Julian Huxley's Undergraduate Years, Oxford Biology, and the Origins of "Epigenetic" Animal Characters in the early 20th-century

Abstract

Julian Huxley is remembered as the author of his 1942 *Evolution: The Modern Synthesis.* But he is nowadays criticised for having reduced biology to selection of genes. Some have however suggested that Huxley's biological views were more expansive – including rather than excluding issues regarding development. In this paper, using hitherto unexplored sources, I show that Huxley's developmental understanding of animal characters was rooted in his education at Oxford in the early 20th-century. He learned to view characters as end-products of 'epigenetic' processes that integrated multiple cross-pollinating causes such as heredity and development. After briefly exploring Huxley's understanding of character development, I show how we can get to grips with Huxley's biological views by exploring the context of his education at Oxford from 1906 to 1909. I then show how Huxley received and used these ideas, before I illustrate how they played an important role in his academic and socio-political work.

Evolution: The Modern Synthesis (1942) is probably Julian Huxley's most famous book, re-printed as recently as 2009 (Huxley, Pigliucci, & Müller 2009). Nevertheless, it is nowadays the subject of criticism for having neglected developmental biology. That is, it is said that the book sees individual development as "of no use for the understanding of evolutionary diversification. Development was all that follows from the genetic information" – having no creative role itself (Esposito 2013, p. 51; see also Walsh 2015; Peterson 2016, p. 10). This is not a universal opinion. The authors of the foreword to the 2009 edition of Huxley's book have noted his concern for the "developmental effects of genes and of the ontogenetic process in general" (Huxley, Pigliucci & Müller 2009, p. 5; see also Baedke 2024). More broadly, this underscores the point that, as Cain has argued, there were multiple "Syntheses" for Huxley himself (Cain 2010, p. 360). This paper examines the origins and development of Huxley's views about animal characters in general. I show that Huxley's view of animal characters, which privileged neither genetics nor development, can be understood when traced back to his education at Oxford in 1906-1909.

Huxley's biological views have already been shown to be more expansive. Kenneth Waters has warned that we should "resist the temptation to define [Huxley's] scientific practice purely in terms of his interest in evolutionary biology" (Waters 1992, p. 21; see also Baedke 2024). Huxley made it evident in his 1942 book that his concern was to see the study of genes and development as complementary. In the *Preface* to his 1942 book, Huxley wrote that "any originality which this book may possess lies partly in its attempting to generalize [Fisher's ideas regarding changes of mutation-effects] still further, by stressing the fact that a study of the effects of genes during development is as essential for an understanding of evolution as are the study of mutation and that of selection."

Development and inheritance were equally important to understand the inconstant "effects of genes", and thus characters.

A "Mendelian Revolution" may obscure Huxley's concern with development (Bowler 1989). After all, the traditional story, partly crafted by Huxley himself, is that the arrival of genetics allowed the revival of Darwinism in a new synthetical form around the 1930s (Huxley 1942; Bowler 1989; Bashford 2022). Kenneth Waters & Van Helden have suggested that this story, with regards to Huxley at least, distorts our understanding of him. Waters, with cues from Churchill, has proposed that Huxley aimed to develop an "embryological synthesis" (Waters 1992, p. 21). Churchill's contribution, and equally Olby's and Witkowski's, in Waters and Van Helden's volume shed much light on Huxley's work on developmental biology. Churchill focused in depth on Huxley's embryological work, particularly his and De Beer's *The Elements of Experimental Embryology* (Churchill 1992, p. 108). Olby briefly mentioned that Huxley, along with his ex-pupil De Beer, aimed to give a "developmental account of gene action" (Olby 1992, p. 66). Neither asked why Huxley had a concern about the developmental action of genes. Witkowski, following John Baker's suggestion that Huxley, in his laboratory work, "was concerned with ontogeny", argued that we should consider Huxley's Oxford tutors: John Wilfred Jenkinson and Geoffrey Smith. He quoted Baker saying that "one can scarcely doubt that it was the memory of J.W. Jenkinson's and Geoffrey Smith's teaching that caused Huxley to devote the whole of his laboratory research to experimental and analytical studies in ontogeny" (Witkowski 1992, p. 84). He looked at Huxley's work on relative growth, while Ridley had looked at the study of embryology in Britain more broadly, with a focus on Oxford (Ridley 1986). But Baker, Witkowski and Ridley did not link Huxley's Oxford education with his interest in the developmental action of genes.

What is novel here, then, is that I show that Huxley's more expansive understanding of characters was nothing inevitable – it was rooted in his Oxford education. In a broader debate about the development of characters, Huxley's tutors sided with what they called an "epigenetic" view, i.e. characters are end-products of context-dependent relative processes, rather than being preformed in cellular nuclei. Other theories debating the relationship between genetics, development and environment have been analysed elsewhere (Sapp 1987; Müller-Wille & Rheinberger 2012). Here I show that Huxley's view about animal characters was rooted at Oxford. We will start with a brief exploration of Huxley's discussion on the action of genes in 1942-1958, showing how Huxley distinguished characters from their complex interacting causes. In the second section of the paper, I show that this was rooted in the "modern" preformationist vs. epigenetic debate that was pervasive during Huxley's education at Oxford. In the third section, through Huxley's undergraduate essays, I show that Huxley accepted the "epigenetic" idea. In the fourth section, we see that Huxley read Weismann and others through these ideas. In the fifth section, I show that Huxley made sense of socio-political issues no less partly through them. In the final two sections, I show that Huxley debated against MacBride, Bateson, and Morgan, by employing his "epigenetic" view of characters, that was implicit in his repeated argument that the expression "gene for" was only a shorthand, while characters were end-products of more complex "epigenetic" processes.

Huxley's view of animal characters, 1942-1958

Huxley made it abundantly clear that the alteration of gene expression is important for evolution. I will pick two books, the first being *Evolution: The Modern Synthesis.* In the book's first chapter, Huxley was careful to make a distinction between "variation" and "characters". He wrote that variations were, broadly, of two types: "modifications" and "mutations" (Huxley 1942, p. 18). The former pertained to "alterations in the environment", while the latter were "alterations in the substance of the hereditary constitution". On the other hand, "characters" were a different business altogether. In all situations, those were combinations between heredity and environment – being products of both mutations and modifications. "Characters as such are not and cannot be inherited", Huxley wrote. For a character is always the joint product of a particular genetic composition and a particular set of environmental circumstances" (Huxley 1942, p. 18). One could not, and should not, equate heredity with a character, as one should not equate it with the environment. To talk about a "genetic factor for a rose-comb" was to have a "one-to-one or billiard-ball view of genetics". No character was "represented' by one genetic factor, or even a combination of factors. Huxley called this a "crude particulate view" that was "a mere restatement of the preformation theory of development: granted the rose-comb factor, the rose-comb character, nice and clear-cut, will always appear". We shall see in section two that it is no accident that Huxley connected this "crude" view of characters with preformation.

In chapter 3, he discussed, in a dedicated section, the relationship between genes and characters. He noted again that the notion of "mendelian characters", of the inheritance of characters, should be dropped. There were multiple ways in which the expression of a gene varied. He noted pleiotropism, the view that a single gene may affect multiple characters, or the view, as I detail more below, that genes interacted with each other, which he owed partly to Fisher's mathematics (Huxley 1942, p. 8). Another way was when genes interacted with the environment during the organism's development. That is, "a given character represents the end-result of a great number of genes interacting with the environment during development, and is not inherited as such" (Huxley 1942, p. 63).

Although characters products of broader relative processes, one gets a sense that Huxley put much emphasis on the role of genes and their interactions in the production of characters, in an asymmetrical sense. But this was no less true for Waddington (Loison 2022; Deichmann 2016). That did not hinder the latter from accepting a view of "reciprocal causation", namely the view that phenotypes were jointly produced by various processes between genotype and environment (cf. Tabery 2014). One may distinguish here genetic *determinism* from genetic *reductionism:* while genes were mainly important for the making of characters, they were integrated in the wider organism (Loison 2022, p. 185).

Huxley's commitment to a view of "reciprocal causation" can be seen in two similarities between his and Waddington's work, evident in Huxley's 1942 book. Just like Waddington, he emphasised the action of each gene as relative to other genes in a system, or a "gene-complex". He wrote that "the most revolutionary change has come in regard to the way in which the expression of a gene can be altered by other genes. The discovery of this fact has given us the two fundamental concepts of genic balance and the gene-complex. Thus the internal or genetic environment of a gene may produce effects upon its expression which are as striking as those induced by the external environment, and of course very much more important from the point of view of evolution" (Huxley 1942, p. 64). Indeed, natural selection did not act on any gene alone, but on a gene-complex. Doubtlessly this is why he focused Chapter 4 on "Genetic Systems and Evolution". Yet another similarity was Huxley and Waddington's adoption of Thorpe's "Organic Selection", according to which the environment was no mere fixed entity selecting the organism, but the organism, in turn, 'preferred" an environment, leading to further character polymorphism (Radick 2017; Loison 2022).

Moreover, the two exchanged a friendly correspondence. Waddington - "Wad" - was seemingly happy in 1957 about Huxley's long-delayed Knighthood. "I have always been shocked that one of the great liberal and progressive influences of our time has received little official recognition". In turn, Huxley viewed Waddington's *The*

Strategy of the Genes favourably, despite criticising it for not giving a more systematic account of "morphism". The book has been hailed as an expression of Waddington's criticisms against what he saw as the excesses of population genetics, including the passivity of the organism and a reductionism to genes. It should be telling that Huxley saw the book none the poorer for that matter. Indeed, Waddington was "glad you [Huxley] found something of interest in it and not too much that you strongly disagreed with".[1]

Huxley openly adopted Waddington's "epigenetics " in his less-known book *Biological Aspects of Cancer* of 1958. There he argued that 'there is no single "cause of cancer'', and hence one should expect a rich taxonomy of different 'cancers". He wrote that one cause was "epigenetic" which was "the analytic study of individual development" (Huxley 1958, 94). Citing Waddington's 1956 *Principles of Embryology*, he said that Waddington tackled the "central problem of differentiation' and showed that much more was needed to understand the 'method by which tissues and organs differentiate in the course of normal development" (Huxley 1958, p. 94). When he discussed the genetics of tumours, he repeated the point he had made at the start of his 1942 book, namely that "characters as such are never transmitted, but that their manifestation depends on the interaction of a large number of genes with each other and with the external and internal environment" (Huxley 1958, p. 36). Huxley's adoption of Waddington's "epigenetics" only in 1958 should warn us against equating the latter's term with what Huxley and his tutors called, as I show below, the "epigenetic" idea (see Deichmann 2016). Huxley's "epigenetic" idea was contrasted with the "modern" preformationist ideas emerging at Oxford in his undergraduate years.

Oxford Biology and the "epigenetic" view, 1899-1906

Walter Frank Raphael Weldon is usually thought of as a biometrician, but he was also an embryologist when he became the Linacre Professor of Zoology and Comparative Anatomy at Oxford between 1899 to 1906 (Provine 1971; Radick 2023). When Weldon arrived at Oxford in 1899, Poulton, a fellow Oxford colleague, had already formulated a Weismannian understanding of characters, according to which characters were preformed in their heredity (Poulton 1908). But Weldon rejected this more restrictive account of mechanistic development. Why?

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[1] Waddington to Huxley, January 1st 1958. Rice University, Fondren Library, Woodson Research Centre, Julian Sorell Huxley MS. 50, Series III: General Correspondence, Box 26, Folder 1

Before 1899, Weldon had studied under F.M. Balfour and then worked as an embryologist (Radick 2023). Gould has made of Balfour (mostly) an adept of Ernst Haeckel's recapitulationism (Gould 1977). To Haeckel, development was pre-determined by evolution (save for ultimately non-significant caveats), while the environment could only change already developed characters. *Pace* Gould, Churchill has shown that, to Balfour, development could be changed by the environment (Churchill 2007, pp. 61-62; for Balfour, see Geison 1978).

In 1882, Weldon noted non-recapitulative variations in the formation of the germ-layers of the lizard *Lacerta Muralis* (the germ-layers, the primary cell layers formed in early embryonic development, had been a core of Haeckel's recapitulationism) (Weldon 1883). By 1890, advances in cytology meant that the test of any theory of development was assessed on the grounds of cell mechanics (Maienschein 2007, pp. 111-114; Müller-Wille & Rheinberger, 2012). Wilhelm Roux and August Weismann's view that the development of characters was determined by the material properties of the cell was influential, although the embryologist Hans Driesch famously rejected it (Maienschein 1991).[2] By the early 1900s, William Bateson made claims about inheritance by arguing that observable characters paralleled factors in the nucleus. Weldon saw Roux, Weismann and Bateson to be sailing the same boat (Radick 2023).

In an unpublished manuscript mainly written in 1904-1905 against Bateson, Weldon rejected what he called the "determinants" of Roux and Weismann (Weldon 1904-1905; Radick 2023; Shan 2020). He favoured Driesch's view that cells differentiated relative to the environments acting on them. Unlike Driesch, Weldon also noted the importance of the internal environment of the cell. The observed and eventual "dominance" - end-form - of any cell was partly due to the developmental possibilities accumulated from the past (Radick 2005, pp. 35-6). Some developmental possibilities were restricted "due to a direct inhibition of certain properties, through the influence of neighbouring cells, rather than to any change in the material constitution" (Weldon 1904-1905). Weldon's pupil, Jenkinson, less inhibited to put labels than his teacher, called what he was against "preformationism", and what he favoured "epigenetic evolution".

There is no evidence that Jenkinson read Weldon's manuscript, but I show that he supported ideas similar to Weldon's. Jenkinson has received some attention in the literature, but not much in relation to Weldon's work

[2] See Churchill 2015 on the distinction of Weismann's work from Weismann*ism* – even Weismann recognised that the environment, broadly, played some part in the making of characters, a point which Huxley would later pick up.

(Gould 1977; Ridley 1986; Sapp 1987; Maienschein 1991; Horder 2008). With a degree in the humanities (*Literae Humaniores*) from Oxford in the early 1890s, he went to study with Weldon at UCL after 1894 (Marrett, 1917). In 1900, in a paper on the development of the mouse, he attacked the doctrine of recapitulation. Based on his observations of the mouse's development, he noted the influence of cytoplasmic "organ-forming stuffs" on the nucleus, concluding that "I believe that all attempts to institute homologies … are foredoomed to failure" (Jenkinson 1900, p. 75; Sapp 1987, p. 17). The development of mammals was "sui generis", i.e. relative to the environment. Jenkinson had acknowledged that "Professor Weldon's laboratory at University College London" was crucial for his work.

Between 1901 and 1905, Jenkinson finished his doctoral work at Oxford. In 1906, he published a series of papers emerging from it. He now focused more on the cell theory, specifically with regards to Roux and Weismann. At the end of a paper on the "Germinal layers of the Vertebrates", he placed Roux and Weismann's theories in a wider context. He contended that "the Roux-Weismann hypothesis of preformation is a modern resuscitation of the famous theory of evolution which was destroyed by Wolff more than a hundred years ago" (Jenkinson 1906, p. 82). Jenkinson thought that preformation was compatible with recapitulation. If the cell was preformed by its nucleus, he argued, then the "prime cause of differentiation – the structure of the fertilized ovum – is itself a heritage from a long line of ancestors, [and] each individual will of necessity repeat in its ontogeny the history of its descent" (Jenkinson 1906, pp. 82-83).

He rejected preformation and recapitulation. He argued that, if one wished to retain the word "recapitulation", one should not use it as a "recapitulation of any adult ancestral type, but merely a repetition of similar ontogenetic functions by cells which have inherited a similar structure. In destiny, however, such cells may be exceedingly diverse" (Jenkinson 1906, p. 87). Jenkinson argued that there were two problems that the "experimental embryologist" had to face. Firstly, to "describe in accurate terms the influence exerted upon the embryo by its environment" and, the second, "to determine the mutual relations which subsist between the parts of the embryo and between the parts of the whole" (Jenkinson 1906, p. 89). That is, "what are the external and what the internal factors which govern the process of differentiation" (Jenkinson 1906, p. 89). "Physiological study", Jenkinson wrote, was important to understand development, which might allow the experimental embryologist to better grasp "the problem of the epigenetic evolution of the complexity of the adult form from the apparent simplicity of the fertilized ovum" (Jenkinson 1906, p. 89). The idea of "epigenetic evolution" – that internal and external factors interact to shape development and characters – was no less adopted by another of Weldon's pupils.

Born in 1881, Geoffrey Watkins Smith studied with Weldon at Oxford, gaining a degree in Natural Sciences in 1903, before going to Naples until 1905, when he started working as demonstrator and lecturer in the Oxford University Museum (Anon, 1916). His first study was on the *Rhizocephala*, parasitic castrators abundant in Naples, whose usual hosts were crabs, the latter also being Weldon's model organisms. When the *Sacculina*, a species of the *Rhizocephala*, infected the crab, the gonads of the hosts degenerated, or barely developed. While female crabs still developed (if modified) secondary female characteristics, Smith observed, males developed only degrees of female characteristics. The male either ended up with a mixture between male and female characters or with complete female sexual characters, depending on the time when the *Rhizocephala* infected the male crab.

Smith concluded that the development of secondary sexual characters could not be determined by the gonads, because the secondary female characters in the male crab developed without an ovary (Smith 1906, p. 84). He contended that an inherited "potentiality" of forming female sexual characters remained in the male, and it might become active under specific conditions, such as when a "sexually formative substance" might act in specific ways. The gonads, then, did not preform sexual characters, but characters were products of specific interactions between inheritance, the gonads, and body substances. The eugenical implications of this developmental flexibility have already been analysed in depth (Brooks 2021, 2023).

What is important is to consider how Smith conceived the biological development of sexual characters. He noted that the formative substance might have different effects on different cells. Why did only some cells differentiate into ova or sperm upon contact with this substance? He reasoned that only those cells "in a particular position and of a particular internal structure are capable of becoming ova under the influence of the sexual formative substance" (Smith 1906, p. 86). In other words, the development of sexual characters was a result of an interaction between the sexual formative substance and the state of the cells at a particular time. Smith wrote that his theory was a "hypothesis" that was compatible with "modern experimental embryology", a "sympathetic grasp", as he called it, "of both epigenetic and evolutionary ideas in embryological theory" (Smith 1906, p. 86). He fell well in line with Weldon and Jenkinson's ideas. The stage was thus set for Huxley's arrival at Oxford.

Huxley's reception of "epigenetic" biology in his undergraduate years, 1906-1907

Huxley adopted his tutors' "epigenetic" ideas in his undergraduate work. He arrived at Oxford in autumn 1906, several months after Weldon died. His personal tutor at Oxford was Smith, and Jenkinson was his lecturer in experimental embryology (Witkowski 1992). No evidence has been found from 1906-1907 that shows the nature of Huxley's interactions with Smith. The earliest notebook with Huxley's notes on Jenkinson's lectures – where he wrote some remarks, for instance, on *Lacerta muralis* – was written in 1907 or 1908 (Huxley 1907-1908). A series of essays Huxley drafted in 1907, however, suggest, as I will show, that Huxley used Jenkinson or Smith's "epigenetic" ideas by 1907.

After finishing his studies at Eton and gaining a scholarship at Balliol, Oxford, Huxley met, in the summer of 1906, Driesch, who by this time was focused on vitalism (Huxley 1970, p. 61). Coming to Oxford in autumn 1906, he had also met the physiologist and philosopher John Scott Haldane around the autumn of 1906, who had been critiquing vitalism (Huxley 1970, p. 65). Jenkinson had, in turn, acknowledged in 1906 the help of "Dr. Haldane". Haldane, who often attended the so-called Oxford Biological Club, argued both against Driesch's vitalism and against reductive mechanistic theory. He was proposing a version of the "organicist" philosophy where he aimed to show that characters were not preformed mechanistically or vitalistically (Esposito 2013; Peterson 2016). Haldane would later figure in one of Huxley's essay.

Huxley read Jacques Loeb's *Comparative Physiology of the Brain and Comparative Psychology* (1900), which showed that the brain, although complex and seemingly "vitalistic", was "determined" materially and could be explained, as Loeb put it, wholly mechanistically, i.e. without recourse to a "mystery" (see Allen 1975). But Huxley also saw evolution and the living conditions of organisms to be crucial. Natural selection, combined with "epigenetic" biology, was his ticket to understanding intricate organisms naturalistically, seeing them more than simple physico-chemical machines.

Writing an essay on natural selection, Huxley explored the different theories about the "origins of variation", which he categorised as either gradual or sudden (Huxley 1907a). As an example of "sudden" variations, he mentioned Hugo de Vries's mutation theory, while of the "gradual" he gave "Weldon's work with crabs".

Although he thought that both were important, he leant towards gradual variation, since, echoing a classic vitalistic argument, small variations allowed for the maintenance of a "harmony" between parts, while large variations disrupted harmonious organisms. In another essay, on the development and functions of the brain, he used his tutors' epigenetic ideas.

To understand the brain, one had to understand the development of its cells (Huxley 1907b; all references in the following two paragraphs, unless otherwise indicated, belong to this essay). Huxley held that the fate of any cell was not pre-formed by its material properties, or a vitalistic mystery, but could be explained in terms of living "epigenetic" processes. Citing Loeb's 1900 book, he began his essay with what was virtually a ladder of complexity of the nervous system, from the "Geotropism of Root", with "v. little specialization", to more complex organisms. Throughout the essay, however, Huxley emphasised how both the internal and external environments, as well as evolution, complicated Loeb's views.

His tutors' biology emerged especially when Huxley discussed the cells constituting the brain, specifically how cells developed and specialised. Cells specialised and divided in labour depending on their "arrangements", i.e. on the collections of cells and their relations. He listed the different specializations which cells could adopt, such as becoming "fibres' and being able to "conduct external stimuli from a sense organ throughout the body" – which allowed some "Protozoa …to perform coordinated movements as a whole in response to a localized stimulus". In all cases, the actions of "ordinary protoplasm' were not "determined" by the protoplasm's properties but "by the arrangement of parts". Huxley wrote that a specific specialisation did not mean that a cell had completely lost "the other functions possessed by the "primitive cell" " (which he also called "undifferentiated protoplasm"). Huxley said that, since the "relative processes" and "relative positions" were important for the destiny of any cell, "the result is mainly given potentially in the germ & partly determined by varying outer influences". He defined the way cells specialised as an "epigenetic idea" - the action of any part was dependent on its location and its relations to other parts.

Just like cells, evolution occurred via the interaction of one generation with another. "Each generation", Huxley said, "is mainly determined by the generation before, but if it should itself alter in certain ways, these alterations will cause alteration in the next & all subsequent generations". That being so, no preformed material made evolution, but any change in one generation could have significant consequences upon the next. Huxley believed that “the development of the race is therefore like that of the individual, epigenetic”. “What the zoologist calls epigenetic processes” was thus characteristic of both development and of evolution (original emphasis). It was in this scheme that one should see the place of “natural selection”. If an organism struck gold with a good arrangement of parts, it could change the general evolutionary course by gaining an advantage over other individuals. Good arrangements were thus saved through “natural selection” in heredity, so that the “organism becomes a storehouse of purposeful arrangements”.

Huxley wrote that such an account dispensed with any “reference to or consciousness of any ideal purpose or goal”, or even a “higher grade of mystery”. For example, one could thus understand the complex vertebrate “system”. Regarding the vertebrates, Huxley noted down on the margins of his essay “qu. JSH”, J.S.Haldane. Again, the latter aimed to show that complex self-regulating organisms were neither preformed nor products of a preforming vitalism, but were “co-ordinated wholes ” whose operations, although naturalistic, were distinct from chemistry and physics (Sturdy 1987). Huxley had a similar ambition. A selection of “epigenetic” arrangements could not be equated with simple physical mechanisms, but was neither vitalistic, no matter how purposeful an organism might seem. Huxley bore the epigenetic or context-dependent differentiation in later years.

Huxley’s reception of Weismann & Jenkinson’s *Experimental Embryology*, 1908-1912

We know from Bowler that there was a continuous “faith in Darwinism” at Oxford against Lamarckian ideas, not least represented by Poulton (Bowler 1983, p. 30; Meulendijks 2021). Poulton was an adept of Weismann’s ideas and, by 1908, Huxley had likely met Poulton, read his 1908 *Essays on Evolution*, and then read Weismann. We can find diary notes in a notebook where, on the 8th of November 1908, Huxley wrote that “after breakfast read a lot of Weismann – finished the first vol. [of *The Evolution Theory*] – it is almost all very convincing” (Huxley 1908a). We can see what particularly struck Huxley in an essay written just after, titled “Natural Selection & Lamarckism” (Huxley 1908b; all references in the paragraph below, unless otherwise indicated, belong to this essay). Darwin’s much-maligned theory of “pangenesis”, Huxley remarked, as all Lamarckian theories, upheld the view that “external conditions’ “act directly on the germ-plasm”. While the environment did not change heredity, Huxley argued, it did change the way in which heredity acted when a character was developed.

Different “determinants” (Huxley put this between inverted commas) in the germplasm could be strengthened or weakened by “use”, and the more they were strengthened, the more “nutriment” they received. Their expression, or, to use Huxley’s word, their “strength”, could be modified by “nutriments” and “use”. This explained to Huxley how, without Lamarckism, traits could degenerate or could become oversized. The non-germplasm-modifying “indirect action of externals”, e.g. nutriment during development, Huxley concluded, “is probably considerable”, especially given recent research in “organ-forming stuffs circulating in the ovum, & by the assumption of similar stuffs necessitated by the effects of parasitic castration”. Jenkinson and Smith’s works thus reverberated in Huxley’s reception of Weismann.

The lesson remained the same that, in between heredity and the final character, there was a process of development and physiology which could change the character, with significant evolutionary effects. With less use, a character could degenerate. When this happened, different inherited possibilities could be brought out, a lesson that Huxley had learnt from Jenkinson and Smith. That is not to say that Huxley completely agreed with his tutors. Jenkinson’s emphasis on the role of cytoplasm, for instance, which has been shown by Jan Sapp, was barely discussed Huxley (Sapp 1987). But the broad epigenetic ideas were taken up, modified to accommodate other data and different purposes.

Opposing Darwin’s pangenesis and Lamarckian ideas, Huxley’s emphasis on use meant that somatic changes did not change the material properties of heredity (as Weldon granted). A new somatic or external environment affected only the actions of the germplasm’s “determinants”, but not their properties. Note that Huxley adopted Weismann’s notion of “germinal selection” - a variation thereof supported by Roux - according to which there was a struggle in the germplasm between “determinants” (Swiatczak 2023, p. 9; Weldon did too, see Radick 2005, p. 37). With a different somatic environment and different use of organs and traits, a determinant might increase its expression through more nutrition, and thus the struggle-between-determinants-within-germplasm would yield different results. Given that the struggle was context-dependent, Huxley did not think a character could be understood as the sole result of either heredity or environment alone, being neither just inherited, nor just acquired. Although, as explained previously, Weldon died before Huxley arrived at Oxford, Radick has shown that the idea that characters were both inherited and acquired was “something of a motto for Weldon” (Radick 2024, p. 109). Characters were results of wider processes, if not altogether co-operative, as Haldane would have had it. As suggested, it is worth noting that Huxley would later adopt J.M. Baldwin’s “organic selection”, which emphasised the integrated actions between environment and the organism in the production and inheritance of characters (Radick 2017; 2024).

None of this, regardless, could have prepared Huxley for the events of November 1908, when his mother died of cancer. Only after several months, on March the 15th 1909, did he finally bring himself to face it. “Dearest mother”, he began, “I can at last write my memory of you, in the hopes that I may cleanse myself – I know what you have loved, what you would have hated, but I can bring it more home, can keep it, more real & effective by putting it down in black-&-white. Now let me tell you [that] I am going to do it every day” (Huxley 1909). Through this type of epistolary therapy, we get a glimpse of Huxley-in-1909, in his final months at Oxford. On April 1st 1909, he wrote that he had a “quite good day – I did a reasonable lot of work, kept at it by Jenkinson’s extraordinary keenness & energy, & it was a lovely day”. In the same month, Huxley received a copy of Jenkinson’s recently-published *Experimental Embryology*. He read it through, richly annotating it (Jenkinson 1909).

Jenkinson’s discussion in the introduction was framed by what he called a “modern” epigenetic vs. preformationist debate. Huxley underlined Caspar Friedrich “Wolff’s *Theoria Generationis*”*,* that Jenkinson said “aroused” evolutionists from their “dogmatic slumbers’, contrasting it with Charles Bonnet’s “preformation” (Jenkinson 1909, pp. 14-16). The modern versions of Bonnet’s preformationism, Jenkinson wrote, were, again, Roux and Weismann’s theories, whose names Huxley again underlined. The alternatives, to be expected, were Driesch and Curt Alfred Herbst (1866-1946), whose names Huxley noted. “Once again”, Jenkinson wrote ending his introduction, “we find ourselves face to face with the old alternative, Preformation or Epigenesis; and it is to the desire of solving this problem that a very considerable proportion of modern experimental research is attributable” (Jenkinson 1909, p. 19).

One remark that Jenkinson made was that one should distinguish between “predetermination” and “preformation”. He wrote that it was obvious that there was “in some sense a predetermined process” in development, namely that development started in certain ways and continued as such. One had to find a “causal explanation” for it, but “without”, he noted, “presupposing the preformation in the germ of morphological units representing every possible inheritable character" (Jenkinson 1909, 20). This predetermination-without-preformaton emerged, Jenkinson wrote, "in Herbst's and Driesch's conception of the events of ontogeny as so many responses to stimuli exerted by the development parts on one another". One thing that Huxley noted from Jenkinson's book was the role of factors in the cell's cytoplasm – the "organ-forming substances", from Edwin Conklin's 1905 research (see Sommer 2014). Jenkinson's distinction between predetermination and preformation – with its accompanying emphasis on the life-cycle of the organism – echoes in Huxley's argument about cooperative evolution.

The continuation of Huxley's "epigenetic" view in his wider work, 1912-1916

Definitions of an "individual" were legion – for Thomas Henry Huxley (T.H.H.) an individual was whatever was differential in the fertilised ovum following sexual fusion (Lidgard & Nyhart 2017). Taking cues from Karl Ernst von Baer, T.H.H.'s "epigenetic" view, with its radical implications of random development relative to environment, was tempered by a view that internal materialistic forces determined development, so that one could predict a developed adult from its fertilised ovum (Richmond 2000). In his 1912 *The Individual in the Animal Kingdom*, Huxley equated his grandfather's view with the mutationist theory he attributed to Hugo De Vries. To Huxley, the trouble was that a "mutation" did not happen only during sexual fusion. "The chain of argument will not hold", Huxley wrote, "for it is found that not all mutations are similar to those we have described: permanent and considerable changes may take place at any time during the life-cycle, and not in the sexual act alone" (Huxley 1912, p. 81). There was no rejection here of some sort of predetermination, but certainly of preformation.

Huxley's "epigenetic" biology – that differentiation and specialisation of parts happened relative to context – emerged in his understanding of co-operative evolution and in his research. In his *Individual in the Animal Kingdom* (1912), Huxley noted how natural selection could act on single individuals, as it could act on individuals dividing in labour and co-operating to survive. Suppose, he wrote, that, instead of a struggle between two organisms to the death, in the "Economy of Nature, the two should conspire together to create a vacuum of their own" (Huxley 1912, 134-5). For, "though it is undoubted that the pressure of the struggle is always forcing life into these vacuums of vacant spaces, we have to look further before we find what the effect on life will be" (Huxley 1912, 134; see Sommer 2014, p. 567). This view was anticipated by a sketch for an essay that Huxley wrote in 1907, where he sundered "evolution" apart from its many "methods" (Huxley 1907c). Competition between individuals was one method. Another was “division of labour’, meaning that single individuals specialised differently relative to each other. Note that Henri Bergson had also emphasised division of labour and cooperation as tendencies in evolution, and Huxley read his philosophy avidly (see Herring 2018). He indeed saw Bergson’s philosophy in the light of epigenetic evolution, writing in his 1907 essay on the brain that “epigenetic processes are those which Bergson says take place in ‘real time’” (Huxley 1907b).

This view played a pivotal role in Huxley’s 1916 “Extension Lectures” at Rice University, where he worked between 1913 and 1916. In “Biology and War”, Huxley formulated a biological argument against war, arguing that human characters, such as behaviours, were products of complex human systems or organisations. It is true that Huxley saw the war as dysgenic – no doubt partly lamenting the death of both Jenkinson and Smith in 1915-1916. War was, however, “dysgenic” not just because people of talent died, but also because nationalism impeded the making of more advanced human organisations that could push the specialisation and differentiation of human parts further. Huxley wrote that “co-operation and community brought out in the ancestor of man all those essentially human & higher qualities which would never have appeared had he remained content with solitary existence” (Huxley 1916, 44). For the same reason, Huxley wrote that women should be given equality of opportunity, since mutual selection between the sexes would increase both their qualities (see Bartley 1995). Biologising social diversification, he was a supporter of democracy (Sommer 2014).

It was nevertheless to be a centralised democracy. Only by adding an international “organ” was internationalism possible – Huxley quoted President Taft’s “League to enforce peace”. At some point, thus, a future scheme “shall be truly international, carried out by co-operation between states, not by one state enforcing its will on others. In other words ... the nation will no longer be the greatest unit of the human race” (Huxley 1916, 40). The need for an organ that enforced international cooperation underscored Huxley epigenetic view of the evolution of human societies. For nations had arisen through processes of increasing division of labour and coordination, just as they could evolve through more such division. “Line upon line, precept upon precept’, referring to the evolution of social organisations, “is the rule of organic development: biologists call it epigenesis [...]” (Huxley 1916, 40). Since nations could change epigenetically, so could “human nature”, given that the latter and the former co-produced one another. Epigenetic evolution was thus the basis for human societies and their advancement. Together with Conklin, thus, Huxley shared a vision of evolution based upon diversity and cooperation leading to greater democratisation (Sommer 2014, pp. 565-569).

Huxley's "epigenetic" characters against MacBride's Lamarckism and Bateson's Mendelian Genetics, 1921-1925

His more expansive view of characters also had repercussions upon his research in the 1920s. He rejected both the embryologist E.W. MacBride's (1866-1940) Neo-lamarckism and genetic determinism at the same time, while claiming a type of reciprocal causation between genes and environment. In an article aimed at MacBride's Lamarckism, Huxley, echoing Driesch and Jenkinson, wrote that "it should not surprise us in the least to find the identical gene-mechanism in every cells of the body". The "gene-mechanism" worked differently in different environments. Piano mechanisms might be the same, but the melodies will differ depending on the pianist or "executant". The "gene-mechanism", or "gene-complex" was the piano mechanism, while the "executant … is represented by the environment … whether intra-cellular, intra-organismal, or external" (Huxley 1921, p. 246). Every cell, indeed, was a "system". He put forward the view that "each cell represents a particular state of equilibrium, and the organism as a whole an equilibrium of all the cells with each other and with the environment. ... The development of an organism is a series of states of equilibrium, usually of increasing complexity". Huxley thought that "from this standpoint the unity of the organism as a whole is not only explicable, but necessary" (Huxley 1921, p. 247).

He admitted that the merit of Weismann had been to dispute the inheritance of acquired characters. But his demerit was "his total failure to construct a physiological theory of development" (Huxley 1921, p. 247). Just two pages before, where he began discussing, as he called it, the "translation of the [genetic] constitution, in certain conditions of environment, into the adult organism", he cited Jenkinson's 1909 book (Huxley 1921, p. 245). In the same vein, Huxley supported Richard Goldschmidt's "physiology of sex determination", arguing that "the earlier rigid belief that sex-determination was entirely a matter of the chromosome-constitution must" be modified (Huxley 1923, p. 928; see Richmond 2009).

In 1924, Huxley co-authored an article Alexander Carr-Saunders (1886-1966) attacking MacBride, calling his Lamarckism a form of "preformationism". Carr-Saunders had studied zoology at Oxford from 1905 to 1908 but then chose to pursue sociological problems (Blacker 1967, p. 365). In 1922, he had published *The Population Problem: A Study in Human Evolution*, where, in a chapter on "Environment among Animals and Plants", he cited Jenkinson's work claiming that heredity and environment "complementary" to each other. He quoted Jenkinson asking his readers to think that, if they were to remove one element from development, "the specific typical end which is reached in normal development will not be attained" (Jenkinson in Carr-Saunders 1922, p. 326). Calling MacBride's characters-inherited-through-habits "preformationism" echoed Jenkinson, for their alternative, unsurprisingly, was epigenesis. "It looks much more as if a chain of reactions was in each case [of development] set going which moved toward an appointed end, but an end not necessarily resembling any of the substances present at the beginning" (Huxley & Carr-Saunders 1924, p. 231). In the same vein, Huxley criticised T.H. Morgan's 1926 *The Theory of the Gene* for being "A Static Theory of Heredity", i.e. for not showing that a character "emerges as the clear-sighted have always seen it - a resultant of a large number of inner agencies, inter-acting with a large number of outer agencies. The term "unit character" should never have been used" (Huxley 1926, p. 581).

It was around this time that Huxley maintained correspondence with William Bateson (1861-1926). In the context of Huxley co-founding the *British Journal for Experimental Biology*, the dispute between Huxley and Bateson underscores the former's support for all-round "epigenetic" biology (see Erlingsson 2013). On June 25, 1925, Huxley, in response to a meeting of the *Genetical Society* that had just taken place, Huxley wrote to Bateson that he was excited with how the meeting had gone. But he had his doubts about the methods people there employed, specifically the "factorial method'. "It seemed to me", Huxley wrote, "that in many of your problems you were getting to a point at which what I might call the factorial method would give out, or at any rate yield rapidly diminishing returns".[3] He proposed that the "physiological method might yield enormous advances". Huxley specifically disagreed with some of the people at the meeting discussing "genetic entities' as if they actually encapsulated traits like "maleness" and "femaleness".

[3] Huxley to Bateson, June 25 1925. John Innes Centre, The Bateson Letters Collection, K50

In December 1925, Huxley gave the example of the aquatic plant *Ranunculus aquatilis* to emphasise his idea of how characters came about, and also how genetics could contribute to them. Take "dd" to mean the genetic factors "for the development of dissected leaves" in the plant. Huxley wrote that "dd in the presence of water habitat -> dissected leaves". While dd in the presence of a land habitat "-> entire leaves". "Here", Huxley continued, "the external environment determines the expression". If the interaction with the external environment was very important in the case of these aquatic plants, the "internal genetic environment", he wrote, "can be equally important." Huxley generalized his point about interactions, saying that "what genetics needs is what physiology has woken up to in the last quarter-century – the fact that [...] the <u>action</u> of a factor is a meaningless abstraction – for its expression depends on interacting with the rest of the genetic constitution. Factors themselves may be, and doubtless are, definite units - but their <u>expression</u> involves 'the organism as a whole'" (original emphasis).[4] It was in this context that Huxley worked with his pupil E.B. Ford on the crustacean *Gammarus chevreuxi.*

Genetics, development, and the "gene for" shorthand: Huxley's work between 1925-1936

Olby has noted Huxley's interest in developmental gene actions in *Gammarus*, but not with regards to the context and controversies surrounding the connection between characters and genes (Olby 1992). As expected, in a note in *Nature* in 1925, Ford and Huxley wrote that "very little is known as to the developmental mechanism by which this correlation [between genes and characters] is brought about. We thus have accurate pictures of the gene-complex and of the character-complex, but these pictures are, we may say, static, and the dynamic relations between the two are obscure" (Huxley & Ford 1925, p. 861). But, in 1926, in response to MacBride and the physiologist Noël Paton, who rejected Mendelian Genetics on account of reducing animal characters to genes, Huxley called the complex connection between genes, development, and characters a future "biological synthesis" (Huxley 1926). While characters were not preformed in genes, the latter contributed to them along with developmental and environmental processes. This ambition to synthesise genetics and development remained with Huxley. He wrote to Frank R. Lillie on 31 March 1928 that "we are getting some nice stuff with Gammarus" which is "helping to bridge

[4] Huxley to Bateson, December 14 1925. John Innes Centre, The Bateson Letters Collection, G2k-18A

the gap between genetics and development".[5] Less concerned with development, Ford remained sensitive to the distinction between genes and characters, writing that "an interacting gene-complex whose results in a given environment have been selected as beneficial to the species" (Ford 1964 [1931], p. 45).

In response to MacBride, Bateson, Morgan, and their supporters, Huxley began reiterating that the expression "gene for" was a shorthand for a more integrated process of biological character-making until 1936, contrasting, as we have seen, his Oxford "epigenetic" approach. In the *Science of Life*, written with H.G. Wells and G.P. Wells, Huxley wrote that "we grow accustomed to using convenient but in a sense misleading shorthand phrases like "the gene for blue eyes", or the "albino gene", that we tend to think of the genes as in *some way little replicas of the characters* with which they are concerned, and of the gene-outfit as being a sort of compressed organism, with a point corresponding to each part of the body" (original emphasis). But this idea was "wholly false". It was "really a survival of the preformationist ideas of the eighteenth century, which so worked on the imagination of one microscopist that he actually drew a human sperm with a *homunculus*, a miniature man, squatting within the head!" (Wells et al. 1931, p. 324).

By 1934, when Huxley co-wrote his *Elements of Experimental Embryology* with De Beer, the point had already become old. They wrote that "the modern view, which combines an epigenetic outlook on development with the particulate theories of neo-Mendelism, denies any such simple correspondence between hereditary germinal unit and developed adult character". "The *function*" was analysed by the "rather special branch of embryology usually called physiological genetics" (original emphasis) (Huxley & De Beer 1934, pp. 4-5). Huxley carried this rather expansive view of the making of characters in his 1936 Galton Lecture.

It is true that to Huxley it was important to equalize the environment to "encourage favorable mutations" for proper eugenics. But he did not equate characters with heredity. In a section subtitled "Environment and the Expression of Genetic Traits", Huxley argued against a preformationist view of genetics. "Characters are not and cannot be inherited", he wrote, "in the sense in which inheritance is used by the geneticist. What are inherited are genes, factors, genetic outfit. Any character whatsoever can only be a resultant between genes and environment".

[5] Huxley to Lillie, March 31 1928. Marine Biological Laboratory Archives, Frank Rattray Lillie Papers (MC-MBL-Lillie), Box 5, Folder 47

Again, “a gene for white flower-colour” was only “a shorthand notation” (Huxley 1936, p. 14). Just like in 1916, doing proper eugenics also meant good social epigenesis. Only a “social system” that encouraged “social traits such as altruism, readiness to co-operate, sensitiveness, sympathetic enthusiasm and so forth”, and which provided “niches” for different specialisation, could allow for a better expression of genes (Huxley 1936, p. 28). Relative interactions between heredity, other people, their development/education, and the socio-political environment, brought about characters. While it is true that Huxley targeted this against growing movements in Germany and was in this sense a “reform eugenicist”, his underlying biological views remained constant (Allen 1992).

The same point – that characters are end-products of interacting processes – is repeated by Huxley in his 1936 well-known “Natural Selection and Evolutionary Progress”. There he wrote, again, that Mendelian *characters* do not exist, because no gene had constant effects. Drawing from Fisher’s work, he argued that, a gene can become “dominant” through other modifier-genes. But this was part of Huxley’s wider argument that the development of characters was a product of complex interacting “epigenetic” process. Developmental processes could change the effects of genes just as much as other genes did. Referring to his work on relative growth, touched upon in his work on *Gammarus*, he wrote that “a large number (possibly the majority) of genes exert their effects through the intermediation of a process operating at a definite rate”, a rate which was “relative – relative to the speeds of other processes of development and development in general” (Huxley 1936, p. 92). Development was not forgotten, nor was gene-development reciprocal causation. This brings us back to 1942, when, again, Huxley wrote that “a study of the effects of genes during development is as essential for an understanding of evolution as are the study of mutation and that of selection.”

Conclusion

With his biology rooted in his Oxford education, Huxley viewed the making of animal characters in a wider sense: “epigenetically” caused by cross-pollinating processes spanning from heredity, development, to various environments. Rather than a “Mendelian Revolution” in Huxley’s thinking, there was much continuation from development to genetics for Huxley (see Hodge 1990). Emphasising the natural selection of genes, and gene systems in his 1942 book was, this paper shows, just that: a matter of emphasis. We have clues as to why Huxley wrote the book in that way. It has been argued that his endorsement of Fisher's mathematics gave him a way to unify the biological sciences in a coherent evolutionary narrative that embraced his wider views about "evolutionary humanism" and progress (Smocovitis 1995, p. 139). Here I have shown the origins of Huxley's aim to synthesise genetics with development. I have not tried to understand Huxley's 1942 book, nor, say, his synthesis with Bergson's philosophy (see Herring 2018), but, in closing, we should note, as Cain has, that "no one synthesis stood out for [Huxley] as more important than the others" (Cain 2010, p. 372).

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