besides that, he made an important technical assessment of the measurements and interpretations of the curves that had been obtained. It is granted, Huxley noted, that we agree that the curves reflect genetic differences among populations, but, as a rule, the distribution of the curves for different ethnic and social groups demonstrate a great degree of overlapping. And such an overlapping of curves can hardly be used for determining the existence of differences among populations. It follows that the evaluation of population phenomena given by Huxley does not compare to the evaluation by the great geneticist and biometrician, Raymond Pearl, who worked with human populations (Kingsland, 1995).

The concept of race

Huxley’s evolutionary and population approaches to analyzing genetic differences in man appeared more clearly in his concept of race. The concept was developed over many years and published in the 1930-1950s. From the mid-1930s, he began to claim that the concept of biological race is simply nonsensical. In order to convince readers of that belief, Huxley drew on the work of the anthropologist, A Haddon, who already had published his views, which completely agreed with Huxley’s. In “*We Europeans*” Huxley and Haddon strove to show that the concept of race in the sense it has been applied to man is highly inconsistent. On a broad

collection of material, the authors showed that race is used as a synonym for “nation” or applied to ethnic groups (the German race or the Jewish race), and as a family line, but not in a biological or semi-biological sense as a synonym for the term “subspecies.” In the latter sense, which was closest to scientific usage, the concept of race remained incorrect. The understanding of “subspecies” is strongly geographical, all subspecies of one species diverging from a single ancestor. The human species to a significant extent is panmictic (freely mixing), yet it hardly has the possibility for such a deep level of divergence, as is common in widely dispersed species. In 1935, Huxley and Haddon wrote: “In man, migration and free mixing creates such conditions that it is completely unclear how we can use the term “race. What do we observe in reality? The relative isolation of groups, their migration and mixing” (Huxley and Haddon, 1935b, pp. 107-108). In several places, they wrote that the term “race” is perhaps worth keeping in order to signify human geographical groups so that they will be absolutely sure that no differences exist between “higher” and “lower” races. This position became key in the race problem, in which previously geographic races were evaluated as non-equivalent. Huxley and Haddon’s credo was the problem of race having no relationship to biology. This is a social problem, and it cannot be solved by biological methods.

After outlining their position on the concept of race, Huxley returned to evolutionary and population problems. He noted that if you consider an organism as a member of a population that has a considerable amount of mutability, which accumulates in a curve with a normal distribution and evolves in constant shifts in the percentage of genes, then that entire collection of ideas is applicable to human populations. Huxley evidently came to the solution of the problem of eugenics from thinking about populations. This was a radical shift in the science of man as a whole.

In the United States, the old generation of eugenicists thought typologically. Species in their view were types, therefore they viewed groups (such as black or yellow people) as homogenous, fixed and also necessarily possessing innate traits. The old eugenicists looked on inter-group mixing as the reason for the ruining of “pure” races—of genetic purity. For Huxley, mixing was the most important eugenic source, but in a completely different sense—he saw in them a factor for the growth of mutability. For him the human species represents a gene pool with internal differences, and he also suggested that within the limits of a studied species, it is impossible to make a classification on an independent biological unity.

In 1941, Huxley supplemented his views on the problem of race in the social plan and added a new article in the book, *The Uniqueness of Man* (Huxley, 1941b). It is clear that the time dictated the direction of the general tone of the work, and Huxley - being a consistent humanist - openly placed the accent on the spreading of Nazi ideology. He sharply criticised all investigations by anthropologists, calling them the product of the pre-Mendelian epoch. In a scientific plan, Huxley broadened even more the concept of “genotype—environment,” which is directly related to the problem of race and nationalism. He noted that for any trait, in any group, there exists great polymorphism with no correlation between intellectual and physical traits. Polymorphism always serves as evidence of genetic diversity and proves the dependence of any trait in the social environment.

He noted that during the reign of Queen Elizabeth I (1533-1603), the English were the most musical nation among the Europeans, but the same could not be said of the English after the Victorian era. What caused this? Did a genetic change occur or was there a change of in the atmosphere of the Reformation and the early industrial society? It was readily apparent, Huxley thought, that the answer needed to be sought in the social sphere. He considered another example

even more convincing. In the time of Carlyle (1795-1881), the German national character was philosophical, musical, and individualistic. After the Franco-Prussian war, the German character became openly militaristic. In such short period, no kind of genetic changes could occur, and thus it was the social atmosphere that had change.

Further on in *The Uniqueness of Man*, he moved to an evaluation of the race problem. It is often claimed, he wrote, that “the Nordic race” stands above others and that all the great achievements of a civilization are the result of Nordic genius. There is absolutely no evidence to support such ideas. And he presented yet another example related to fascist politicians. It is accepted that the Jews form a “racial type” and therefore there should be a Jewish character. From a biological point of view, the problem of the Jews is especially interesting. It is known that the ancestors of the Jews formed by the mixing of various groups. Later the Jews mixed within different countries with other groups (for example, the black Jews of North Africa). The population processes led to Jews having a different genetic identity in different regions. In each country, the Jewish group overlaps with other non-Jewish groups for almost every trait. Huxley wrote: “The word ‘Jew’ is actually not a genetic term in the strong sense, and, not surprisingly, does not belong to a strong national understanding. The Jews are a socio-religious group and a pseudo-nationalistic description. ‘Jewish’ traits, without a doubt, are significantly more than the product of Jewish tradition, and despite reactionary claims, it is impossible to prove their inheritance” (Huxley, 1941b, p. 116). After the analysis of race, nations, and ethnic groups, the investigator, for Huxley, should concentrate on the uniqueness of man, and then many local problems lose meaning or stand in a completely different light. The uniqueness of man appears in the most important species traits: intellect, mentality, and temperament. All the key traits are under the control of nature. As in other species, however, there is variation in man. Any local population, he noted, “carries” in itself a part of nature and a part of inherited mutability. Any species is made of sub-species, of geographic races. This complete conceptual basis does not work directly in man. Man’s tendency to migrate is so great that it outweighs that trait in all other animals. And finally, the physical difference between groups, as if it had once not existed, is never a barrier to interbreeding, as in wild animals. Africans, Chinese, and even the Nordic races, he noted, are always inter-fertile. General panmixia is the uniqueness of man, which is a serious barrier to any theory of race. The general panmixia in the history of man led to there being in general no pure races or even nationalities. Native Africans carry a multitude of Caucasus genes, and an Indian is genetically even more mixed than an American. Mongolia began to spread from the East and left its traces in Prussia, Russia, and Central Asia. And yet, how did the differences arise that are preserved among human groups, in spite of their mixing over tens of thousands of years? Undoubtedly this is a problem that requires a special investigation. In a series of examples, Huxley convincingly showed that the elementary laws of population genetics act among any groups. Therefore the main types in body structure and temperament are repeated throughout all ethnic groups—black, white, brown, and yellow. However, all basic constructions and classifications were made by anthropologists in the pre-Mendelian epoch.

Huxley again accentuated the fact that human groups have a mixed origin. Contemporary procedures of population investigations indicate that inside every group one will find differences which overlap the rest. This is principally important. The old concept of race gave no answer to the question of quantitative variation. The new concept leans on the ideas of quantified, or multifactorial, inheritance. Inside every main type, there are geographic trends of variation, and among types there are connecting links. Gradations are observed between Negroes and

Europeans, between White and the Yellow peoples. There is a clear gradation between the Yellow man and the now existing dark-brown Asiatic type. At present, panmixia is growing literally at a geometric rate. Not in a single case can the origin of a nation be traced to a common ancestor.

Considering the historical conditions and contemporary genetics, Huxley came to the following conclusion about race. The word “race” - in the sense that it is applied to man - loses any kind of formal meaning. It is a pure abstraction, which, from a scientific point of view, differs strongly from the sense in which it is usually used. In the literature, there is a great mixing of the ideas of race, culture, and nation. It is desirable that the term “race”, in the sense that it is applied to man, is simply removed from the scientific lexicon. The meaning of that term really is unclear even in evolutionary biology. In biology, race is usually understood as a variant, that is, as a poorly defined sub-species. Migration and free mixing are processes that literally destroy the sense of the term “race” (Huxley 1941b, p. 125).

Huxley returned to an analysis of race several times. He spoke out most radically in 1941. This was completely understandable—the racist fascist ideology was for him unacceptable.

Huxley's eugenics program

Thus Huxley showed that the environment is the most important component in the formation of human qualities. Genes also participate in the formation of traits. Human subgroups (social classes, races) are grouped only by human criteria. What should the eugenicist do in this case that would set himself apart from the social reformer? Huxley completed a series of investigations, in which he outlined his arguments. His main argument was that there is no scientific basis for the idea that many human traits are controlled by genes to significant level. Furthermore, he claimed that human groups differ genetically in traits of personality, intellect, and behavior. But the present and layered environmental factors can mask that difference very well. In the very terms of evolutionary theory, Huxley tried to explain why true genetic differences can be “carried over” from one ethnic group to another. He showed that the difference between “pre-selected” and “post-selected” influences existed. Pre-selected influences were predisposed in an organism or group of organisms to the choice between one or another environment. As a classic example, he used cave fauna. Animals with weak vision can purely accidentally fall into a cave and easily develop its form of life. Pre-selection simply means some accidental processes, which become determinative processes, “deciding” which animals fall into caves and which do not. Inside the cave, post-selectionist influences begin to work. Post-selection acts on populations, thanks to defined evolutionary trends in a given environment. For example, in a population with weak vision, which is in some way stabilized inside caves, post-selectionist forces would increase tactility or the sense of smell.

From a eugenic point of view pre-selective influences, Huxley suggested, can work well in the beginning period of sorting people into social classes. Hereditarily weaker people were “pre-selected” for the lower classes. People with more “intelligent” inheritance or were more energetic were “pre-selected” for the higher classes. Literally immediately in these different social and economic environments post-selection began to work in different directions. Thus, in the next generations, a genetic difference might arise between the social classes. Huxley wrote that: “With time, a great number of unsatisfactory people will accumulate in the lower level, when at the higher level there will be collected to a greater percentage successful types” (Huxley, 1936e, p. 59). This type of process can work in the creation of support of ethnic or other geographical sub-populations.

Practically all eugenic programs suggested measure, which should maintain differences in the birth rate of lower and higher classes. The birth rate of lower classes should fall sharply, and the higher classes should raise their birthrate. Huxley was under complex political and social influences. In any case, he did not think that such a simple eugenic approach would lead to the desired positive result. He believed more in his own concepts of pre- and post-selection. But in conditions of economic crisis, he could not directly relate social success to one aspect of biology, not even genetics. He wrote: "It would be good if success was directly connected with biological and social values: one strata reproduces faster, and the other, slower. However it is known that reproduction demonstrates reversibility, and making levels with desirable qualities is a naïve rationalization" (Huxley, 1936e, p. 59). With the concepts of pre- and post-selection there constantly arose difficult problems. Undoubtedly, these forms of selection are acting, but their results always depend on the socio-economic environment in the framework of their expansion. Huxley, Haldane, and Needham thought that human environments are a matter for the creative hands of man himself, and not a "fact of nature." It is interesting that, discussing the problem of human environments, Huxley was not able to find a single solid source. And this is understandable, for such work could be completed only with the cooperation of almost all specialists on social, biological, and even geological questions. Huxley began with a general eugenics assumption that human beings can undergo genetic selection like any other species. He wrote: "Undoubtedly, genetic variations in temperament, including the tendency for social and antisocial acts, an inclination to cooperation of individuality, exist. But man, like domesticated animals, suppresses these traits. If we did not live in a society, but chose another form of living together, then there would exist a constant danger of similar antisocial tendencies of its members" (Huxley, 1936e, p. 75). Furthermore, he recalled the simple truth that selection always acts in a particular environment, and not in the environment in general. He wrote: "Any eugenic ideal will always be different from that, with which we have connected it. For example, with the feudal order of things, with primitive industrial society or with the market economics. These are different worlds, just like capitalistic or socialist orders, militaristic or the general order of peace" (Ibid., p. 63).

Such comprehensive acceptance, which Huxley placed on the environment with its variations and infrastructures, permitted a broad evolutionist to show eugenicists a social environment, and that they should become social reformers. Any eugenicist has the right to choose his own actions depending on the social environment, in the frameworks in which he practices. As a rule, choice leads to three possibilities: 1) the eugenicist can admit that the social order always remains unchanged, and therefore can confidently practice genetic selection; 2) the eugenicist can imagine some ideal environment and take selection in an ideal direction, hoping the social environment will change in that desirable direction; and 3) the eugenicist can lead a united attack on both the environment and the germ plasma, qualifying his effort as the work of the "future." In a future, more harmonized environment selection can lead to a truly positive, progressive end. The third alternative, for Huxley, is a striving to understand rationally the ideal.

And did Huxley himself defend such an environment, in order to start in it a new eugenic selection, or, as he said, a new eugenic practice? In 1936, he was greatly impressed by the Soviet practice, which, as it seemed to him, more humanely and productively used group values. And here, Huxley suggested, it is also necessary to develop a positive eugenics, that is, selection for altruism, cooperation, enthusiasm, etc. The process of such a selection should replace the traits, which are right now selected for in capitalist society, primarily egoism. But now, he lamented, it is impossible to select all desirable traits, because the expression of such

genes are often suppressed or masked by environmental effects. For him the existing social structure of his time, capitalism, was unacceptable primarily because of nationalism and the unavoidable penchant for war. The existing layers of society in capitalism, he noted, are artificial, and there should be a natural stratification - primarily a division along genetic-biological traits. At the same time, he insisted that the environment should be equal for all members of society. Until the creation of such an environment, the prolonged action of eugenicists will not be realized. Thus eugenicists and social reformers should always present a single face. Without such unity, any action loses meaning.

How does one plan the results of the action of eugenics even in the best environment? And more concretely: what methods should be used in the practice of eugenic selection? The dependence of the birthrate on the level of education and socio-economic status was widely accepted since the beginning of the 20th century. The equalization of the social environment will mean the raising of the socio-economic level of the lower classes and thus the lowering of their fertility. But this is only an indirect approach. Positive eugenics should still find a way to raise the birthrate of the professional classes.

Control over the birth rate and sterilization

The idea of controlling the birthrate was part of old eugenics of the most varied types. This idea was widely discussed in English society, and at the beginning of the 20th century in the United States, thanks to Pearl's publications. English scientists, even independent from eugenicists, often turned to that idea after the publication of Malthus's 1798 "*On Populations*." In all periods of Huxley's research, he was an active supporter of the idea of controlling the birthrate. On the feelings between men and women, he wrote entirely loftily; however, he thought that these feelings had nothing to do with reproduction. He wrote: "The reproduction function—is a completely different land." The most difficult aspect of controlling the birthrate was, he suggested, how to put that ideology into practice. And an even more difficult problem was how to prepare society for such a radical social action. He suggested that solving the problem of controlling the birthrate must begin with the "problem group." In this group, there should be people with defects. In Great Britain' they make up five-ten percent of the population, therefore making an experimental group with such people is also important for social reasons. The methods of sterilization are the most voluntary, but they are necessary. Subsequently, Huxley suggested, laws are required to end voluntarism. He became an active supporter of sterilization at the end of the 1930s-1940s, and before that he adopted a moderate position in comparison to other eugenicists (Allen, 1992, p. 211). Thus, when Gregory put forward a plan for the mass sterilization of members of the lower classes of Wales and Ireland, Huxley rejected his idea. But from the end of the 1930s to the 1960s, Huxley began to speak out at the Eugenics Society in defense of sterilization. On all his trips to the United States, he supported American eugenicists on the question of sterilization. He was especially active in California, where 12,000 sterilization operations had been performed. Huxley wrote: "You in your country are the great pioneers in sterilization. California has impressive results on the behalf of social health. We in England are lagging. If we could make similar operations legally, the result would be good" (Huxley, 1936e, p. 78).

In the mid-1930s, he presented a report at the Eugenics Society on the legalization of sterilization by forceful measures. After some time he presented a special report on forced sterilization of intellectually retarded people. He once more declared himself a follower of the scientific method in solving any social problem. He claimed that the issue at stake was about the

scientific method, and not the dictate of a religious person or nationalist. The contents of the report, Huxley stressed, were not driven by class or political motives—they were simply humanity entering a new era. He wrote: “If human progress will continue, the next great step will be man’s control over his own environment. Our fate is in our hands. And the problem of reproduction is in our hands. This is humanist soul, and our instrument lies only in the scientific method” (Huxley, 1936e, p. 76).

Huxley proposed a more complex task, than that of the older generation of eugenicists. But the older generation better understood the difficulties, which arise in legalizing sterilization and controlling the birthrate. In addition, they mistakenly viewed eugenics and social reforms as in opposition. Moreover, as the theories of the biometricians and Mendelians complement one another in the study of inheritance, just as sociology and human genetics draw on supplemental approaches to control human evolution. Eugenicists should not only establish that the studied trait is inherited, but also that it actively contributes to social politics. Thus the goal of eugenicists is to control the evolution of the human species in a desirable direction. The new eugenics should unite theory and practice, inheritance and the environment, genetics and social theory.

The planning and control of human evolution

The investigation of Huxley’s eugenics views provides an excellent model in the history of science. On the example of one scientist, one can see the interaction of such completely different and occasionally incompatible ideas, as individualism, collectivism, social planning, liberal politics, evolutionary theory, and genetics. The interaction of these ideas represents a certain fusion of social philosophy. Huxley’s study of eugenics in the context of the history of ideas permits discovering the complex motivations, which formed and stimulated social action. Unlike the older eugenicists, burdened by traditional ideas and stereotypes, Huxley moved from the pure ideology of eugenics to the problem of the birthrate and, finally, to the control of the birthrate.

Perhaps, Huxley was the first to unite eugenics ideology with population control (but it was really Raymond Pearl, a biometrician, geneticist, and broad populationist, who expressed similar ideas, see Allen, 1991). Before Huxley and Müller, the problem of eugenics and population control was viewed separately. After World War II, the idea of controlling the birthrate, as the most important eugenics idea, led to the development of methods that limited family size, and had an influence on many programs of human populations. At the basis of such a program lay the simple idea of the differential fertility between classes, races, or ethical groups. Huxley almost left eugenic ideology and moved to the problems of population control. At the same time, he broadened the eugenic ideology to a global level. Moreover, this connected with preparing documents for forming UNESCO and the related work of that global organization. In 1964, in work on evolutionary humanism, Huxley repeated the exact Müller’s words on the necessity of eliminating “sick” genes, stressing that human populations would otherwise become a continuous genetic load (Huxley, 1964, p. 250). Thus, from the old, individual, or family eugenics, Huxley moved to a completely new discipline, which can be called evolutionary population eugenics. The reason for such a “jump” is easily explained, when one considers Huxley’s evolutionary legacy. The common evolutionary interest, the consistent thoughts on population, and an excellent knowledge of genetics significantly broadened Huxley’s scientific horizons, transforming him from a “defender” of eugenics to a “defender” of population control.

Communism or liberalism in eugenics

At the beginning of the 1930s, in a period of financial crisis in the West and while sympathizing with the Soviet Union, Huxley worked aggressively to form a non-governmental organization in the sphere of economics and society. The idea of planning totally conquered Huxley's ideas—he viewed it as the social result of evolutionary progress. But at the end of the 1930s, Huxley's regard for the Soviet Union changed. The reasons were the political processes and the destruction of great geneticists, most of all Vavilov. Huxley never fell under the influence of Communist ideology, as had, for example, Haldane, who joined the Communist party of Great Britain. And the ideology the evolutionary humanism, which Huxley formed, was incompatible with the ideology, or better, the Soviet practice of Communism. He wrote two books on Soviet Russia, in which he was one of the first to use the expression “totalitarian society.” In all his scientific and popular works, Huxley clearly separated Russia of the 1920s from Stalinist Russia with all of its inhumanity.

Even so, Huxley introduced a leftist-liberal element into eugenics. Mostly his liberalism developed into a sharp critique of all racist theories and imperialistic ideology. Huxley seriously analyzed Marxism as a social theory, which made possible the advancement of social thought. In Marxism he saw a theory, which uses knowledge of the past to change the social order in the future. But nowhere did Huxley write of the necessity of the “conversion” of Marxism from theory to real practice. In addition, he was not an eager defender of capitalism, accepting the imperfect traits of many of its forms. Huxley was always ready to accept new radical ideas, if they deserved his attention.

Eugenics in scientific (evolutionary) humanism

For Huxley, it was important to keep together the ideas of humanism and deny formal religion. Evolutionary humanism was for him a philosophy of belief, based on the application of scientific methods to understand man, morals, and ethical life. It was typical naturalistic philosophy, which excluded mysticism and all notion of the supernatural. In addition, this was not the typical nature philosophy or positivist philosophy, which had been described in monographs and textbooks of academic philosophy. In the concept of evolutionary humanism, there simply was no reductionism and social physics. In the publications on evolutionary humanism, Huxley applied biology to understand human behavior. He was a consistent supporter or even the most active defender and propagandist for science and the scientific method. Regarding biology and man, the higher methods of knowledge, Huxley suggested, are found in the area of evolutionary theory. Without knowledge of man's evolutionary past, he claimed, one will be unable to understand his contemporary life and to predict his fate. He wrote: “The fundamental postulate of evolutionary humanism is that the intellectual and spiritual forces effectively act in all man's practical matters and are not outside of man, but are inside him. The most important evolutionary mechanism of man is the psycho-social mechanism. It is necessary to understand its mechanism and the point of its application” (Huxley, 1964, p. 295). Huxley noted many times that evolutionary humanism allows man to take life into his own hands and to control his fate. This should be conducted on the individual and the collective level.

He understood well the importance of controlling the social processes, just like controlling the natural processes. He suggested that among the most important general human problems that require uninhibited control is that of birthrate. Here, this problem automatically includes nature itself, and does not work against it. So any problem of evolutionary humanism acquires a cosmic scale, becoming a part of global evolution, the “guardian” of which is man. In essence, Huxley included two important components in the reform of eugenics: an evolutionary

view of the studied processes and the scientific control of social processes, as well as social planning.

An evolutionary perspective

The eugenicists of the early period were Darwinian evolutionists. But, as is known, in the 1920-1930s a new evolutionary view arose. Huxley's views on evolution formed primarily under the influence of natural history in the broad sense of the word, including the study of bird behavior. In addition, he had experience as an experimental biologist and geneticist. It was completely natural that he made an "evolutionary synthesis." How did his evolutionary synthesis influence his views on eugenics?

The historian of science, Allen (1992) noted that the influence of Huxley's evolutionary synthesis on eugenics occurred in several non-standard ways. In the first place, Allen suggested, were the population ideas, i.e. to accentuate the saturation of human populations (as in any animal population) with many mutations and recombinations. Beginning in the 1950s, however, Huxley simultaneously used the term "population" in a broad demographic sense in connection with the problem of the unlimited growth in the human population (Malthus' parameter). In the 1962 Galton lecture, it is apparent that these two concepts of populations interacted in different ways in Huxley's thought.

Mutations, in his estimate, were the source not only of inheritable defects, but also of the variations upon which future evolution occurs. The literate contemporary eugenics approach should include the idea of the selection of desired genes from the gene pool, as well as the idea of negative selection, which acts against the "defective" genes. Population genetics introduced a principally new idea into eugenics, according to which human populations are in a state of evolutionary dynamics.

Through an analysis of the problem of species and their structure, Huxley also added much that was novel to eugenics. In this regard, he was able to avoid a typological approach to *Homo sapiens*. The old eugenics relied on the concept of race and ethnic groups. Moreover, the history of the human species represents numerous migrations and mixings; i.e. *Homo sapiens* is a global panmictic population, with subdivisions that occurred through the exchange of genes over hundreds of thousands or even millions of years. Therefore, neither racial nor ethical "types" are pure in a genetic sense.

A constituent part of Huxley's eugenics was the idea of planning, which he developed over his entire scientific career. An especially sharp problem arose in the 1950s, when Huxley began a series of intensive publications on the problem of controlling the magnitude of the human population on the Earth (Huxley, 1950). Since the beginning of the 20th century, the ideas of controlling the birthrate and generally having social control were widely discussed, becoming subjects of investigation for many historians (Freeben, 1979; Jones, 1982; Paul, 1984). Thus, the idea of planning among Anglo-American eugenicists appeared significantly earlier than when Huxley entered into that field of activity. It is interesting that the idea itself arose as a kind of philosophical doctrine, aimed at the search for ways and methods of gaining rational control of the natural and social worlds. From these ideas grew Huxley's notion of the necessity for an Institute of Planning, the members of which should be experts in the study and evaluation of processes that occur in the natural and social sphere. A contingent of experts should be formed from the representatives of the middle class. But Huxley did not agree with the old eugenicists, who claimed that it was necessary to control the material of human inheritance in a literal sense

of the word (besides, of course, the inheritance of sick people). Control used on agricultural animals should not be applied to humans.

Enthusiastic about planning in the 1920-1930s, Huxley joined a number of planning organizations. He was a member of the committee for economic planning, the duties of which covered the processes ongoing in all of society. He joined the group “Five Years,” the name of which was borrowed from the experiences of the Soviet five-year plans. He found himself in constant discussions with the supporters of the ideas of “pure” market economics, attempting to supplement these ideas with planned approaches. Why did Huxley so persistently defend the compromising of ideas between capitalism and socialism? The problem deserves to be considered from a broad historical perspective. From 1890 to the end of the 1930s, the reason for Huxley’s interest in the area of social stability and human evolution was war and depression. It is strange that he was not politically right, or left. He applied the ideas of control to social life without harsh dictatorial methods.

Of the founders of the evolutionary synthesis, he most broadly studied the social sciences and considered himself an equal specialist among the other actors in the sphere. He was a global politician not only because he occupied the post of Director General of UNESCO, but also in the spirit of his own evolutionary social views. The idea of controlling the birthrate, was clearly connected by Huxley with preserving humanity and the biosphere—this is the best evidence of his humanitarian and global views of the world.

Genetics and eugenics: a dispute

The well-known American geneticist and eugenicist, Diane Paul, published an article on Huxley. The article is principally unlike other publications because it aims to compare the position of Dobzhansky and his school with Huxley’s views on the question of human genetics. Paul recalls that in the 1950-1960s, Müller widely polemicized with Dobzhansky about the significance and size of genetic variability. In this polemic, Huxley seemed closer to Dobzhansky’s position than to the views of his old friend, Müller (Paul, 1992, Pp. 225). Paul cites Dobzhansky’s letter to Huxley from 11 July 1953. Dobzhansky wrote: “It is extremely desirable to see that balanced polymorphism plays a great role in the adaptive evolution of an organism, which reproduces sexually. From this it entirely follows that in reality, lethal genes and heritable illnesses, forming co-adaptive combinations of genes, from the point of view of the structure of species represent only the raw material. This is highly important to understand in comparison with the old problems of human genetics and, of course, eugenics” (Op. cit.; Ibid., p. 226). Paul added that illnesses might provide the flexibility of species on the whole. However, from her article it is not clear whether Huxley answered Dobzhansky’s letter.

From the end of the 1950s, Dobzhansky placed the so-called balancing selection at the center of his investigations, that is selection, by which heterozygotes have an advantage over both homozygotes (overdominance). At the basis of the theory was Bruce Wallace’s experiments with X-rays of *Drosophila melanogaster*. X-rayed heterozygotes below a dose of 500 roentgen were more vital than the control flies. Such a “gift,” Dobzhansky did not expect (Beatty, 1987). Heterozygote advantage is a way of explaining the preservation of defective genes in a population and maintaining them at a high rate. And here appears another “gift.” In sickle-cell anemia, the homozygotes develop a serious illness that is lethal, but the heterozygotes develop a compensatory defense against the illness. After such a discovery, the historian Müller asked who would raise a hand to guide selection against genes of such a type? Moreover, it is noteworthy

that nothing is known about the other genes which in double doses act like typical lethals. In agreement with Müller (1960), sickle-cell anemia is convincing, but is in no way a universal fact.

After the publication of Dobzhansky's work in the 1950s-1960s on the balancing concept of the genetic structure of populations, the discussion between Dobzhansky and Müller became even more lively. In Dobzhansky's book, *Mankind Evolving*, most of the citations are from Müller, and it is primarily a critique of Müller as the main opponent of Dobzhansky's fundamental evolutionary population genetics. One of the sections of this book, called "The Most Brave New World of Müller", is a real caricature of the philosophy of him, whose name is always connected with the selection of "the ideal man, or ideal woman, or even the entire population of the world, which in the final stage will become the bearers of an ideal genotype" (Dobzhansky. 1962, pp. 329). Dobzhansky's sarcasm was not accidental [Dobzhansky well knew the friendship between Müller and Huxley and, possibly, therefore called the section in his book, in which he criticized Müller's views, in correlation to Huxley's brother's book, Aldous Huxley's *Brave New World*, London, 1932).] The idea of genetic diversity was never accepted by Müller, and the concept of the genetic structure populations negated the balance concept and was built on the idea of greatest adaptability of a small class of ideal homozygotes, which selection maintains or eliminates, if mutations arise with a lower adaptability. The selection of highly adaptable homozygotes, Müller suggested, is the main path of evolution.

Nevertheless, Dobzhansky greatly simplified Müller's views in order to "get satisfaction from his opponent." Müller never supported the ideas of a unified human genotype. Even in the 1930s, when he suggested a program of the artificial fertilization of women with the sperm of tested males. In his 1935 book entitled *Out of the Night*, Müller wrote that the artificial fertilization of women should be done with the sperm of the strongest males in an intellectual regard and with social sensibilities. Examples of such men for him were Lenin, Newton, Beethoven, Pushkin, and Marx. It is correct that later Müller softened his position. But this did not inhibit Dobzhansky drawing him out for general ridicule.

Moreover, Müller wrote about Dobzhansky with great respect. Not denying his differences with Dobzhansky, he stressed, however, that he never taught the idea of absolute uniformity, although, of course, he did not attribute as much significance to diversity as did Dobzhansky.

The experienced historian of science, Diane Paul, and the experienced geneticist, Bruce Wallace (who was a student of Dobzhansky), suggested that the concept of diversity requires more weighty and careful evaluation (Wallace, 1957; Paul, 1992). Unlike Allen, Paul was convinced that support of the idea of genetic diversity in populations does not always indicate the progressiveness of a scientist. Wallace, who had suggested and completed the decisive experiment in support of the concept of -over-dominance, declared at a conference on "The Influence of Radiation on Human Inheritance" that the given concept is "morally deficient" (Wallace, 1957). Undoubtedly, the concept of over-dominance cannot be moral or amoral, but why did Wallace express it in such a way? It is believed that the reason was that heterozygotes and -over-dominance act as an elite group, in spite of the diversity and possibilities of the genotype, in Dobzhansky's words, which transfer from one class to another. Dobzhansky's methodology demonstrated the democratism and equality of the possibilities, it "obtained satisfaction" from the concept of genetic load. And all the same, Wallace did not establish such a democratism. [The discussion between Dobzhansky and Müller on the problem of the genetic structure of populations became a subject for analysis by the historians and specialists (Beatty, 1987; Crow, 1987; Paul, 1987). It is interesting that Dobzhansky's student, Richard Lewontin,

and the propagandist for Müller's views, James Crow, came to the same conclusions at the end of the 1980s (Crow, 1987; Lewontin, 1987). They suggested that it is necessary to make a unified neutralist-selectionist concept of genetic polymorphism, and then the tension that arose between Müller and Dobzhansky would be taken to a new historical turn of developmental genetics and evolutionary theory.]

In *Mankind Evolving*, Dobzhansky wrote: "The equality of the possibilities is inclined towards the differentiation of the assimilated environment [read "niche"] in unity with the genetic polymorphism of the populations. . . . But the equality of possibilities has nothing in common with the unintelligible phrase of the identity of the genotypes" (Dobzhansky, 1962, p. 244). Translated into the social sphere, Dobzhansky's words mean that genetic polymorphism is the premise for the division of labor and the necessary condition for people to do their own work, while doing it in the very best way. The equality of possibilities, for Huxley and for Dobzhansky, make the process of social sorting entirely effective. It is correct, Huxley wrote, that science should actively participate in the division of labor and here is its perspective on the life of humanity. But contemporary life hardly can support Huxley's optimistic words.

The dispute had not yet ended. Allen and Paul as experienced historians of genetics and eugenics were able to work and "present" the material. However, a series of important problems were simply left out of their analysis. In such a situation, naturally, it follows to continue the discussion of the above-mentioned problems.

In their publications and correspondence, Dobzhansky and Huxley discussed natural selection, especially in the aspect of eugenics problems. Dobzhansky published in a eugenics review an article called, "*Natural Selection and Fitness*," and in his correspondence asked Huxley to support his idea of "Darwinian fitness." At the time, Huxley was preparing to publish a review of Dobzhansky's *Mankind Evolving* (Dobzhansky, 1963). Huxley's critique of Dobzhansky's concept in the eugenics journal spilled out into a full version in the Galton lecture of 1962 (Huxley, 1963d). The basic critical position regarding Dobzhansky's views on the nature of the action of natural selection, Huxley outlined also in a new introduction to his well-known book, *Evolution: The Modern Synthesis* (Huxley, 1963a, Pp. xviii-xxi).

In the introduction to the new edition of the book in 1942, Huxley made a short survey of the successes in evolutionary theory over the twenty years since the first edition. The range of criticism included one Dobzhansky. Already in the review, Huxley noted that Darwinian fitness did not change in terms of reproductive success, as Dobzhansky had suggested. As any population geneticist knows, how many scientists supported Dobzhansky. In the 1942 book, Huxley wrote: "As a result of the well-known increase in interest in population genetics, in counterbalance to formal genetics, the theory of natural selection underwent significant changes. In particular, are the undesirable novelties regarding the concept of *fitness*. The term fitness is defined in terms of the differential reproductive success, without any reference to phenotypic fitness, which provides or grants individual survival. Several authors, for example, Dobzhansky, go so far as to call differential reproductive success "Darwinian fitness," although Darwin never used fitness in that sense. The first to use this term in evolutionary theory was Spencer with the help of the unsuccessful phrase "*survival of the fittest*." In the early editions of Darwin's *The Origin of Species*, Spencer's expression simply does not appear" (Huxley, 1963a, p. xviii).

Further, Huxley moved to a similar analysis of Dobzhansky's views and their consequences. The basic source for the analysis was *Mankind Evolving*, where Dobzhansky, in particular, wrote that Darwinian fitness is measure only in terms of reproductive experience or proficiency, and that only the trend or direction, visible in the life and its evolution, is the

product of a large life. In correspondence with this position, natural selection means the differential reproduction of the carriers of various genetic investors (Huxley, 1963a, Pp. XVIII-XIX). It is curious that Dobzhansky cited Müller, who criticized the expression “Darwinian fitness,” noting that *fitness* and *Darwinian fitness* are not identical, and in a certain sense may even be contrary. [Müller’s article on the theme of natural selection in connection with human evolution was published simultaneously in two issues (H Müller, “*The Guidance of Human Evolution; Evolution after Darwin* (Chicago, 1960), Vol. 2, pp. 423-462; the same article is in *Perspectives in Biological Medicine*, 1960, Vol. 3, pp. 1-43).] In the Dobzhansky-Müller polemic, Huxley was clearly not on Dobzhansky’s side.

A very small group of critics of Dobzhansky’s views on the nature of the action of natural selection, as has already been noted, was supported by Huxley in the most varied directions. Huxley wrote: “When we evaluate the problem more critically [than Dobzhansky], it will be necessary to draw a sharp distinction between two forms of natural selection, which lead to such evolutionary trends as survival selection and reproductive selection. JBS Haldane in 1959 also saw a distinction between these forms of selection, but called them correspondingly *phenotypic* and *genotypic* selection. I prefer my own terminology or semantics of natural selection, but use *phenotypic* and *genotypic* for the corresponding types of social selection” (Huxley, 1963a, p. xix).

In connection with this, it is appropriate to recall that in 1972, my tutor Cirill Zavadskii suggested that I write a review of Dobzhansky’s book, *Genetics of the Evolutionary Process*. The timing was good, because the first volume of the collection, *The History and Theory of Evolutionary Study*, was then being prepared. It was difficult to write, despite the fact that Dobzhansky’s language was simple and he expressed his thought very clearly. The review ended with the wish to publish the book in Russian. Before the publishing corrections the following words were in it: “That Dobzhansky’s works are not published in Russian does not help the development of evolutionary theory in our country.” An experienced editor and wonderful person objected: “How can the non-publishing help or not help? The phrase removed, although in my soul I protested. I will cite my own evaluation of the asked question: “In close connection with natural selection Dobzhansky was led to the analysis of the problem of adaptation. This question addresses two divisions under different names, *viz.* adaptedness and Darwinian fitness. However the definitions, which are given by this understanding, all the same concur. In both cases the relative contribution of the genotype to a population’s gene pool is stressed. The meaning of separating these two understandings, thus, remains unclear. In addition, the expression Darwinian fitness brings to mind the idea of the existence of some kind of non-Darwinian fitness. . . . The fitness of organisms is not a property of the gene, but is defined as the united result of the entire genotype and phenotype” (Gall, 1973, p. 154). This citation is used to show that many leading Russian evolutionary biologists (II Schmalhausen, GF Gause, MM Kamshilov, and others) always interpreted natural selection as the differential reproduction of phenotypes, suggesting that only on this basis over a series of generations does the selection of the genotype occur.

The views of Huxley and Schmalhausen on the evolutionary role of natural selection are surprisingly in agreement. Huxley wrote: “In the process of biological evolution selection has its effect primarily through the phenotype and acts by way of its differential success. These processes will have evolutionary effects, which Darwin describes well: a) the majority of individuals, which survive to the adult stage, will mate and leave offspring; b) the majority of phenotypes, which survived, have a genetic basis. Natural selection can also act by way of the

differential reproduction of adult individuals, but actually this is reproductive selection, which has exclusively small evolutionary effects” (Huxley, 1963a, p. xix). Schmalhausen separated selection into fertility and selection for higher organization (or selection for vitality). Selection for fertility in content agrees exactly with selection for reproduction. Even the examples, which Schmalhausen and Huxley agreed. For example, Schmalhausen wrote: “If in the general destruction of eggs, embryos, and at times young (in the presence of caring for the offspring) most often entire clutches die, then a positive significance is acquired by the increase in the number of clutches although at the expense of decreasing the number of eggs in each clutch. A positive significance is also gained by the divisibility and polytypy of the clutches” (Schmalhausen, 1939, p. 194). In turn, Huxley, proving the action of reproductive selection, wrote: “This type of selection acts on the side of making optimal clutches, high in offspring, or, in general terms, on the side of the number of offspring” (Huxley, 1963a, p. xix). In interpreting survival selection, Huxley also spoke as Schmalhausen’s “twin,” having suggested the concept of selection for vitality. Schmalhausen wrote: “If this selection moves along the line of increasing the vitality in different environmental conditions, and this is possible in the case of the increase in organization with the complexity of a broader adaptability, which is connected with morphogenetic and physiological correlations, then the evolution of an animal can lead to *aromorphosis*, that is, to the spreading of the habitat environment with the use of new possibilities”(Schmalhausen, 1939, p. 195). Correspondingly, Huxley wrote: “Selection for vitality . . . unavoidably supports and even raises the status of all species, trends, leading to biological improvement, specialization, functional effectiveness of the system of organs, or to the improvement of the general organization” (Huxley, 1963a, p. xx).

Such an agreement in thought between two evolutionary biologists is completely natural when one looks at their creative path. But it is important that the Russian and British scientists, having rich experiences in embryology, growth, and morphology, and having solved the problem of large evolution, thoroughly understood that in any interpretation of natural selection, the field of action should be the phenotype.

Huxley’s new introduction to his 1942, *Evolution: The Modern Synthesis* allows for another look at his book. Actually, the idea of phenotypic selection as the main, and perhaps, only form of natural selection was extremely necessary for Huxley. Natural selection as the differential reproduction of genes or genotypes is convenient for population geneticists, who also consider themselves evolutionary geneticists. But they all worked in the field of microevolution. The genetic, or as is still said, contemporary theory of natural selection automatically reaches a dead end, in principle as an unsolvable situation in the area of interpreting macroevolution. Macroevolution implies the origin of higher taxa, the origin of organs, that is, phenomena at the phenotypic level. Of course, at the base of the majority of evolutionary changes lie genetic changes, but in a broad evolutionary perspective the investigator always works with phenotypes, which are selected in populations. In such a viewpoint, it is possible to construct a single united concept of evolution, without dividing it into macro- and micro-evolution, without questionable extrapolation and panselectionism. In fact, there is a great fork in genetics itself, between population genetics and the genetics of development. If the genetics of development is introduced to evolutionary theory, the simple schema for selection are automatically eliminated and we come closer to understanding the genetic basis for large evolution. In the beginning of the 1950s, when investigations on population genetics intensified, which extended to the experimental study of the evolutionary process, it was no accident that Huxley immediately expressed doubt about the possibilities for genetics to understand fully the evolutionary process

and demonstrate the multitude of varied and necessary approaches to studying the process of evolution on different levels (Huxley, 1954a).

In the eugenics lecture of 1962, Huxley noted that “Biologists often ask, which is the more important, inheritance or environment? I have repeatedly stressed that such a question cannot be posed. It would be just as irrelevant to ask a biologist at a legal meeting, when did he stop beating his wife. There is a phenotype, which is biologically significant, and that phenotype forms a complex of interacting inheritances and factors of nature. *Eugenics together with evolutionary biology needs a more general phenotypic approach*” (Huxley, 1962b, p.132; author’s emphasis). With regard to the combination of genotypic and phenotypic approaches in an acceptable form for eugenicists, Huxley demonstrated the fundamentality of evolutionary theory in the following way: “*The evolution of man flows on two different levels and by way of two different methods: the genetic, which is based on the transmission and variation of genes and combinations of genes, and the psycho-social, or cultural, which is based on the transfer and variation of knowledge and ideas*” (Ibid., pp. 132-133; author’s emphasis). This hierarchical evolutionary approach, as has been noted, was suggested by Huxley as a basis for studying man, ethics, and humanism. By all appearances, it was also central to his eugenics approach. In support of this, in particular, is Huxley’s critique of a lecture by his student, Medawar, on “*The Future of Man,*” in which evolution is described as a process that occurs, in Huxley’s words, only on the phenotypic or even lower cultural level, and is called a new type of biological evolution. Here Huxley demonstrated precisely the hierarchical nature of the evolutionary process and the global consequences (in his words, “cosmic”) evolution of man at a phenotypic level (Huxley, 1962b, p.132). And yet, even though Huxley had an excellent knowledge of genetics thanks not only to his own investigations, but also to his constant reviewing of the newest investigations in genetics in the 1920s in British and American journals, such as *Nature*, *Science*, the *Journal of Genetics*, he nevertheless retained such a great role for the phenotype in evolution.

Apparently, the reason for this was that Huxley was first and foremost an evolutionist and viewed genetics from that direction. For example, more important for the evolutionary biologist is not the number of mutations, but the phenotypic effects which they produce. In fact, selection always works on phenotypes. This became very clear in the early 1970s, when the Britten-Davidson model for the evolutionary role of regulators and structural genes in eukaryotes appeared. A revolution in evolutionary theory might occur in the near future, thanks also to the best understanding of the interaction between the genotype and phenotype. There are now new experiments and theoretical foundations of the interaction genetics (in the broad sense) and developmental biology, primarily thanks to the discovery of a small group of common genes, which control even the structural plan and general morphology to different extents in the advancing groups of organisms (the research of E Davidson and R Carroll). As is well-known, from the problem of developmental biology and evolutionary theory came Huxley’s great belief in the importance of the phenotype in evolution, and this occurred when the attention of the evolutionary geneticists was directed at the genotype.

When Huxley was preparing a new edition of *Evolution: The Modern Synthesis*, he worked a good deal on the problems of eugenics and the global problems of human survival. Therefore in discussing the problems of natural selection, he also touched on eugenics. He wrote: “The situation with man so strongly differs from the biological situation, that it is possible to easily to overturn attempts to apply concepts, like the concept of natural selection, to contemporary human affairs. All evolutionary differences in reproduction and survival are acting

right now, but their roots should be sought in the special psychological character of human evolution. The simplest of all would be to accept the fact, that a new form of selection, *psychosocial selection*, or simply, *social selection*, is acting right now. Fisher said that evolution in the early stages of human society continued by way of the “social contribution of fertility,” when in the majority of contemporary societies there is the “social selection of infertility.” I reciprocate with the same coin: the word *euselection* signifies the premeditated selection of supposed desirable genetic qualities. Brewer used *euteleogenesis* in order to define improvement through artificial fertilization from selected donors. Müller openly said that it is possible to get an effective yield, using the contemporary technology of deep freezing and, thus, preserving sperm (the corresponding eggs and embryonic cells).

Eugenics and human genetics, which relate to human evolution (noted by Dobzhansky, Crow, Müller, Medawar and others) recently discussed these problems. They came to the conclusion that social selection (eugenic selection for the genetic improvement of man) would differ, radically, from an artificial selection directed at improving the genetics of domesticated plants and animals, and also will be different than natural selection, which acts automatically to make biological improvements in groups of natural species. Eugenic improvement all the faster and faster will become the main goal of evolving man, although for reasons of such tragedies as overpopulation, atomic war, and the ruthless exploitation of natural resources” (Huxley 1963a, pp. xx-xxi).

Beginning with the Galton lecture of 1962, Huxley tried to give some substance to the term *fitness*. When Medawar used the word *fitter* for the estimate of variations in the survival and propagation of offspring from ancestors, Huxley noted: “This I believe to be an unscientific and misleading definition. . . . I will call this evolutionary fitness, in opposition to the purely reproductive *fitness of the evangelists of geneticism*, which I prefer to designate with the descriptive etiquette: *the complete or differential reproductive advantage*” (Medawar, 1960; Huxley 1962b, p. 131). It is easy to see that the definitions of Dobzhansky and Huxley are similar.

Huxley discussed the problem of fitness once more in connection with the relationship between positive eugenics and population genetics (Huxley, 1962b, pp. 137-138). He noted that there is only one scientific definition of *fitness* for Medawar and for Dobzhansky, *reproductive fitness*. Thus Huxley exposed the meaning of *evolutionary fitness*. He wrote: “We should explain direct phenotypic *fitness* and *fitness* on the scale of large evolution. If *fitness* is measured by the differential survival of offspring, then this is simply a mechanism for improvement on the scale of large evolution, which is realized by way of a truly biological *fitness*.”

Genetic polymorphism was the subject of investigations of a large school of American geneticists and zoologists, which was led by Dobzhansky. But in not much less volume similar research occurred in Great Britain (Ford and his students, and Mather and his school). Therefore, when shifting from the general evolutionary conclusions on fitness to the concrete analysis of questions at the level of population genetics, Huxley made no author citations. But he organized a good connection between population genetics, human genetics, and eugenics. Having outlined the essence of genetic polymorphism, which is dispersed in animals and to a certain extent in man, he moved to his evaluation from a eugenics point of view. The problem of polymorphism comes under the field of the critique of the representatives of contemporary positive eugenics, for Huxley, on the basis that in the case of heterozygote advantage over the homozygote the way for prolonged and scaled improvement will be closed. The “average” of heterozygote intelligence in a given environment will more fertile than the homozygotes that surpass them in

talent. He sharply answered his imagined opponents. Nature is not stable, and, it would seem, stable polymorphism sooner or later is “overthrown.”

Huxley's care regarding Dobzhansky's views on the nature of balanced polymorphism was possibly related to fact that the arguments of positive eugenics had weighty evidence. In fact, having achieved a balanced polymorphism, populations lose many talented people, although it also protects the sick, if they are heterozygotes. Medical genetics has provided a large amount in this field of study.

Huxley suggested looking at the problem from the point of view of evolutionary theory. The representatives of positive eugenics often recall that initially an effective selection requires authoritarian methods and therefore can act only by way of some kind of dogmatic tyranny. The idea, which was widely disseminated in the press, Huxley claimed, is evidence of the incompetence of the authors of positive eugenics in the problems of psycho-social evolution. In the evolutionary approach, one can actually discuss what can be called genetic expressions, but they fall into the framework of the theory of biological evolution. In other words, evolutionary theory proves the absence of faith in man's evolutionary potential. Geneticists and eugenicists simply support that fact of evolutionary theory, since they study already realized life. In the sphere of eugenics Huxley felt a genuine Dictator. In 1934, he even wrote a long essay on the problems of planning in society on the basis of scientific humanism, which was entitled “*If I was Dictator*.” In 1932, he became a steady member of the committee for political and economic planning, and thanks to him, eugenics became a component of the committee's duties. The question of tyranny did not worry Huxley in the eugenics plan, although he actively discussed that question in his works on evolutionary (scientific) humanism and evolutionary ethics. He introduced the term “totalitarianism” itself, analyzing the situation in the Soviet Union after 1937. He wrote: “In the contemporary world grows self-tyranny: in part, like a dogma, it is in principle non-scientific, but in part it is entirely tolerable.”

He concluded the Galton lecture with the words, which can be found in any work on human biology, evolutionary theory, and genetics. He declared: “In an evolutionary perspective on eugenics—the progressive genetic improvement of the human species—the primary goal becomes human evolution. How should the eugenicist plan his work for the long-term perspective? Undoubtedly, it is necessary to continue investigations on human genetics, reproduction, including the methods of sterilization. Establish Darwin research stipends in the area. We should all the time support negative eugenics, especially in the field of investigating social group problems. We should continue to investigate the field of human population growth and should immediately support all agencies and organizations, which conduct scientific politics in the field of the control of human population size. In such a plan, we should support all agencies which provide eugenics consultations and advice at after marriage. Since significant eugenic improvement depends on donor fertility, we should constantly improve that practice, primarily by developing new systems of testing, and we should publicly support artificial fertilization by way of donors. In general, we should bring real genetic improvement into our home. *We should finally do something so that people will understand that social and cultural amelioration is insufficient* [These words are a direct argument against including Huxley amongst the “*environmentalists*” in eugenics; author's emphasis.] If people are limited to half-measures, then they simply will turn into poor environmental thinkers, they should combine social amelioration with genetic improvement, or finally, with hope that all this will come in the future.

Undoubtedly, not only eugenicists should help educate the public and especially the members of the professions, such as physicians, teachers, scientists, administrators, and others in regards to eugenics, but this should lie at the foundation of all educational systems. Moreover, the educational system at all levels should be improved, in order to provide at least the minimum of biological understanding of the problems of the reproduction of populations (human population), genetics, selection, ecology, nature preservation, the evolutionary process at all levels, including man and his significance in the Universe, and his corresponding responsibilities.

If this will all come to be, and I believe it will, Huxley highlighted, the role of man will become better and he will come to control the evolutionary process on the planet and direct the future path of evolution in a desirable direction. The full realization of genetic possibilities is the primary motivation for man's efforts, and eugenics is one of the fundamental sciences of man" (Huxley. 1962b, pp. 139-140).

By way of a Conclusion

In scientific biographies it is hardly necessary to make general conclusions. But the life of Huxley is undoubtedly evidence of how diverse a person can be in contributing simultaneously to the most varied fields of biological and social sciences, although the latter were touched upon only in passing in analyzing the strictly biological problems. Huxley was a great scientist, a popularizer of science, and organizer of science on the national and global stage.

It is completely natural that, in investigating the very broad activities of Huxley, many events in his life will remain untouched. In addition, some well-known moments of his biography conform to a simple logic. For example, in 1915 at the Rice Institute, Huxley and Müller daily discussed the problems of genetics and the genetic basis of evolution. They constantly spoke of the role of recombination processes and, of course, the role of mutations. This disturbing theme became a subject for their further correspondence. Moreover, after World War I, Huxley chose to investigate experimental embryology, which had no connection with genetics or evolutionary theory. The reason for choosing experimental embryology as a fundamental object of investigation remains obscure.

But an even greater secret remains how Huxley's immeasurably great activity conquered his permanent depressions. There is a book, *"Darwin—the Invalid"*. One could easily write the book *"Huxley—the Invalid"*. Juliette Huxley, his wife, fully described in her autobiography how difficult it was for Huxley to overcome his depressions. She noted: "The first time was in 1919 when I took him to Doctor Vittoz in London. He was in a terrible state. After the visit to the doctor, he became completely physically immobile, and the depression became much less acute. Only now do I understand that we were in great trouble" (J Huxley, 1987, pp. 83-84). On Huxley's second nervous-psychic breakdown Juliette wrote: "When we were in Africa, he, possibly, contracted malaria and took a large dose of metacrine, a good drug against malaria. Upon return home he was still shaking. His liver was in a poor state, but there was something else even more serious—his deep depressive condition. Even before his departure, he had serious conflicts at the Zoological Society, but who could know that the soul is located in the liver. This was my second experience of observing Julian in a period of complete loss of his work abilities" (Ibid., p. 188). Later Juliette regularly described in her husband's words his state of health and general condition. Huxley twice underwent electroshock therapy. In 1944, when he first took this

electroshock procedure, Juliette wrote: "This was a complete nightmare, but with great anxiety I signed the agreement for the treatment." Further she added Julian's words: "I was never able to forget the doctor's eyes, which glanced at me at the moment of attaching the electrodes to my head. There was an especially frightening moment of shock, during which I lost consciousness. However the treatment helped me, although to this time no one can understand why electroshock lessens depression. Possibly, it erases previous events from the memory without leaving any trace. In any case, there is an influence on the memory, and after a month follows complete recovery" (Ibid., p. 87).

Somehow, after the next depression, Huxley received an invitation to visit the Soviet Union for a jubilee of the Soviet Academy of Sciences. Juliette wrote: "I insisted on the trip because I knew that the voyage would re-establish his complete belief in himself. He described in his *Memories* what an anger Lysenko's lecture produced in him. Upon returning home, he felt completely recovered" (Ibid., pp. 192-193). It seems that Huxley's anger in the event of intellectual disfigurement extinguished other undesirable feelings.

Thus, the diversity of Huxley's activities existed despite spiritual invalidism. Perhaps this "point of invalidism" to some extent defined his investigatory themes? It is possible that his interest in unlimited progress, including the evolution of man, in eugenics, ethics, humanism, and the global consequences of overpopulation in one way or another depended on Huxley's spiritual state, from his spiritual world on the whole.

Chronological Table

1887 – Julian Sorell Huxley is born in London on June 22.

1889 – His brother Trav is born.

1892 – Julian enters grammar school.

1894 – His brother Aldous was born.

1895 – His grandfather Thomas Henry Huxley dies.

1897 – Julian enters preparatory school.

1900 – He entered Eton College.

1906 – He enters Balliol College at Oxford University. Trip to Heidelberg to study German.

1908 – Wins the Newigate Prize for literature. Julie Huxley died from cancer on November 29.

1909 – Julian takes a first-class degree in natural history (zoology) at Oxford University. Participates in the celebrations at Cambridge of the centenary of Darwin's birth, and the 50th anniversary of the publication of the *Origin of Species*. He is awarded the Napoli stipend from Oxford University.

1909 – 1910 – He begins his investigations at the Napoli Marine Biological Station.

1910 – He becomes a lecturer at Balliol College and a demonstrator as the Department of Zoology and Comparative Anatomy at Oxford.

1910 – Publication of the work on regeneration in *Sycon*.

1912 – With his brother Trev he investigates courting in *Podiceps cristatus*. Assistant of the biological sciences at Rice Institute in Houston, Texas. Visit to T. H. Morgan's laboratory in New York. Agitates for Muller to move to Houston. Visit to the New York Museum of Natural History. Conversations with Osborne. Publication of *The Individual in the Animal Kingdom*.

1913 – Works with Otto Warburg and Richard Hertwig in Germany. Assistant Professor at Rice Institute. Depression of medium severity.

1914 – Return to England. Nervous breakdown.

1914 – 1915 – Professor of Biology at Rice Institute.

1916 – Work at the Marine Biological Station at Woods Hole, Massachusetts. Returns to England to participate in World War I. Work on the censor committee. Meeting with future wife, Juliette Baillot near Oxford.

1917 – Service in Army. His brother Andrew is born.

1919 – Work in the New College and demonstrator at the Department of Zoology and Comparative Anatomy at Oxford. Marries Juliette. Strong nervous breakdown.

1920 – Completed the investigations on the Mexican salamanders.

1921 – Member of the expedition to Spitzbergen. Visits to Norway, Denmark, and Germany.

1923 – Publishes *Essays on Biology*.

1924 – Visit to Rice University to deliver lectures.

1925 – Professor of Zoology at King's College, London University.

1926 – Invited by Wells to collaborate and his son to write an encyclopedia *Science of Life*.

1927 - Becomes Head of the Zoological Department at King's College. Works on *Science of Life*.

1927 – 31 – Lecturer at King's College, and full professor of physiology.

1929 – Visit to East and Central Africa at the invitation of the Colonial Committee on Education.

1930 – President of the Association of Scientific Workers.

1931 – Visit to the Soviet Union with Intourist. Participates in organizing the Planning Committee.

1932 – Publishes *Problems of Relative Growth*.

1933 – Death of Leonard Huxley.

1934 – Publishes *Elements of Experimental Embryology* with de Beer. Vacation in Switzerland.

1935 - 1942 – Becomes Secretary of the Zoological Society of London.

1935 – Lectures in Canada and the United States. Publishes in *We Europeans* (with Haddon).

1936 – Publishes *Natural Selection and Evolutionary Progress*. Makes an attempt to create a continental zoo. Takes part in forming the committee on human population and the Association or the study of systematics from the point of view of general biology, and also becomes one of the founders of the Institute for the Study of Animal Behavior.

1936 – 1941 – Prepares *Evolution: The Modern Synthesis*.

1936 – 41- Takes part in the founding committee for population investigations in the Association for the study of systematics from the point of view of general biology.

1938 – Selected member of The Royal Society. Summer vacation in Switzerland.

1940 – Publishes *New Systematics*. Becomes patron of the Free German League of Culture in Great Britain.

1941 – 1942 – Lecture in the United States supported by the Rockefeller Fund. Publishes *Evolution: A Contemporary Synthesis* and *The Uniqueness of Man*.

1943 – Romanes' Lecture at Oxford on evolutionary ethics. Radio work.

1944 – Visit to Western Africa as member of the commission for higher education in the British Colonies. Participates in the movement to found UNESCO. Works actively in the Institute of Intellectual Cooperation for the League of Nations. Nervous breakdown.

1945 – Visit to the Soviet Union on invitation of the Soviet Academy of Sciences. Secretary of the Preparatory Commission for founding UNESCO. Visit to the United States. Lectures in New York on the dangers of atomic weapons.

1946 – 1948 – Becomes first Director General of UNESCO

1946 – Session of UNESCO in Venezuela.

1947 – Visit to Haiti and the United States for UNESCO. General Assembly of UNESCO in Mexico. Publishes report on preserving wild nature in Great Britain. Publishes Romanes' lecture "*Evolution and Ethics*." Visits to Central America, Haiti, South America.

1948 – Visits to Czechoslovakia, Hungary, Yugoslavia, Austria, Holland, the countries of the Near East, Northern Africa. Visit to Poland as a tourist. General conference of UNESCO in Beirut, at which he decides to prepare a history of humanity.

1949 – Participates in the formation of the ecological society and society for the study of animal behavior in England. Vice-president of the UNESCO commission on writing the history of humanity. Prepares recommendation for forming the committee on national parks for the government.

1950 – Lecture at the Swedish Academy of Sciences on ritualization in birds. Short visit to the United States. Participation in the UNESCO session in Florence.

1951 – Lecture at Munich University at Rensch's invitation. Visit to the United States to participate in the forming of the society for the study of evolution. Lecture at Indiana University on Muller's initiation.

1951 – 1952 – Nervous debilitation.

1953 – Awarded the Kalinga prize for the popularization of science. Lecture in Italy. Scientific visit to Australia.

1953 – 1954 – Visits to the United States, islands of the Pacific Ocean, Australia, Tasmania, East India, Iraq, Iran, Syria to deliver lectures on demographics. Publishes *Evolution in Action*. Becomes Editor of *Evolution as a Process*.

1955 – Lecture in New York on cancer.

1956 – Awarded the Darwin medal at the London Royal Society. Lecture at The Royal Society in honor of the Queen-Mother. Trip to Spain to discuss the problem of preserving wild nature. Nervous breakdown.

1957 – Publishes "*New Bottles for Old Wine*." Nervous breakdown.

1959 – Takes part in the conference for the Darwin Jubilee (Chicago). Lecture on planning in Delhi.

1959 – 1962 – Becomes President of the Eugenics Society of London.

1960 – Trip to South and East Africa, reports to UNESCO on the problem of preserving wild nature.

1961 – Trip to West Africa. Lecture at Ghana University. Visit to Canada and the United States.

1962 – Personal visit to the United States. Visit to Norway.

1963 – Trip to Jordan, Ethiopia. Reports on national parks. Death of Aldous Huxley.

1964 – Publishes *Essays of a Humanist*.

1965 – Organizes discussion at The Royal Society on the problem of ritual behavior in animals and man. Visits to Israel and Africa.

1966 – Nervous stress.

- 1967 – Vacation in Tunisia. Honoring his 80th year. The BBC organizes a jubilee program.
- 1968 – Translates the article “Courting in the Greater Crested Grebe”.
- 1969 – Vacation in Yugoslavia.
- 1970 – Awarded the Gold Medal for a great contribution to scientific investigations in the field of preserving wild nature. Publishes first volume of *Memoires*.
- 1971 – Visit to Paris for the 25th anniversary of UNESCO. Visits the national parks of East Africa.
- 1972 – Visit to the Department of Zoology at Oxford University.
- 1973 – Publication of the second volume of *Memoires*.
- 1975 – Dies on 14 February from pneumonia.

Julian Huxley's Publications

1912

Some phenomena of regeneration in *Sycon* ; with a note on the structure of its collar – cells.// *Phil. Trans. Royal Soc. London. B* **202**. P. 165 –189.(a)

A first account of the courtship of the redshank (*Totanus calidris* Linn)// *Proc. Zool. Soc. Lond.* V. **2**. P. 647 – 655.(b).

A “ disharmony “ in the reproductive habits of the wild duck (*Anas boschas* L)// *Biol. Zbl.* V. **32**. .P. 621 –623.(c)

The great crested grebe and the idea of secondary sexual characters.// *Science.* V. 36. P. 601 – 602. (d)

The individual in the animal kingdom. Cambridge. Univ. Press. (e)

1914

The courtship habits of the great crested grebe (*Podiceps cristatus*) ; with an addition to the theory of sexual selection.// *Proc. Zool. Soc. Lond.* V. 2. P. 491 – 562.

1916

Bird watching and biological science. Some observations on the study of courtship in birds. // *Auk.* V. 33. P. 142 – 161.

1919

Some points in the sexual habits of the little grebe, with a note on the occurrence of vocal duets in birds. // *Br. Birds.* V. 13. P. 155- 158.

1920

Metamorphosis of axolotl caused by thyroid feeding.// *Nature. Lond.* V. 104. P. 435.

1921

Further studies on restitution bodies and free tissue – culture in *Sycon*.// *Quart. J. micr. Sci.* V. 65. P. 293 – 322. (a)

Studies in dedifferentiation. 11. Dedifferentiation and resorption in Perophora.// *Quart. J. Micr. Sci.* V. 65. P. 643 – 697.(b)

Obituary of W. W. Fowler. // *Br. Bird.* V. 15. P. 143 – 144. (c).

Review of H. E. Howard. Territory in Bird Life. // *Discovery.* V. 2. P. 135 – 136. (d).

The accessory nature of many structures and habits associated with courtship. // *Nature. Lond.* V. 108. P. 565 – 566. (e).

1922

Experiments on amphibian metamorphosis and pigment responses in relation to internal secretions. // *Proc. R. Soc. B.* V. 93. P. 36 – 53. (With L. T. Hogben).(a)
Ductless gland and development. Amphibian metamorphosis considered as consecutive dimorphism, controlled by glands internal secretion. // *J. Hered.* V. 13. P. 349 – 358. (b)
Preferential mating in birds with similar coloration in both sexes. // *Br. Birds.* V. 16. P. 99 – 101.(c).
Some observations on the habits of the red – throated diver in Spitsbergen. // *Br. Birds.* V. 18. P. 34 – 46. (With G. van Oordt). (d).

1923

Ductless gland and development. Amphibian metamorphosis considered as consecutive dimorphism, controlled by gland internal secretion. // *J. Hered.* V. 14. P. 3 – 11. (a)
Studies in dedifferentiation. IV. Resorption and differential inhibition in *Obelia* and *Campanularia*. // *Quart. J. Micr. Sci.* V. 67. P. 473 – 495. (With G. R. De Beer). (b).
Courtship activities in the red-throated diver (*Colymbus stellatus* Pontopp.) ;together with a discussion of the evolution of courtship in birds. // *J. Linn. Soc. Zool.* V. 35. P. 253 292. (c)
Essays of a biologist. London : Chatto and Windus.(d)
An essay on bird mind. // *The Cornhill Magazine.* V. 54. P. 415 425. (e).
Progress, biological and other. // *The Hibbert Journ.* V. 21. P. 436 – 460. (f).

1924

Studies in dedifferentiation. 5. Dedifferentiation and reduction in *Aurelia*. // *Quart. J. micr. Sci.* V. 68. P. 471 – 479. (With G. R. de Beer). (a)
A note on the reactions of chick chorio – allantois to grafting. // *Anat. Rec.* V. 28. P. 385 – 388. (With P. D. F. Murray).(b).
Early embryonic differentiation. // *Nature. Lond.* V. 113. P. 276 – 278. (c)
The variation in the width of the abdomen in immature fiddler crabs considered in relation to its relative growth – rate. // *Amer. Nat.* V. 58. P. 468 – 475.(d)
Constant differential growth – ratios and their significance. // *Nature. Lond.* V. 114. P. 895 – 896.(e)
Eugenics and heredity. // *The New Statesmn.* V. 23. P. 281 – 283. (f).
Some further notes on the courtship of the great crested grebe. // *Br. Bird.* V. 18. P. 129 – 134. (g).
Some points in the breeding behaviour of the common heron. // *Br. Bird.* V. 18. P. 155 – 163). (h).
America revisited. The Negro Problem. // *Spectator.* November 29. P. 821 – 822. (i).
Absence of prenatal effects of lens – antibodies in rabbits. // *Brit. J. Exp. Biol.* V. 1. P. 215 – 248. (With A. Carr – Saunders). (j).

1925

Studies on amphibian metamorphosis. 11. // *Proc. R. Soc. B.* V. 98. P. 113 –146. (a)
Mendelian genes and rates of development. // *Nature. Lond.* V. 114. P. 861 –863. (With E. B. Ford). (b).
The absence of “ courtship “ in the avocet. // *British Bird.* V. 19. P 88 – 94. (c).
Studies on the courtship and sexual life of birds V. The oyster – catcher. // *Ibis* 12th ser. V. 1. P. 867 – 897. (with F. Montegue). (d).

1926

Studies in dedifferentiation. V1. Reduction phenomena in *Clavellina lepadiformis*. // *Pubbl. Staz. Zool. Napoli.* V. 7. P. 1-35. (a)
Modification of development by means of temperature gradients. (Record of reading of paper only.). *Anat. Rec.* V. 34. P. 100.(b)
The annual increment of the antlers of the red deer (*Cervus elaphus*). // *Proc. Zool. Soc. Lond.* V. 2. P. 1021 – 1035.(c)
The stream of life. London : Watts. (d)
Essays in popular science. London : Chatto and Windus. (e)
Animal biology. London : G. Allen and Unwin. (With J.B.S. Haldane) (f).
The biological basis of individuality. // *J. Phil. Stud.* (g).

1927

Further work on heterogenic growth. // *Biol. Zbl. Bd.* 47. S. 151 – 163. (a)
Discontinuous variation and heterogeny in *Forficula*. // *J. Genet.* V. 17. P. 309 – 327. (b)
On the relation between egg – weight in birds. // *J. Linn. Soc. Zool.* V. 36. P. 457 – 466. (c)
Studies on heterogenic growth. 1V. The bimodal cephalic horn of *Xylotrupes gideon*. // *J. Genet.* V. 18. P. 45 – 53.(d)
The modification of development by means of temperature gradients. // *Arch. EntwMech. Org.* Bd. 112. S. 480 – 516.(e)
Mendelian genes and rates of development in *Gammarus chevreuxi*. // *Brit. J. exp. Biol.* V. 5. P. 112 –134. (With E. B. Ford).(f)
Religion without revelation. London : Benn. (g)

1928

Sexual differences of linkage in *Gammarus chevreuxi*. // *J. Genet.* V. 20. P. 145 – 156. (a)

1929 – 1930

The science of life : a summary of contemporary knowledge about life and its possibilities.
London : Amalgamated Press. (With H. G. and G. P. Wells).

1930

Spemanns “ Organisator “ und Child Theorie der axialen Gradienten. // *Naturwissenschaften*
Translated by H. Spemann. Bd. 18. S. 265. (a)
Bird watching and bird behaviour. // London : Chatto and Windur. (b)
Ants. // London : Benn (c)
Bird mind. // *Atlantic Monthly.* V. 146. P. 473 – 482. (d).
The courtship of birds. // *The Listener.* V. 3. P. 935 – 937. (e).
Eugenic sterilisation. // *Nature.* V. 126. P. 503. (f).
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