ИССЛЕДОВАНИЯ

What Was so Upsetting about the Inheritance of the Acquired Characteristics? W.L. Tower, C.H. Waddington and the Evolution of the Evolutionary Synthesis

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This article asks the question why was the notion that acquired characteristics can be inherited so deeply resisted in early 20th century biology? The article begins with the case of William Lawrence Tower, a biologist at the University of Chicago whose career ended in scandal over his attempts to improve the inheritance of striping patterns in the Colorado Potato Beetle. Though less well-known than the more notorious example of Paul Kammerer (whose work is today being reconsidered in light of epigenetics), the controversy concerning Tower's claims reveals a strong mistrust for the inheritance of acquired characters during the period. Next I consider some of the most important figures in the evolutionary synthesis of genetics and evolution — H.J. Muller, Julian Huxley, L.C. Dunn, J.B.S. Haldane and Theodosius Dobzhansky — in terms of their reaction to the work of C.H. Waddington, whose ground-breaking research in epigenetics provoked a similar level of suspicion due the fact that it also implied acquired characters are inherited. The article concludes with the suggestion that the history of the evolutionary synthesis be reconsidered in light of why ideas such as Waddington's were rejected as incompatible.

Keywords: C.H. Waddington, W.L. Tower, genetics, evolution, Lamarckism, T.H. Morgan, H.J. Muller, Julian Huxley, L.C. Dunn, J.B.S. Haldane, Theodosius Dobzhansky.

> *The garden path has its attractions for the likes of us, and all of us who want to understand living systems in their more complex and richer forms are fated to look like suckers to our colleagues who are content to make a quick (scientific) buck whenever they can build up a dead-sure pay-off.*
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> C.H. Waddington. *The Evolution of an Evolutionist*[1]

[1] Waddington C.H. (1975) *The Evolution of an Evolutionist,* Ithaca, NY: Cornell University Press.

Introduction

The evolutionary synthesis of genetics and natural selection was a central development in the history of twentieth century biology. The idea most explicitly left out of this merger was that acquired characteristics can be inherited. In recent years the rise of epigenetics — the science invented by Conrad Hal Waddington — has renewed belief that environmental factors can affect evolution. For this reason some epigeneticists argue biology is undergoing a "neo-synthesis" that undermines a fundamental assumption of neo-Darwinism. The circumstances surrounding these events, as well as a strategy for further investigation, are outlined below.

Though it is possible to support the epigenetic belief that the environment changes DNA without necessarily claiming these effects are inherited, the desire to do so is widely evident in the published research[2]. This begs the question why. What is so important? Is the desire to prove acquired characters can be inherited such a recurrent theme in the history of evolution because the idea is attached to something biologists want to be true?

I am not going to attempt a definitive answer in the essay that follows. Rather, I am going to outline a strategy for research. In the first part I will examine a case study where a geneticist, William Lawrence Tower, claimed to have proven the inheritance of acquired characteristics; in the second I will give an overview of the evolutionary synthesis in terms of five of its most important architects — all of whom were familiar with Tower's work; in part three I will describe their relationships with Waddington, who they all knew as well.

Though Waddington's ideas were never accepted during his lifetime, the growth in epigenetic research during the past decade-and-a-half has been exponential[3]. The pace suggests that a reassessment of what was not so long ago dismissed as "Lamarckism" is due[4].

The Case of the Colorado Potato Beetle

William Bateson was on a lecture tour of the United States in 1907 when he wrote his wife Beatrice back home in Britain. Bateson's attraction-repulsion theory was drawing criticism from his colleagues for its numerous inconsistencies, however his lectures still drew crowds in the hundreds — an experience he found "exhilarating" (Cock, Forsdyke, 2008, p. 229). As far as Bateson was concerned, "the one blot on [his] expedition" was an encounter with William Lawrence Tower at the University of Chicago. "Tower's story about the beetles", Bateson wrote, caused "fear I shall have trouble with him in the future" (Cock, Forsdyke, 2008, p. 300–301).

Tower had recently published *An investigation of evolution in chrysomelid beetles of the genus* Leptinotarsa, in which he claimed to have discovered evidence of the inheritance of acquired characteristics in the striping patterns of the Colorado potato beetle (Tower, 1906). Four year later Tower published two experiments providing further confirmation of his findings, however

[2] The best example is Jablonka, Lamb, 2014.

[3] See, for example, BMG LABTECH (2012) *Fun Fact: Right now, Epigenetic is one of the fastest growing fields of life science,* available online at http://microplate-readers.blogspot.com/2012/11/fun-fact-right-now-epigenetic-is-one-of.html, http://www.nyas.org/Publications/Ebriefings/Detail.aspx?cid=adb8dd47-cf5e-46d8-ac32. Burggren W.W. (2014) *Epigenetics as a source of variation in comparative animal physiology — or — Lamarck is lookin' pretty good these days*, available online at http://jeb.biologists.org/content/217/5/682.

[4] Ibid.

T.D.A. Cockerell, a zoologist who conducted fieldwork in Colorado, pointed out that they were actually mutually contradictory (Cockerell, 1910). Tower denied any wrongdoing, but his behavior caused raised eyebrows. He agreed to withdraw one experiment and substitute it with another, but still claimed the withdrawn experiment had been correct (Weinstein, 1998).

Three years later, in his book *Problems of Genetics*, Bateson expressed renewed skepticism of Tower's research. By now Bateson's notion of attracting and repulsing traits had been debunked by crossing-over. As for Tower, Bateson stated that though, "[t]his work has attained considerable celebrity and has been generally accepted as making a definite extension of knowledge", he was "still in doubt as to the weight which should be assigned to this contribution" (Bateson, 1913, p. 219–227). Meanwhile Tower continued to arouse suspicion for reasons like claiming that his experimental results were lost in a fire (Weinstein, 1998, p. 352–353).

In 1917 Tower underwent a highly publicized divorce trial that would ultimately force him to resign from the University of Chicago. On August 7 of that same year, Charles Davenport responded to a letter from the president of the Carnegie Institution, R.S. Woodward, asking his opinion of Tower. Davenport responded that he was "somewhat embarrassed at the request as I do not know how I ought to counsel in the matter. I have known Tower ever since his undergraduate days at Harvard", where "he was not approved of by other members of the Department of Zoology". Davenport said Tower was "headstrong", and added that he found "nearly universal doubt about the reliability of Tower's reports", which he judged was "due first of all to the fact that Tower has consistently declined to subject his findings to the criticism of his scientific colleagues".

Davenport could "recall three occasions on which Tower was to give an account of his work, with specimens, before scientific meetings", but, "either failed to appear himself or failed to show the critical specimens". Tower's colleagues had come away from his lab feeling he was "peculiarly secretive or is very much afraid of a critical examination of his method and results". "Although most of his findings are certainly worthy of credence and have brought him a well-deserved reputation", Davenport added, "still there are many which will not stand critical analysis and there are many persons who declined to accept his conclusions". "It is best", he concluded, "to proceed slowly"[5].

"The warning you send will be heeded", Woodward responded[6].

Over a year later, December 31, 1918, Woodward sent a copy of Tower's *The Mechanism of Evolution in* Leptinotarsa to Thomas Hunt Morgan at Columbia University, asking his opinion[7]. Woodward referred to Tower's, "severities of domestic difficulties, which have led to the breaking of his connection with the University of Chicago and to a suspension of his connection with the Institution". "Tower", Woodward said, "has not been held in high esteem by his colleagues in biology". Nevertheless, Woodward was still curious to hear what Morgan thought of Tower's work.

Morgan liked Tower. According to his protégé, Sturtevant, Morgan "found Tower interesting personally, and that at a society meeting the two men had stayed up all one night talking to each other" (Weinstein, 1998). Morgan's lab had also nearly burned down in a fire, making it more likely he

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[5] Correspondence, Charles Davenport to W.S. Woodward, August 7, 1917. William Lawrence Tower. Carnegie Institution of Washington, Archives. Genetics: Director, Charles B. Davenport, 1902–1931. Folder 3. Thanks to Marsha Richmond for this correspondence, as well as the letters from the Carnegie Institution Archives noted below.

[6] Correspondence, W.S. Woodward to Charles Davenport, August 8, 1917. William Lawrence Tower. Carnegie Institution of Washington, Archives. Genetics: Director, Charles B. Davenport, 1902–1931. Folder 3.

[7] Correspondence, W.S. Woodward to T.H. Morgan, December 31, 1918. William Lawrence Tower. Carnegie Institution of Washington, Archives. Genetics: Director, Charles B. Davenport, 1902–1931. Folders 3 and 4.

would accept Tower's claims about his missing research[8]. Yet Morgan responded regretfully, that while he was in "sympathy with his insistence on the use of the experimental method, and also with the mechanistic view that he extols", Tower failed "to give the crucial evidence on… where crucial evidence could have been obtained by the very methods which he advocates". "When the work is carried to the point where the real difficulties of the situation arise", Morgan reported, "he resorts to generalities and phrases, so that one is left at the end with the impression that no important step has been made"[9].

In a letter to *Nature* the following year, Bateson explicitly linked Tower to the more well-known controversy surrounding the work of Paul Kammerer on the inheritance of acquired characteristics in the midwife toad:

> The copious and astonishing observations said to have been witnessed by Professor Tower, of Chicago University, and by Dr. Kammerer of the Vienna Versuchsanstalt, naturally called for exceptionally careful examination. The results of both these authors have been widely accepted, and had begun to pass current in text-books. In the case of Professor Tower's paper … close textual criticism revealed features which suggested that implicit confidence should be postponed pending confirmation — a conclusion to which I had come when, on a visit to Chicago in 1907, I had seen illustrative specimens which Professor Tower was good enough to show me (Cock, Forsdyke, p. 301).

Doubts surrounding Tower continued to mount to the point that on December 13, 1919, Hermann J. Muller, penned a letter to his good friend in Oxford, Julian Huxley, on the latest gossip about Tower. "Please forgive me for not answering your inquiry about Tower sooner", Muller replied,

> Somehow nothing in connection with Tower ever makes any impression on me and I promptly forgot your question. I'm enclosing the only criticism I know of his work by one of our own Columbia men; this, however, covers only the new report of Tower's — not his work on manufacturing variations. Tower is regarded seriously by very people here; he's muddle headed and Morgan privately explains lots of his "results" as downright lies (sh!). The fact that he's dropped all reference to his earlier motif in his later work, where he should have had plenty of chance to notice the same effects, seems very significant.

Muller also mentioned Bateson's criticism of Tower in *Problems of Genetics* and concluded that, "There's absolutely no work on genetic variation as influenced by environmental conditions which has been done in such a way as to be interpretable under the factorial theory"[10].

Despite the skepticism Tower's work provoked in the U.S. and U.K., one of his publications was picked up by Nikolai Vavilov as he gathered literature on the latest in genetics to deliver back to the USSR. Here it was read by the man who would soon emerge as one of the foremost geneticists in Russia, Theodosius Dobzhansky. As Dobzhansky later recounted,

> The book which I picked out that seemed important. Now we know it was a very bad book. There was a man by name of Tower, who was working for the Carnegie Institution, had a laboratory at the University of Chicago. He wrote a number of most "remarkable" papers claiming hav-

[8] "Fire Destroys University Hall", *Columbia Daily Spectator* LVIII/17, October 10, 1914, pp. 1–2.

[9] Correspondence, T.H. Morgan to W.S. Woodward, February 1, 1919. William Lawrence Tower. Carnegie Institution of Washington, Archives. Genetics: Director, Charles B. Davenport, 1902–1931. Folders 3 and 4.

[10] Correspondence, H.J. Muller to Julian Huxley, December 13, 1919. Huxley, J.S. 1919–1920. Muller MSS. Series I, Box 23. Lilly Library, Indiana University.

ing made very startling discoveries with a species of beetle, the so-called Colorado potato beetle, *Leptinotarsa*.

At that time it was quite exciting, so I wanted to know what Mr. Tower wrote, so it was Tower's monographs of the genetics of Colorado potato beetle which was my English textbook. I regret to say that later on, all his discoveries were shown to be faked. In fact, there is good reason, I am told, to suspect that the man was a plain cheat, and simply invented things without doing any of that. It's one of the scandalous cases in American science, which, as far as I know, is not published anywhere. I don't know whether Mr. Tower is still alive; probably not. Probably nobody takes a chance, of writing about it, but since approximately 1925 or thereabouts, the name of Tower is not longer mentioned anywhere. Before that time, there was no book on genetics or evolution which did not mention him[11].

The Evolutionary Synthesis

Morgan's 1910 discovery of the *white*-eye mutation in the model organism, *Drosophila melanogaster*, marks the turning point when it became possible to identify where genes are and how they're inherited. Among the first to visit Morgan's "fly room" was Huxley, in the fall of 1912, passing through on a lecture tour of east coast universities. Huxley was heading south to found the biology department at the William Marsh Rice Institute in Texas, where his fame as the grandson of "Darwin's bulldog" T.H. Huxley provided him with a salary twice he was earning at Oxford[12].

However, this was a difficult moment for Huxley. Morgan's lab had reoriented the center of what Bateson had named "genetic" research to the United States. Huxley was not only insecure that his reputation relied solely upon the family name, but also that the value of that name had depreciated significantly. Though geneticists like Bateson and Morgan might disagree on whether genes are located on the chromosome, they were unanimous in their belief that evolution was too speculative a question to be studied in a laboratory. Even worse, by the last edition of *On the Origin of Species*, Darwin had conceded to the idea that acquired characteristics could be inherited.

Meanwhile Muller's relationship with Morgan was contentious for many reasons. Among these was Morgan's refusal to adhere to the agreed upon terminology when discussing the science they were in the process of inventing[13]. When Huxley asked Morgan if he had someone to recommend for his laboratory at Rice Morgan told him to take Muller[14].

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[11] Reminiscences of Theodosius Dobzhansky, p. 122. Butler Library, Columbia University; It is also worth noting that one of Tower's students was Warder Clyde Allee, known for his argument that species are naturally inclined to cooperate rather than compete. Though influential, the popularity of the "Allee effect" was diminished by the theory of Allee's contemporary, George C. Williams, that species are biologically programmed to behave selfishly. Williams would benefit from the promotion of his vocal advocate, Richard Dawkins, whose concept of the "selfish-gene" would dominate evolutionary thinking by the end of the century. See Mitmann, 1988; Dawkins, 1976.

[12] The name was changed to Rice University in 1960.

[13] When Muller took Morgan's class in the spring of 1911, Morgan used the letters W to represent wrinkled peas and R to represent round peas in his lecture on Mendelism. When it came time to discuss his own experiment with the *white*-eyed mutant fly he used W again to represent white and R to represent red. The students were thus left totally confused about the idea of sex-linked inheritance. This detail is particularly significant in terms of Waddington's critique of genetics as detailed below. See Carlson, Genes Radiation and Society, p. 57.

[14] Public lecture, Elof Axel Carlson. Cold Spring Harbor, Long Island. Feb. 25, 2015.

Another aspiring geneticist attracted to the Fly Room was Leslie Clarence Dunn. Dunn had studied botany as an undergraduate and only recently learned of genetics after being given a copy of Morgan's *Heredity and Sex* by his mentor at Dartmouth. By this time Morgan had no room for students lacking background in genetics, so Dunn went to work with W.E. Castle at Harvard instead[15]. Like Bateson and Morgan, Castle was more interested in heredity than evolution.

Castle's Bussey Institute was a farm laboratory where the focus of research was mammals. Though Dunn was taken away from his research to construct wire models displaying Castle's alternative theories to the belief that genes were located in a straight flat line on the chromosome, he still found time to replicate fly room concepts like linkage and crossing-over in mice. After graduation Dunn worked with chickens at the Storrs Agricultural College in Connecticut. Just as he had shown fly genetics could be replicated in mice, Dunn found that "hybrid vigor" demonstrated by the genetics of maize, also increased hatchability. This discovery led Dunn, who was by now thoroughly disillusioned by genetics' doppelganger — eugenics — to argue inter-racial breeding was beneficial to humans[16].

Dunn's contemporary J.B.S. Haldane was repelled, rather than attracted, by the fame of the Fly Room. As Haldane watched friends like Huxley abandon Britain for the wealth provided by universities in the U.S. he, like Huxley, realized his own country had been replaced at the forefront of research in heredity and evolution[17]. Haldane also, like Dunn, replicated *D. melanogaster* genetics in mammals (Haldane, Sprunt, Haldane, 1915, p. 133). Then, in a series of papers published in the 1920s, Haldane provided the mathematical model of population genetics, showing the theoretical proofs by which genetics might operate outdoors in the laboratory of nature[18].

The qualitative counterpart to Haldane's quantitative data was provided by Dobzhansky, who arrived as a Rockefeller Fellow in Morgan's lab in 1927[19]. Unlike the U.S. or Great Britain, Darwin's reputation had never gone into "eclipse" in Dobzhansky's homeland[20]. Muller's discovery the year before that genes could be mutated by radiation increased the pace of production, accelerating understanding of mutations' role as the building blocks of evolution[21]. Dobzhansky's studies of *D. melanogaster*'s wild cousins like *Drosophila pseudoobscura*, traced the pattern of how genes are spread in nature to create population "gene" pools, who procreate among one another to form new species (Lewontin, Moore, Provine, Wallace, 2003, p. 228).

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[15] The Reminiscences of L.C. Dunn, 1960, p. 27. Butler Library, Columbia University.

[16] For the memory of Castle's challenges to the chromosome theory see Reminiscences of Leslie Clarence Dunn, 1960, pp. 94–95. Oral History Collection, Butler Library, Columbia University. For representative publications see Dunn, 1916; 1919; 1920a; 1920b; 1920c; 1920d; 1921a; 1921b; 1923a; 1923b; Dunn, Dobzhansky, 1946.

[17] There is abundant evidence of Haldane's lifelong antipathy for the U.S. in his publications and personal papers at the National Library of Scotland and University College, London. See for example: Haldane, 1926, as well as Correspondence, Francis Harwain to J.B.S. Haldane, December 24, 1947. Haldane Box 34. 4 (1946–1951). J.B.S. Haldane Papers. University College London; Correspondence, J.B.S. Haldane to Ruth Moore, March 18, 1952. Haldane Box 21. General Correspondence, 1951–1952. J.B.S. Haldane Papers. University College London.

[18] These papers became the basis for Haldane's most important work, *Causes of Evolution* (1932).

[19] Dobzhansky used the evolutionary mathematics of Sewall Wright in his research. See Lewontin et al., 2003.

[20] "Eclipse" was the term Huxley used in his landmark work *Evolution: The Modern Synthesis* (1942).

[21] For a recent work which puts Muller's research in context see Campos, 2015.

The fruits of this research, coupled with the mathematical side of population genetics described by Haldane, helped Huxley consolidate what he termed the "modern synthesis" of genetics and Darwinian natural selection in 1942 (Huxley, 1942).

According to the founders of the neo-Darwinian synthesis — Muller in particular — the gene was the source of life (Muller, 1926). Just as splitting the atom had revolutionized our understanding of the physical laws of the universe, manipulating the gene would provide the means to establish mastery over nature. However, the synthesis may also be regarded not as a moment when ideas previously seen as mutually exclusive — Mendelism and Darwinism — were united, but as a moment when notions which did not fit the paradigm were excluded. Among these were belief in the influence of environmental factors upon development and heredity, as described in the revolutionary theories of Conrad Hal Waddington.

C.H. Waddington and the Synthesis

Waddington studied geology as an undergraduate at Cambridge University, where he ignored the required reading because he was more drawn to the philosophy of Alfred North Whitehead. Whitehead, who, like Huxley, was on his way out the door to join the exodus of British academics accepting more lucrative positions in the United States, was interested in reality as a process, rather than a stable arrangement of objects (Whitehead, 1978).[22] It is likely that Whitehead's influence was part of what prepared Waddington to later become skeptical that the gene was an irreducible unit of heredity, or that one could define a simple relationship between phenotype and genotype.

Waddington never bothered to finish his dissertation, and his position at Cambridge was tenuous until 1929 when he received a research fellowship. During this period Waddington was introduced to genetics by Gregory Bateson (1904–1980), son of the man who had coined the term just four years before Morgan discovered the *white*-eyed fly. Among Waddington's first scientific papers were two on genetics, one of which he wrote in collaboration with Haldane. Though Waddington was interested in genetics, the subject was still so esoteric that he believed pursuing it would mean never being able to find a job. Waddington decided to pursue embryology instead (Robertson, 1997, p. 597).

The interests of embryologists and geneticists did not coincide during this period. As Dunn put it in the introduction to Dobzhansky's *Genetics and the Origin of Species*,

> Variation and heredity had first to be studied for their own sakes and genetics grew up in answer to the interest in these problems and to the need for rigorous methods for testing by experiment all ideas we might hold about them. The requirements of this search drove genetics into the laboratory, along an apparently narrow alley hedged in by culture bottles of Drosophila and other insects, by the breeding cages of captive rodents, and by maize and snapdragons and other plants. Biologists not native to this alley thought sometimes that those who trod along it could not or would not look over the hedge; they admitted that the alley was paved with honest intentions but at its end they thought they could see a red light and a sign "The Gene: Dead End" (Dobzhansky, 1937, p. xii).

[22] In 1924 Harvard University recruited Whitehead from University of London.

As for the geneticists' point of view, in his 1926 *Theory of the Gene* Morgan stated that research problems in genetics and embryology were mutually exclusive (Morgan, 1934)[23]. In his own embryological work Waddington began formulating the ideas which he hoped would bridge this gap and link his field with genetics. Waddington showed that the organizer in amphibians — a region in the embryo that can produce a second embryonic axis to form a separate body — also existed in the embryos of mammals and birds. Next, Waddington studied the chemical nature of the organizer and the means by which it induced the formation of a secondary body, which led him to focus on the inducing signal by which development happened (Slack, 2002).

In 1934, Morgan published *Embryology and Genetics*, which inspired Waddington to declare to his colleagues that Morgan had,

> "firmly advocated the point — and should have fully established it, if people had been ready to listen to him — that the fundamental agents that bring about embryonic development are the genes, and that the only satisfactory theory of embryology must be a theory of how the activities of genes are controlled" (Robertson, 1997, p. 592).

Waddington was also, like Haldane, a member of the college of Cambridge Marxists including J.D. Bernal and Joseph Needham — both of whom he convinced that the chromosome theory of heredity was correct (Wersky, 1978, p. 206–207). Waddington continued his voluminous outpouring of publications in embryology and, in 1938, was awarded a Science Doctorate post-hoc by the University.

In June of that year Waddington left on a ten month Rockefeller Fellowship which he spent in the United States working at Cold Spring Harbor, Columbia University, as well as Morgan's new fly room at the California Institute of Technology. In Pasadena, Waddington worked with Dobzhansky, as well as another of Morgan's students, and Alfred Sturtevant, on wing development in *Drosophila melanogaster*. It is significant that it was at this point Dobzhansky was immersed in his research on *D. pseudoobscura*, the fruits of which would constitute his most important contribution to the evolutionary synthesis (Waddington, 1940). Waddington would take things the opposite direction. Waddington was not interested in the environment surrounding the flies, he wanted to know more about the milieu the Neo-Darwinists ignored — the landscape within.

When he returned to England, Waddington published "The Genetic Control of Wing Development in Drosophila", which would lay the groundwork for a later publication on "Genetic Assimilation of an Acquired Character in Drosophila" (Waddington, 1940b; 1953). Waddington also published a book, *Organisers and Genes*, where he introduced the term "epigenetics" for the first time. Meanwhile Waddington coined the word "competence" to describe the ability of cells or tissue to respond to an inducing signal, and outlined its influence on genes responsible for the development of eye color or antennae in *D. melanogaster*. The diagrams contained in the book provide the first visual representations of what Waddington would later present as the "epigenetic landscape".

It is worth noting that the frontispiece of *Organisers and Genes* foreshadowed the confusion which would greet Waddington's ideas in the years that followed. Waddington had a keen interest in contemporary art and the image he used to represent his burgeoning notion of the "epi" (i.e., environment) in which genes developed was produced by John Piper (1903–1992), a friend since the 1930s[24]. The different paths genes could follow in their development was

[23] See also Gilbert, 1991.

[24] Waddington even published a book on Modern Art towards the end of his career, see Waddington, 1969.

shown metaphorically as water flowing through the ravines down away from the viewer towards a distant sea, however the perspective made it appear as though the water was actually flowing towards the viewer. Though trivial, I believe this detail is symbolic of the reception towards Waddington's theories as his career continued.

Waddington served his country in World War II, and in 1945 he was asked to replace Francis Crew as Chair of Genetics at Edinburgh University. In 1947 Waddington was elected as a member of the Royal Society and set about establishing a genetics program at Edinburgh. However by this time, as mentioned above, the Neo-Darwinian paradigm was well-established without any apparent role for embryology. Even worse, a counter-reaction led by Soviet biologist T.D. Lysenko positioned genetics in opposition to the dynamics of evolution implied in Waddington's epigenetics, which insisted upon alternate developmental pathways beyond current conceptions of genetic inheritance. Dobzhansky, among others, claimed Waddington was rejecting the Neo-Darwinian synthesis and siding with Lysenko (Gilbert, 2015, p. 205)[25].

Waddington's affiliation with the likes of Haldane, Bernal and Needham gave the argument currency[26]. The upshot was his theories were rejected for reasons that ultimately had little to do with what he was actually saying. Things came to head for Waddington at an Oxford Symposium of the Society for the Study of Experimental Biology in 1953, where Waddington noted that though the advances of the past 30 years showed that biologists were reaching "some degree of finality" in uniting their interests under a common research goal, there was still no place for his field (Smocovitis, 1996, p. 24).

It is telling that the significance of the discovery of the chemical structure of DNA that same year went unmentioned in Waddington's 1956 *Principles of Embryology*, or *The Strategy of the Genes* published one year later. Waddington was not interested in the nature of the gene. He was, as an embryologist, focused on the cytoplasmic factors between the cell wall and the nucleus, and how cells were influenced by external factors as they developed. In these publications Waddington further refined the epigenetic landscape. *Principles* included an image with balls set at the top of a slope carved with alternate grooves they might follow in their development. Waddington used the term "evocation" to refer to the effect of the inducing signal to which tissue responds by selecting one of a few possible pathways for development. He coined the word "canalization" to describe the idea that a given cell will still become a thorax or a wing despite whatever mutational or environmental factors might intervene.

Waddington also sought to undermine the absolute integrity of the gene, a move that countered the belief of geneticists like Muller that it was the source of life[27]. Referring to Morgan's paradigm-altering discovery of the *white*-eyed mutant fly 46 years earlier, Waddington said that "in the usual genotypes met with within *Drosophila melanogaster* a substitution of w+ for w will change the eyes from white to red. The whole of the genotype other than the particular gene in which we are interested can be referred to as the genotypic milieu or genetic background". In other

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[25] I have found not published criticism of Waddington from Muller, which could be explained by two reasons:

1. Muller was attempting to distance himself from his prewar reputation as a communist, and criticizing Waddington would only have highlighted this period in his personal history;

2. Muller did not necessarily disagree with Waddington.

[26] Haldane in particular suffered for his initial willingness to be open-minded to the idea that Lysenko might be on to something. See deJong-Lambert, 2017.

[27] This is evident as early as his 1939 textbook, *An Introduction to Modern Genetics* (Cambridge, U.K.: Cambridge University Press, 1939), where he makes the case that geneticists must acknowledge themselves to be part of a wider "physiology of descent". See also also Speybroeck, 2002.

words, terms like "*w*+" and "*w*" were over-simplifications obfuscating a far more complex process (Waddington, 1956, p. 163)[28].

In *Strategy of the Genes*, Waddington mapped out the landscape further. Within the canals where cells develop are branching pathways called "chreodes" — a term derived from Whitehead's notion of "concresence" — the joint formation of a single entity (Robertson, 1977, p. 598; Speybroeck, 2002, p. 72)[29]. On the landscape chreodes are the buffered pathways charting the different trajectories according to which a cell destined to become a wing or an antenna might develop — structuring the different outcomes which could result based upon the environment they are exposed to. The landscape itself was underpinned by "guy-ropes" (representing "chemical tendencies") and "pegs" (representing genes) supporting it from below (Jablonka, Lamb, 2002, p. 83; Allen, 2015). It is clear that in this geography the notion of any one-to-one relationship between gene and trait falls apart.

By this time an honors course in genetics had been established and Edinburgh was becoming renowned as one of the global centers of genetics research. However Waddington was on to other things. In 1965 he garnered financial support to establish the Epigenetics Research Group. The following year he convened the first of four meetings at the Villa Serbelloni in Bellagio, Italy on the topic of Theoretical Biology[30]. It was the height of the revolution in molecular biology enabled by the discovery of DNA and RNA hybridization techniques. However for this reason Waddington's epigenetics was increasingly ignored by developmental biologists (Robertson, 1997, p. 11). Meanwhile, Waddington also, thanks to the ongoing conflict between his "Lysenkoist" *sic* views and the Neo-Darwinian paradigm, continued to be rejected by geneticists. Thus neither of the groups which he had sought to bring together on the epigenetic landscape were willing to go there.

Waddington's Epigenetic Research Group was dissolved in 1970 and five years later he died. In his final book, *Evolution of an Evolutionist*, Waddington said that since the rediscovery of Mendel's Laws "[t]hree basic changes in 'paradigm' (in Kuhn's sense) of the Theory of Evolution have become accepted:

1. Variation between individual organisms is due to changes in discrete units (genes) which do not 'blend'…
2. Evolution is to be considered in terms of changes in frequencies of *individual* genes in *populations* of organisms…
3. Evolution is concerned with populations of genes (gene pools) in populations of organisms".

However, "a fourth change is still waiting in the wings for full acceptance". By this he meant the inheritance of acquired characteristics:

> The battle, which raged for so long between the theories of evolution supported by geneticists on one hand and by naturalist on the other, has in recent years gone strongly in favour of the

[28] See also Speybroeck, 2002, p. 65, as well as Muller's criticism of Morgan's use of genetic terminology above.

[29] "Chre" comes from the Greek word for "necessity" and "hodos" from trajectory — i. e., "chreode" meant necessary trajectory.

[30] For a description of the symposia see Squier, 2015. See also the program for the 13th Altenburg Workshop in Theoretical Biology 2015, *Arriving at a Theoretical Biology: The Waddington Centennial*, 22–25 September 2005. Available online at: http://www.kli.ac.at/Modules/Assets/events/12/13AWTB_Program+Abstracts.pdf.

> former. Few biologists now doubt that genetical investigation has revealed at any rate the most important categories of heredity variation; and classical 'naturalist' theory — the inheritance of acquired characters — has been very generally relegated to the background because, in forms in which it has been put forward, it has required a type of hereditary variation for the existence of which there was no adequate evidence (Waddington, 1975, p. i, 16).

Waddington illustrated his theoretical interpretation of how acquired characteristics were inherited, followed by a practical example in terms of wing venations in *D. melanogaster*. However in the book Waddington also conceded that he was not a man of his time: "Thus my particular slant on evolution — a most unfashionable emphasis on the importance of the developing phenotype — is a fairly direct derivative from Whiteheadian-type metaphysics" (Robertson, 1997, p. 597)[31]. In other words, just as the philosopher Waddington idolized refused to reify objects as stable entities, Waddington refused to accept the gene as a solid unit of heredity, unaltered by the epigenetic landscape upon which the cells containing the genes developed.

Conclusion

The significance of Waddington's contributions to developmental biology were definitively acknowledged by the founding of the Waddington medal in 1998 — the only award given by the British Society of Embryologists. As for genetics, by 2001 the meaning of the term epigenetics had become so muddled that Joshua Lederberg suggested it should be abandoned (Lederberg, 2001, p. 6). However, a turning point arrived in 2008 when The Cold Spring Harbor Laboratory organized a special symposium to define once and for all what epigenetics meant[32]. At this juncture, it was determined that: "An epigenetic trait is a stably heritable phenotype resulting from changes in a chromosome without alterations in the DNA sequence" (Berger, Kouzarides, Shiekhattar, Shilatifard, 2009). In other words, Waddington was right.

But what about Lamarck, Tower, Kammerer, and Lysenko? In light of the above it is unsurprising that Kammerer's experiments are now being reconsidered in light of epigenetics and who knows — maybe Tower might be next? Dunn also referred to Tower's work when recounting the influences that led him to become a geneticist. However unlike Bateson, Davenport, Morgan, Muller and Dobzhansky — Dunn simply recalled that Tower's research on striping patterns of the Colorado potato beetle "stood me in good stead when I had to go down and defend myself, the next year, in seminars at Harvard" (Dunn, 1960, p. 42).

Dunn made this comment in 1960 — long after Tower had been disgraced. Maybe he still thought there might be something to it? The point is syntheses are never settled and the details underlying their construction may contain the reasons they are ultimately replaced. As Waddington suggested, the promise of a "dead-sure pay-off" might be as important a factor in what scientists accept to be true as the evidence right in front of them.

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[31] See also Waddingon, 1953.

[32] Cold Spring Harbor was where the members of Morgan's lab spent their summers and to this day the legacy of the Fly Room is celebrated in its library and archives. In a symposium devoted to Muller on Feb. 25, 2015 at which I was present, the director of Cold Spring Harbor, Nobel Laureate James Watson, declared that Muller was "the most important geneticist of the 20th century". See 1:50 at http://library.cshl.edu/Meetings/muller/h.j. — muller-event — videos.html.

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Что так подрывало концепцию наследования приобретённых признаков? В.Л. Тауэр, К.Х. Уоддингтон, и эволюция эволюционного синтеза

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В этой статье ставится вопрос, почему представление о том, что приобретённые признаки могут быть унаследованы, встретило такое сильное сопротивление в биологии в начале XX века. Статья начинается с рассмотрения случая Уильяма Лоуренса Тауэра, биолога в Чикагском университете, карьера которого закончилась скандалом из-за его попыток улучшить наследование признака чередования полос у колорадского картофельного жука. Хотя менее известное, чем печальный пример Пола Каммерера (чья работа сегодня пересматривается в свете эпигенетики), противоречие относительно заявлений Тауэра показывает сильное недоверие к наследованию приобретённых признаков в тот период. Также рассматриваются некоторые самые важные фигуры в эволюционном синтезе генетики и эволюции — Г.Дж. Мёллер, Дж. Хаксли, Л.К. Данн, Дж.Б.С. Холдейн и Ф.Г. Добржанский — с точки зрения их реакции на работу К.Х. Уоддингтона, инновационное исследование которого в эпигенетике вызвало похожий уровень подозрений из-за того, что оно также подразумевало, что приобретённые признаки наследуются. Статья заканчивается предположением, что история эволюционного синтеза должна быть пересмотрена в свете того, почему такие идеи, как идеи Уоддингтона, были отвергнуты как несовместимые.

Ключевые слова: К.Х. Уоддингтон, В.Л. Тауэр, генетика, эволюция, ламаркизм, Т.Х. Морган, Г.Дж. Мёллер, Джулиан Хаксли, Л.К. Данн, Дж.Б.С. Холдейн, Феодосий Добржанский.