Review of: Julian Huxley, *Evolution: The Modern Synthesis – The Definitive Edition*, with a new forward by Massimo Pigliucci and Gerd B. Müller. MIT Press.

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Science, philosophers and sociologists of science often tell us, is inherently an ahistorical enterprise, with scientists at most dealing with Whiggish history and hero-worship. If this is the case, one has to be suspicious whenever a science book of historical significance is reissued. It is not hard to explain the flurry of editions of Darwin's famous texts, republished to coincide with the Darwin bicentennial and the sesquicentenary of *On the Origin of Species*. The republication of books by less iconic figures urges us to ask *Why this book? Why Now?* Julian Huxley's 1942 classic *Evolution: The Modern Synthesis* (ETMS), recently reissued by MIT Press, is rich in biological examples and evolutionary argument, and is of enough historical significance, to merit republication and discussion.

1942 saw the publication of two books that came to represent the Modern Synthesis in evolutionary thought, which was the guiding framework for evolutionary biology for most of the twentieth century: Ernst Mayr's *Systematics and the origin of species, from the viewpoint of a zoologist* and Julian Huxley's *Evolution: The modern synthesis*, which gave the evolutionary synthesis its name. Both books are milestones in the history of evolutionary thought. The two books however are very different.

Huxley's book, sometimes described as ponderous and, remarkably from a contemporary perspective, also described as a popular account, is more massive than Mayr's shorter book, spanning close to 800 pages in the edition under review. Huxley set out, as he puts it in the introduction to the book, to promote a "synthetic point of view" on evolution. The synthesis he envisions is not restricted to a synthesis of Darwinian natural selection and Mendelian heredity, as the Modern Synthesis is often presented, but includes genetics, developmental physiology, ecology, systematics, paleontology, cytology, and mathematical analysis. Not all of these receive the same amount of attention in Huxley's presentation, but they ground his explicitly multifaceted approach to evolution. An important aspect of this pluralistic approach is that for Huxley it is abundantly clear that different groups are expected to show different kinds of evolution, depending on the organization of their genetic material, their reproductive strategies and more (p. 45). This guiding perspective and the question of evolutionary trends and progress are the two axes along which the book moves. Fittingly, the second chapter of the book, which follows an introductory chapter on natural selection, is concerned with the "multiformity" of evolution while the last is dedicated to evolutionary progress. The rest of the book deals with *Mendelism* (chp. 3), and in particular the importance of particulate heredity, the relation between genes and characters, and factors affecting gene expression, *Genetic Systems and Evolution* (chp. 4), including the early evolution of genetic systems, and the effects of hybridization and polyploidy, *Species and speciation* (chps. 5-7), covering geographical as well as other kinds of speciation and a discussion of taxonomy, *Adaptation* (chp. 8), including a discussion of preadaptation and a repudiation of Lamarckism, and *Evolutionary Trends* (chp. 9), in which Huxley gives an account of evolutionary trends which is based on natural selection and the effects of development rather than on orthogenesis.

ETMS was a successful book. A second edition was published in 1963, and supplemented the original text with a long introduction attempting to bring the book at least partly up to date. A third edition, published in 1974, also featured a new introduction aimed at reciting recent developments and kept the original text unchanged. This time around the introduction was not written by Huxley, but by a group of nine of Huxley's associates, each an authority on a specific topic, an illustration of the scope of the book. Included in the Definitive Edition now published by MIT Press are the introductions from the 2nd and 3rd edition. Alas, the new edition lacks an introduction summarizing how current knowledge affects the arguments Huxley makes in the book, let alone relevant notes throughout the book offering a contemporary perspective. As the editors rightfully note in their forward, doing justice to current knowledge and theoretical considerations in an introductory chapter hardly seems possible. The editors direct the reader to the volume they edited entitled *Evolution – The Extended Synthesis* (MIT Press, 2010). The reader of the present volume, however, is left feeling shortchanged. Huxley's book deserves to be brought to the present.

I already mentioned that Huxley appreciated the multi-formity of the evolutionary process. Indeed, Huxley's book has the atmosphere of a more tolerant, pluralistic, view of evolution than we have come to expect in the wake of the "hardening of the synthesis" (as Stephen Gould so aptly put it). The Synthesis came to represent a hard-line view of evolution that privileged accumulation of small mutation via natural selection over any other evolutionary process, marginalized the evolutionary consequences of development, and took speciation to be almost universally the result of geographical isolation. Two authors that receive a perhaps surprisingly sympathetic hearing in Huxley's book are not only a reminder of an earlier era, prior to the hardening of the synthesis, but are reasons to revisit the book when considering the future of evolutionary thought. They are Cyril Darlington and Richard Goldschmidt. Much maligned, and at times misunderstood, the two rebels are far from dismissed out of hand in Huxley's book. Indeed, Darlington's conception of the evolution of genetic systems (the subject of chp. 4), and Goldschmidt's views on speciation and, more significantly, developmental genetics, suffuse the book.

Darlington published *The Evolution of Genetic Systems* in 1939 (while already forcefully hinting at them in the final chapter of *Recent Advances in Cytology* in 1932). Goldschmidt's avowedly anti-neo Darwinian views are the subject of his 1940 book *The Material Basis of Evolution*. The centrality of these works for Huxley is made apparent in the following quotation:

> "The nature of an organism thus influences the mode of evolution… However, there has been hardly any attempt to survey the problem as a whole. Darlington's *Evolution of Genetic Systems* is a notable essay in this direction though limited to chromosomal and reproductive mechanisms and Goldschmidt's *Material Basis of Evolution* attempts the same for modes of development. A small but increasing number of writers realize that such a general approach is not only possible but necessary. Comparative Evolution is destined to become as important as Comparative Anatomy." (p. 127-8)

Both Darlington and Goldschmidt were deeply concerned with the functional and evolutionary consequences of the organization of the genetic material. Darlington attempted to relate the karyotypic organization of a species (e.g., polyploidy, sex chromosomes) with its reproductive strategy, and in particular the differences between inbreeding and outbreeding species. Goldschmidt's views about evolutionary saltations are well known, his views about the genome perhaps less so. Goldschmidt forcefully argued against the idea of "atomic" genes organized on the chromosomes like beads-on-a-string. He thought that the chromosome is a hierarchically organized system, consisting of chromosomal segments of increasing size. These ideas were intimately connected to Goldschmidt's views on macro-evolution, which for him involved "systemic mutations" which are essentially chromosomal rearrangements. While he did not go as far as Goldschmidt, Huxley emphasized that chromosomes cannot be considered random assortments of genes and should instead be understood as functional gene arrangements. Huxley also explored the evolutionary implications of mutations that involve changes in whole sets of chromosomes, which he termed “genome-mutations” (pp. 85-87).

While accepting that evolution may at times be more rapid than typically assumed, as Goldschmidt argued, the editors of the present edition are quick to reject Goldschmidt's ideas about genome-wide upheavals. It seems that this conclusion may be somewhat premature. A wide and growing array of examples suggest that genomic-wide changes, often epigenetic in nature, may be triggered in various conditions. For example, nutritional stress, heat shocks, and hydrostatic pressure, cause genome-wide epigenetic changes in organisms such as rice, *Brassica* and flax, and transposable elements are often activated as a result of stress, such as wounds, and, notably, hybridization, and can lead to changes throughout the genome (Jablonka & Lamb 2008). While not identical to Goldschmidt's ideas from before the molecular revolution, the similarities are remarkable. The role such epigenomic changes play in evolution has yet to be fully investigated. Possible evolutionary consequences include (a) the fixation of the changes, when the affected population is small or during evolutionary bottlenecks; (b) increased evolvability, due to increased variation; (c) specific adaptation, in species that exhibit repeatable and specific genomic restructuring, such as wheat (Levy & Fledman 2004). As a result, induced epigenomic changes may establish genetic constraints and lead to preferred evolutionary trajectories.

The evolutionary importance of hybridization and lateral gene transfer is being increasingly recognized (Arnold et al. 2008; Rieseberg 2009). The importance of hybridization, and the polyploidy that might result, were recognized by Huxley who discussed it in relation to the arguments made by Darlington and noted that it might lead to increased variation (see chp. 6, sec. 8 and 9 in particular). As Huxley noted, the results of hybridization depend on the genetic and cytological mechanisms that are operative in each particular case, and thus hybridization and its genomic aftermath combine the interests of Darlington and Goldschmidt. Clearly disrupting the Tree of Life metaphor, these evolutionary processes can lead to a variety of evolutionary consequences, notably the transfer of adaptive traits between populations and species (Arnold et al. 2008) and increased variation. It is striking that hybridization may be an adaptive response to environmental conditions: Female spadefoot toads are likely to choose heterospecific mates in conditions in which hybridization is favorable (Pfennig 2007). Polyploidy and hybridization are involved in speciation in many taxa, though most common in plants. The genomic consequences of polyploidization deserve further study, but current knowledge indicates that they may involve a variety of epigenomic mechanisms and lead to massive genomic alterations, and include changes in methylation patterns, histone modifications, as well as targeted genetic changes (see Lamm & Jablonka 2008). Once again, the ideas of Goldschmidt and Darlington seem prescient, and fundamentally interrelated.

A large body of work is devoted to trying to explain, using the framework of the Modern Synthesis, the evolution of prominent genome functions, such as error correcting mechanisms, and genomic phenomena, such as supposedly selfish genomic parasites. Genome mechanisms are thus typically portrayed as adaptations for achieving reliable heredity. Genomic parasites, as transposable elements are typically understood, are explained as "selfish" genetic elements that further their own evolutionary success. Whether focusing on the organism or the gene as the appropriate unit of selection, these paradigmatic explanations presuppose the existence of genes as independent units of function and neglect the consequences of the ontogenetic developmental propensities and constraints of genomes. We now know, however, that the genome is highly dynamic and that the functioning of the genome depends on the constant activity of a variety of molecular mechanisms, epigenetic and otherwise. The result is an active and responsive system that exhibits complex developmental dynamics.

The significance of the development of organisms for understanding their evolution is the focus of the Evo-Devo research program. As the editors note, this insight was already emphasized by Huxley in *ETMS* but has only recently begun to be taken seriously. Alas, this research approach has yet to grapple with the genome as a significant developmental system whose understanding requires close attention to the interaction between the developmental properties of the system and its evolutionary dynamics (see Lamm, forthcoming).

The growing knowledge of genome dynamics and mechanisms, epigenetic and otherwise, should play a critical part in any contemporary attempt to rethink the evolutionary "synthesis". A revitalizing of the Modern Synthesis of Mendelian Genetics and Darwinism will necessarily have to replace classical genetics with contemporary epigenomics. Huxley's discussion may be rewarding and inspiring. At the very least, his demand for a pluralistic view of evolution, that pays attention to the evolutionary forces unique to different groups, has become increasingly hard to ignore.

I have focused this review on some aspects of Huxley's portrayal of evolution that I find particularly powerful for thinking about evolution and that are perhaps underappreciated. It goes without saying that various aspects of the book have not withstood the test of time as well as others. In particular, Huxley's discussion of evolutionary progress, especially its relation to the future evolution of humans seems to me to show that Huxley was fundamentally a man of his time (I find it irresistible to mention that Huxley expressed hope for work on telepathy and extra-sensory perception). Be that as it may, some of his arguments may offer insight, as well as serve as a cautionary tales, to those thinking about notions of transhumanism, and those such as Ray Kurzweil and Eliezer Yudkowsky who suggest that "the singularity is near." The notion of “singularity,” as used by these thinkers, refers to an “intelligence explosion” we are about to experience as result of successive generations of intelligent machines, each able to design a next generation of even more intelligent machines. While arguably all too optimistic about progress, Huxley concluded his book by noting that our optimism about the future progress of human evolution "may well be tempered by reflection on the difficulties to be overcome."

Before concluding this review of Pigliucci and Müller's Definitive Edition of *ETMS*, we must turn our attention to the questions I mentioned at the outset. Why this book? Why now? It should be apparent at this point, that I am generally sympathetic with the impulse that led to the decision to republish this classic of evolutionary thought. The book, as well as the notion of an evolutionary synthesis, played a significant role in the history of evolutionary thought. It has long been debated whether the so-called Modern Synthesis was overall a positive force in biology, or whether its lacunae undermine its contributions. More recently, voices have been heard claiming that the time is ripe for a new, extended, evolutionary synthesis. It is no coincidence that *ETMS*, with its historical role yet pluralistic outlook, resurfaces as an imagined precursor. The editors' hope that their own work will push forward such a revised view of evolution is laudable; naturally, as is apparent in my review, each of us working in the trenches will have their own views about the direction this endeavor should take.

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