Embryology and the Evolutionary Synthesis: Waddington, Development and Genetics.

by

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The candidate confirms that the work submitted is his own and that appropriate credit has been given where reference has been made to the work of others.

Abstract.

The role of embryology, genetics and morphology within mid twentieth century evolution theory, is discussed in the context of the growth to dominance of natural selection as the orthodox mechanism of adaptive evolution. The unification of neo-Mendelian heredity and neo-Darwinian selection theory, is described as the core of modern synthetic neo-Darwinism as it emerged in 1930s mathematical population genetics. As selectionism strengthened within synthetic neo-Darwinism, embryological development was excluded from its traditional causal role in adaptive evolution within the "old synthesis" of Haeckelian recapitulation and neo-Lamarckian inheritance. A two-tier embryology was created, as embryology was understood to deal separately with the experimental analysis of ontogenetic development, and the historical descriptive analysis of phylogenetic lineages. Neither tier informed the other, or played any direct causal role in the mechanism of the creation of adaptive evolutionary novelty. That adaptive evolutionary mechanism was entirely the preside of natural selection. However, as the selectionist synthesis hardened in the 1940s, late nineteenth century Darwinists' concerns over the hereditary fixation of highly specific adaptive somatic modifications resurfaced. Consequently, the strategic defence of the synthetic theory against any resurgence of neo-Lamarckian heredity, involved an appeal to the principles of modern synthesis developmentalism; namely, the developmentalist syntheses of Waddington and Schmalhausen. The unforeseen implication of these moves by founding supporters of the synthetic theory, was that the disciplines upon which 1940s developmentalism rested--namely, Western chemical embryology and Soviet evolutionary morphology--did after all play a central and causal role in the mechanism of adaptive evolution. Attempts to characterise the alternative and developmentalist syntheses of Waddington and Schmalhausen as the "missing links" to an otherwise incomplete modern synthesis, are historically evaluated. These attempts are thought to embody either a mistaken understanding of the essential nature of synthetic neo-Darwinism, or an obfuscation of the continuing issue of its synthetic adequacy.

Contents.

Preface.

This thesis is about one major consequence for the modern evolutionary synthesis of its move towards an ever stricter selectionist-adaptationism in the 1930s, 1940s and 1950s. That consequence was the return of late nineteenth century concerns over phenotype-genotype relations in adaptive evolution and, by the same token, of the threat from the "old synthesis" of recapitulationism and the inheritance of acquired characters. It is, therefore, also about evolutionary embryology, genetics, and morphology, as those three disciplines came together to form a powerful nexus in modern synthesis developmentalism. Much has been made of the supposedly minimal contributions made to the modern synthesis by embryology and morphology. It is hoped that the current history will at least serve to reopen debate over these issues, and perhaps serve to show that embryology and morphology made a much more powerful contribution than has hitherto been suspected. To paraphrase Churchill's comment after researching the history of embryology in the modern synthesis period, one's instincts tell one to dig deep in one place, in the hope of striking the taproots that feed the tortuously intertwined developments on the surface. I have tried to follow this excellent advice as closely as possible.

The personal motivations for investigating the issues below are easily related. For a biology major in the mid to late 1980s, Sussex University was a tremendously stimulating environment. But it was a veritable dream come true for one excited by the supposed crumbling citadels of synthetic neo-Darwinism, though nonetheless stimulated by the precise and powerful pleasures of genetic chance and evolutionary necessity. At Sussex, such dichotomies were very soon displayed before one's very eyes, having the likes of Maynard Smith and Lewis Wolpert, Brian Goodwin and Gerry Webster available to see and listen to in close proximity and quick succession. Embryology, development and genetics were particularly stimulatingly taught in the genetics department, with Waddington's Edinburgh co-worker James Sang heading a very strong team including Robert Whittle and Jonathan Bacon from Cambridge, and Janet Collett from Johns Hopkins. As undergraduates, we were taken to the cutting edge of empirical and philosophical issues concerning development in an exciting way, culminating in our inclusion within a final year retreat conference for serious academic debate.

The following is, therefore, primarily an intellectual history of the conceptual issues surrounding modern synthesis developmentalism between 1930 and 1960. Apart from having a liking for such histories for the reasons made clear above, I also felt that this method appropriate for what, in many ways, is a new area of investigation. Historians need to have some grasp of, for example, what Simpson understood by organic selection, and what Waddington felt was the theoretical relationship between genetic assimilation, stabilising selection, and the Baldwin effect. Thus there have been very few places where I have focused on socio-political issues at the level of institutions, or professional interest groups, or on broad styles of thought or psychobiographical explanations.

This is not an expression of aversion to any of these historiographical methods. In fact it is readily apparent where they might be applied to the very substance of my topic. For example, ill-feeling between Mather at Birmingham and Waddington at Edinburgh, according to those closely involved at the time, was due in no small degree to Waddington's charismatic group attracting the lion's share of the limited supply of graduate students and research funding available to genetics in the 1940s and 1950s. Similarly, the constant proliferation of different kinds of natural selection, with little or nothing apparently to distinguish them, might well be related to the difficulties (reflected upon by Waddington himself) of achieving status in the new field of evolutionary genetics in the 1930s and 1940s. Again, there was a clear stylistic divide across modern synthesis developmentalism. Hence T. H. Morgan's transmission genetics and the Pasedena group's interests strongly influenced Waddington's 1950s research; whilst Woltereck's conception of the norm of reaction, Baur's particular brand of neutralism, and Haecker's phenogenetics evidently strongly influenced Schmalhausen.[1] Lastly, Waddington's autobiographical

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[1] Whilst acknowledging the importance of Harwood's 1993 *Styles of Scientific Thought*, I have not made extensive use of his analysis of German interwar genetics for several reasons. Firstly, Harwood's history is all but completed as mine begins. Secondly, and more importantly, Harwood himself explains that "strict selectionists were few and far between in interwar German biology" (Harwood 1993, p. 104). However, my history is built around the central theme of dissent among strict selectionist-adaptationists in the Anglo-American tradition, whilst the roles of such German anti-selectionists as Goldschmidt, and weak selectionist dualists as Plate, are somewhat peripheral to it. Thirdly, Waddington and Schmalhausen were

writings and self-professed penchant for Whiteheadian process philosophy, would provide rich material indeed for a psychobiographical approach to the Waddingtonian epigenetics programme.

Nevertheless, whilst these approaches may be applied to this material in future, I feel that the current history as written provides for its own defence. It does so, through being an important first look at a interesting topic in the history of the modern synthesis; namely, the debate over the evolutionary significance of adaptive modifications to the organism, with all its negative implications for the status of the current neo-Darwinian synthetic theory. Lastly, as Gould stated in 1976: "It is rather remarkable how many current controversies in biology are a continuation of long-standing arguments" (Gould 1967, p. 221; in Provine 1983, p. 43). It is certainly true that the issues of unilinear regularity versus branching irregularity, orthogenetic internalism versus selectionist externalism, and gradualist continuity versus saltationist discontinuity in evolutionary theory, are all well represented within the current history of modern synthesis developmentalism. These issues--Gould's "eternal metaphors" in evolutionary thinking--add another dimension of complexity and interest to the intellectual issues at hand, and constantly coloured the background to the debates. Occasionally, also, they came to the foreground and influenced those debates directly--as in the case of Huxley's lone strong support, among the synthesis' founding supporters, for neo-organic selectionism in the 1940s.

The reader who wishes to can go straight to the Summary conclusion in Chapter 5, and in particular to the 10 point general summary in section 5.4, for an advance overview of the whole before reading the detailed chapters. Finally, I should like to thank my Supervisor, Jonathan Hodge, without who's tremendous patience and even greater generosity, this thesis would never have been completed. I should also like to thank those who have provided useful feedback and encouragement during my travels, particularly Gerry Webster, Michael Ghiselin, Elihu Gherson, and Peter Stevens. Others who have given encouragement and stimulation include Paul

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both staunch nucleo-cytoplasmic interactionists, and could not be described as dualists in the sense in which Harwood discusses Winkler, Fick, Plate and others (1993, pp. 106-107). Waddington and Schmalhausen were, I maintain, unique in having synthesised orthodox 1930s interactionist Mendelian genetics and 1950s strict selectionist-adaptationism within their particular theories. Inheritance for them constituted a unity between Mendelian genetic, epigenetic and morphogenetic factors, and did not incorporate any equivalent to the German dualist notion of the *Grundstock*.

Griffifths, Bill Wimsatt, Fred Churchill, and many others at the very stimulating Leuven and Seattle ISHPSSB conferences who's names I do not now recall.

Introduction.

The Evolution of Synthetic Neo-Darwinism: The Emergence of Strong Selectionism and the Adaptationists' Dilemma.

> The adaptationist tradition, on the other hand, has been an English pastime for at least two centuries. If continental thinkers glorified God in nature by inferring the character of his thought from the laws of form linking his created species, or incarnated ideas (as Agassiz maintained), then Englishmen searched for him in the intricate adaptation of form and function to environment--the tradition of natural theology and Paley's watchmaker. Darwin approached evolution in a quintessentially English context--by assuming that adaptation represented the main problem to be solved and by turning the traditional solution on its head. Few continental thinkers could have accepted such a perspective, since adaptation, in their view, was prevalent but superficial.[1]
>
> Stephen J. Gould

0.1. Evolution Before the New Synthesis: The Several Challenges to Selectionism.

The history of Darwin's classic theory of evolution, during the period leading up to the emergence of the synthetic evolutionary theory of the 1930s, is far from one of smooth rise to scientific hegemony. Rather it is one of rise, decline and fall, followed by resurrection. Darwinism, or the gradual evolution of adaptive forms, via the natural selection of small hereditary variations occurring spontaneously in natural populations, was in its heyday in the 1870s and 1880s. It took hold in Germany, where the morphologists Gegenbaur and Haeckel applied Darwin's theory of descent in opposition to non-transmutationist ideal morphology, and began trying to decipher the historical connections between transmuted forms. During this period, many young Darwinian anatomists and embryologists joined the Haeckelian research programme, and attempted to reconstruct actual phylogenetic pathways in evolutionary development, based on the embryological principles of Haeckel's "biogenetic law" (Bowler 1989, p. 202). As Nyhart observes from *On The Origin of*

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[1] Gould 1983, p. 91.

Species, "Darwin's assertions that morphology was 'the most interesting department of natural history, and may be said to be its very soul,' and that embryology was 'second in importance to none in natural history,' lent weighty authority to this group's claims that their endeavours were truly scientific" (Nyhart 1995, p. 141).[2]

Nevertheless, evolutionary morphologists began to lose faith in the Haeckelian doctrine, along with the results of the research it promoted. Limited fossil evidence had precluded any rigorous testing of the highly speculative phylogenies that were being constructed. Yet reaction against "phylogenizing," or the embryological reconstruction of hypothetical genealogies, did not represent a turn against evolutionism itself; very few late nineteenth century paleontologists still accepted creationism (Bowler 1989, p. 202). However, the paleontological morphologists who were committed evolutionists did not remain committed to Darwin. Not only did the fossil record include troublesome gaps which post-Darwinian morphologists had summarily failed to speculate away, it also contained evidence of mysterious long-range developmental trends; and some of which were clearly mal-adaptive developments which had led to extinction of the lineage. Such trends, although still open to Darwinian gradualist explanation, were increasingly felt to be beyond explanation by the theory of natural selection.

Hence in America, the anti-Darwinian paleontologists Hyatt and Cope were both neo-Lamarckists. They had developed, from the mid 1860s to the late 1880s, a unique approach to evolutionary gradualism. From early on, their ideas were based upon the combination of recapitulation with the action of internal orthogenetic hereditary forces, and only later upon the neo-Lamarckian inheritance of acquired characters. Both were very influenced by creationist idealism, especially Agassiz's notion of a transcendent parallelism existing between paleontological and embryological development (Bowler 1989, p. 261). They completely ignored Darwinian adaptationist natural history, seeing evolution as being driven by non-utilitarian goal-directed or teleological forces in embryological development, with an

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[2] For Nyhart, "as is suggested by Haeckel's case and as . . . for members of the generation just embarking on their professional careers in 1860, Darwin's theory offered a new takeoff point for developing a personal program of research, for it provided a way of justifying the long-held belief that embryology, classification, and the study of the history of the organic world were all legitimate and mutually reinforcing realms of morphological enquiry" (Nyhart 1995, p. 142).

internal law of "acceleration of growth" accounting for recapitulation.[3] For both Hyatt and Cope, then, Darwinian random variation and selection could have no role, because evolution was merely the unfolding of a predetermined (and in Cope's view Divinely preordained) orthogenetic sequence of changes (1989, p. 262). However, both men later turned to a more utilitarian explanation of evolution, and therefore adopted Lamarckian use-inheritance. As Haeckel knew, the Lamarckian inheritance of acquired characters, including specific use-inheritance, suited recapitulation very well by providing an explanation of the terminal additions to development which his "biogenetic law" required (ibid.).

However, elsewhere in the late nineteenth and early twentieth century, European conceptions of orthogenesis such as Eimer's "definitely directed evolution" stood independently of paleontologists' concerns with long-term evolutionary trends: for example, Eimer's lifetimes work had been on coloration and patterning in butterflies (Eimer 1898). Similarly, the challenge to Darwin from European neo-Lamarckism was not tied to non-utilitarian orthogenesis as it was among the American paleontologists. Lamarckism had re-emerged as an independent (if disparate) movement in the wake of Darwinism having made species transmutation scientifically acceptable. Furthermore, as was often pointed out by neo-Lamarckians, both Darwin and (most especially) Haeckel had appropriated their ideas.[4] Neo-Lamarckism was a peculiarly protean movement, accepting many non-selectionist adaptive evolutionary mechanism's including Geoffroy's evolution via direct

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[3] For evolutionary (that is, historical and phylogenetic as opposed to ideal) recapitulation to occur, the length of ancestral ontogenies, or individual organism's life-cycles, must be shortened. As Gould explains: "Nature must make room for the new features added to the end of ontogeny. Recapitulationists, from Haeckel onwards, have offered a standard explanation for this condensation: it occurs as a result of a law of heredity; the law's causes are as unknown as its results are manifest. But what law of heredity? Here the recapitulationists disagreed. Some spoke of a universal tendency towards acceleration of the developmental rate: descendants would pass through stages more quickly than their ancestors had. Others, Haeckel included, favoured a law of 'deletion'--certain stages would be exised, allowing the remaining ones to complete their appearance more rapidly" (Gould 1977, p. 83).

[4] Neo-Lamarckism and Darwinian selection both assumed adaptation to the environment was the primary cause of evolutionary change; hence Darwin could relatively easily assume a limited role for Lamarckian use-inheritance. However, orthogenetic regularities occurred independently of the environment, and were therefore positively anti-utilitarian, and anti-Darwinian (witness the harsh criticisms definitely directed towards the pan-selectionist Weismann from Eimer in my section 2.3.3.). In Bowler's view, "the supporters of orthogenesis reveal the last vestige of the influence of idealism on modern biology" (Bowler 1989, p. 265).

environmental influences, and a variety of forms of orthogenesis (Mayr 1980, p. 5).[5] The term neo-Lamarckism had been coined by Packard in 1885, in opposition to Weismann's "neo-Darwinian" insistence upon natural selection as the sole mechanism of adaptive evolution. This insistence of pan-selectionists such as Weismann and Wallace, combined with Weismann's doctrine of the insulation of the germ plasm from all environmental stimuli to adaptive modification, created a strong polarity in the period's understanding of heredity (Bowler 1983, p. 59). Weismann tellingly insisted that neo-Lamarckians provide specific evidence that acquired modifications were directly causally responsible for the production of identical germinal variations; that is, that they provide specific evidence for somatic induction. Yet, in the new century's shifting emphasis from field based to laboratory and experimentally based methods, neo-Lamarckian's lacked any experimental evidence acceptable within the narrow Weismannian criteria. Furthermore, in the 1920s Lamarckism was under renewed threat from a resurgence of selectionism, and the notable efforts of committed Lamarckists such as McDougal and Kammerer still failed to convince the pan-selectionist Weismannians.

A third major challenge to classical Darwinian selection, namely neo-Mendelian mutationism, also emerged forcefully at the beginning of the twentieth century. However the particular path of its development is closely bound up with the resurrection of natural selection, and is therefore better examined within an historical overview of the emergence of synthetic neo-Darwinism in the first half of the twentieth century.

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[5] As Bowler explains, "there were two kinds of Lamarckians: those who wished to link the theory with the idea of regular evolution and orthogenesis, and those for whom the inheritance of acquired characters was purely a mechanism of adaptation, more purposeful than Darwinism but no more likely to generate regular patterns of evolution" (Bowler 1983, p. 56). Neo-Lamarckians clearly occupy the second of these categories, and classical Lamarckians the first. Burkhardt states: "Neo-Lamarckism arose less as a continuation of Lamarck's own thinking than as a legitimate response to problems left unanswered in Darwin's *On the Origin of Species*. The idea of the inheritance of acquired characters, the defining characteristic of neo-Lamarckian thought, was indeed central to Lamarck's thinking. But it was never an issue for Lamarck himself; he and the vast majority of his contemporaries simply took the inheritance of acquired characters for granted" (Burkhardt 1980, p. 345).

0.2. The Foundations of Synthetic Neo-Darwinism: Development of the Mendelian-Hereditarian Research Programme.

The emergence of a synthesis in modern evolutionary biology in the 1930s and 1940s, is a very broadly accepted category within the historiography and philosophy of biology, although the significant period of its emergence is contested.[6] The nature and status of that synthesis is still more problematic, and has caused considerable controversy. Many historians, most notably Provine, have characterised the content of the synthesis more narrowly, focusing on the integration of classical Darwinian selection, and theoretical population genetics, as the significant core of the synthesis (Provine 1971, 1983, 1986; Beatty 1986; Wallace 1986). From this perspective on the significant events, the synthetic theory was fully formulated by the early 1930s with the publication of the works of Fisher's 1930 *Genetical Theory of Selection*, Haldane's 1932 *The causes of Evolution*, and Wright's 1931 paper "Evolution in Mendelian populations." Hence Dobzhansky felt that Fisher, Haldane, and Wright in the West, along with Chetverikov in the Soviet Union, "may be considered founders of the modern analysis of evolutionary phenomena" (Dunn 1951, p. 575; in Provine, 1980, p. 491). Others, most notably Mayr, maintain that systematists from several fields made a non-trivial contribution during the 1930s and 1940s to a broad-ranging synthesis, which was not itself reducible to the simple fusion of Mendelian genetics and Darwinian selection theory (Mayr, 1980, p. 40; Provine 1983, p. 44).[7]

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[6] Provine stated of the 1980 meeting of the Committee on the Recent History of Science and Technology, gathered specifically to discuss the purported synthesis: "One certain conclusion emerged from the conference. All participants, whether scientists or historians, young or old, agreed that a consensus concerning the mechanism of evolution appeared among biologists during the 1920-1950 period. Darwin, despite all his influence, was unable in his lifetime to produce a corresponding consensus, and none coalesced until the second quarter of the twentieth century. Whatever it is called--evolution, the modern synthesis; the evolutionary synthesis; or twentieth century Darwinism--every participant agreed that a comprehensive and compelling view of the mechanism of evolution appeared during this time" (Provine 1980, p. 399). In the present history, I apply the term "synthetic neo-Darwinism."

[7] Mayr robustly defended his view that the synthesis proper began in 1937 with Dobzhansky's classic work *Genetics and the Origin of Species*, and was "completed in principle in the 1940s" (Mayr 1980, p. 42), asserting: "For this reason [supporting Laudan's view that the synthesis did not instantiate a Kuhnian revolution] to state that the synthesis was merely an acceptance by the naturalists of the newer findings of genetics ignores the numerous concepts that the geneticists took over from the naturalists: population thinking, the multidimensionality of the polytypic species, the biological species concept (with the species defined as a

From the point of view of the present history, there is acceptance of the widely held notion that, in the early 1930s, a transforming union was finally instituted between neo-Mendelism and neo-Darwinism. The resulting doctrine, which I will call synthetic neo-Darwinism, engendered a new and readily identifiable central dogma, if not active research programme, that has persisted within adaptive evolutionary biology to the present day. This use of synthetic neo-Darwinism as a working historical category is not intended to undermine the claims of any others historians, that such a conception of the synthesis denies the obvious input from other biological disciplines and research traditions. Rather, my use of the concept serves to support the legitimate sentiment behind those claims: namely, that supporters of the doctrine in the 1940s and 1950s marginalised problematic disciplines, excluded potentially subversive individuals' viewpoints, and rationally reconstructed their theoretical writings, in a way that has historically fuelled deep suspicions over the new orthodoxy's synthetic adequacy. The present history, therefore, focuses upon the obvious exclusion of the phenogenetics of modern synthesis developmentalism (as expressed within the embryo-genetics of British chemical embryology, and Soviet functionalist evolutionary morphology), from making their contributions to a genuine synthesis.

The development of synthetic neo-Darwinism has been described in detail by several historians of biology (Provine 1971, 1986; Mayr 1980; Bowler 1988, 1989). A review of the historical background to its development, is essential to an appreciation of its rise to dominance as the accepted mechanism of adaptive evolution. As outlined in the previous section 0.1., Darwinism was in marked regression at the end of the nineteenth and beginning of the twentieth century. Considerable general resistance had developed to Darwin's (and Wallace's) insistence on gradual organismic change as the normal mode of evolution under natural selection--along with particular resistance to the mechanism of natural selection itself (Panchen 1993, p. 122). In the 1890s, controversy over Weismann's synthesis of cytology and heredity, with its central doctrine of the absolute isolation of the germ plasm, was likewise reaching a high point. Weismann's consequent insistence upon a rigid distinction between acquired somatic (somatogenic) and inherited germinal

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reproductively and ecologically autonomous entity), the role of behaviour and change of function in the origin of evolutionary novelties, and so on" (1980, p. 40).

(blastogenic) characters, was unacceptable to Lamarckians, for whom a purely germinal source of variation was unthinkable (Bowler 1983, p. 78; see my concluding section 5.1.). Weismann's ideas symbolised the hard heredity and dogmatic selectionism Lamarckians so avidly opposed.

However, Correns and de Vries, after their (in de Vries' case disputed) rediscovery of Mendel's laws of inheritance in 1900, suggested that they held the key to a completely new and alternative theory of heredity. Bateson, who became the British champion of the new "Mendelism," had been a recapitulationist, but had become utterly disaffected with speculative post-Darwinian morphology. His prior saltationism (as expressed in his 1894 *Materials for the Study of Variation*), found its apparent vindication with the Mendelian rediscovery, and began for him a particularly acrimonious conflict with the Darwinian gradualists of the biometric school; namely, Pearson and especially Weldon (Provine 1971; Bowler 1989). Unfortunately, Bateson could not personally accommodate the new science of heredity to any mechanism of adaptive evolution since, for him, mutations creating new genetic factors were always degenerative. De Vries, nevertheless, had developed the concept of mutation as an explanation of saltative evolutionary change, independent of natural selection. Such "sports" minimised the importance of Darwin's minor individual variations: as long as a sufficient number of individuals were thus mutated, a new form could be created as a distinct breeding population.

Hence, a third candidate emerged in the contest for the mechanism of evolutionary change; one which simultaneously explained the origination and separation of varieties and species, and did not require the complex biological and geographical isolation mechanisms of the Darwinians (Bowler 1989, p. 276). Furthermore, neo-Mendelian mutationism appeared to obviate the need to invoke environmental adaptation as evolution's *sine qua non*. Hence some naturalists, weary of the Darwinism versus Lamarckism debate over the true mechanism of adaptive evolution, enthusiastically supported the mutation theory. Furthermore, adaptation was seen, by many of the new breed of experimentalists, as an unscientific doctrine suggestive of the reintroduction of teleological and purposive agencies into evolution.

These, then, all appeared to be excellent reasons for rejecting Darwinism, particularly since Weismann's extremism over natural selection had become so strident. Hence, as Mayr reflects, the Mendelians--meaning Bateson, de Vries, and Johannsen--both ignored the comprehensive findings on speciation made by Darwinian systematists, and also "took a dim view" of natural selection (Mayr 1980, p. 7). As the neo-Mendelian Johannsen stated, further to the findings of his "pure line" experiments on self-fertilising bean plants: "Even the most careful experiments with cross-fertilizing plants and animals confirm most convincingly our interpretation of an inability of selection to achieve more than a mere isolation or separation of previously existing constitutionally different organisms: Selection of differing individuals creates nothing new; a shift of the 'biological type' in the direction of selection has never been substantiated" (Johannsen 1915, p. 609; in Mayr 1980, p. 7).

In consequence of the Mendelian's evidences, the neo-Lamarckians were forced to accept the existence of saltation, but refused to accept its significance to adaptive evolution. Thus, in Mayr's words, "to dislodge the proponents of soft inheritance from their last toehold, it was necessary to establish two important facts: (1) that there is no difference between large and small mutations--that is, between de Vriesian mutations and Darwin's individual variation; and (2) that the components into which Darwin's individual variation can be dissected show the same hard inheritance as sports or conspicuous mutations" (Mayr 1980, p. 19). For Mayr, supporting evidence for these propositions was begun by several geneticists; such as Nilsson-Ehle in 1909, East in 1910 and 1916, Baur in 1925, Emerson and East in 1913, and Castle in 1916. By the 1920s, in Mayr's estimation, "it was reasonably clear to those who kept up with the genetic literature that there was only one kind of variation"; a kind completely conformable to Darwin's original theory. However, confusion was evident, even up until the 1930s and 1940s. The writings of palaeontologist and Lamarckian H. F. Osborn (1927), for example, epitomised the lingering interpretation of mutation in the de Vriesian sense amongst field working evolutionists (ibid.).

It was the remarkable progress in resolving and cytologically mapping transmissible variations in *Drosophila*, that enabled T. H. Morgan to designate any minor heritable phenotypic change as a genetic mutation.[8] Significantly for Soviet

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[8] Morgan, however, was by no means an ardent selectionist. Yet although Mayr's view in 1975 was that "Morgan's opinions . . . impeded the eventual synthesis," other historians such as Allen think this view unjustified, and see Morgan as struggling to integrate the new genetics with Darwinism, and making "several significant modifications on his views on Darwinian theory

research into genetic mechanisms of adaptive evolution, Chetverikov in 1926 attempted unsuccessfully to institute the term "genovariation" into the language of heredity; with genovariations (as opposed to non-transmissible phenovariations) supposedly differentiating Morgan's mutations from the de Vreisian macromutations.[9] De Vries, according to Mayr, compounded the confusion that Chetverikov had sought to alleviate, "by never making it clear whether mutation referred to a change in the phenotype or in the genotype" (Mayr 1980, p. 21). A further consequence of the confusion over mutation, was that so-called "mutation pressure" was thought essential to evolving beyond the restrictions of Johannsen's pure lines. Thus Haldane wrote in his *The Causes of Evolution*: "The fundamental importance of mutation for any account of evolution is clear. It enables us to escape from the impasse of the pure line. Selection within a pure line will only be ineffective until a mutation arises" (Haldane 1932, p. 57; in Mayr 1980, p. 21).

The first three decades of the century, therefore, laid the foundations for synthetic neo-Darwinism, as characterised by the integration of neo-Mendelian heredity and classical Darwinian selection. Nevertheless, many field naturalists, especially the American school of palaeontologists, continued to reject selectionist explanations; some adhering to neo-Lamarckism and orthogenesis, others to neo-Mendelian saltationism, and some (like H. F. Osborn) to both. Only by a general recognition of the complexity of the genetic structures of natural populations, could Darwinism regain the ascendancy in explaining adaptive evolution. As Mayr has stated: "Unless one adopts population thinking and considers every individual as representing a uniquely different genotype, natural selection does not make much sense" (Mayr 1980, p. 29; see also Bowler 1989, p. 308). Such a recognition of the genetic complexity of populations was also congruent with the rapprochement between neo-Mendelism and Darwinian biometrics (Provine 1971). As early as 1902,

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between 1903 and 1932" (Allen 1980, p. 356). Also, Weinstein believes that Morgan's reputation in respect of his supposed anti-selectionism "does not represent his ideas with complete accuracy" (Weinstein 1980, p. 432).

[9] See section 2.6.1. for the neo-organic selectionist Gause's controversial use of the genovariation-phenovariation distinction to explicate his substituting selection concept in 1940. Adams lists many more important contributions made by Chetverikov at Kol'tsov Institute in Moscow. As Adams States, those contributions included "one of the first theoretical papers synthesizing biometric, naturalist, and genetic approaches to evolution in a Darwinian framework" (Adams 1980b, pp. 242-243; see also Dobzhansky 1980, pp. 234-235).

then, Yule had suggested that the continuously varying characters of the Darwinians could be explained by accepting many Mendelian factors to be responsible for small hereditary variations in a single character (Bowler 1989, p. 309).

This landmark realisation--namely, that selection for adaptively advantageous genes within such genetically complex populations could be the driving force behind adaptive evolution--was comprehensively embodied in the mathematical formalisms of R. A Fisher and J. B. S. Haldane in Britain, and Sewall Wright in America. This was the major theoretical departure characterised above as synthetic neo-Darwinism. In the West, Fisher, Haldane, and Wright agreed upon several matters: the immense power of selection to change gene frequencies in reasonably few generations, the relative insignificance of mutation pressure, and (much more controversially) which formal variables were most important (for example selection rates, effective population size). For Provine, their work was "a crucial element in the vast narrowing of the controversies over the mechanisms of evolution in nature" (Provine 1986, p. 232). However, despite broad agreement among these founders of the synthetic theory, Wright and Fisher differed greatly in their views.[10] Drawing on his pre-synthesis work on guinea pigs, Wright's 1925 original typescript of his "shifting balance" theory of the mechanism of evolution, did not emphasise mass selection in large populations, but selection within smaller (though not too small) partially isolated subgroups, or "demes" (Provine 1983, p. 45). Within demes, gene frequencies were subject to Wright's own evolutionary mechanism of random genetic drift, as well as natural "interdemic" selection--the latter working by selective diffusion from demes with the more adaptive gene combinations (ibid.). According to Wright himself, his famous 1931 paper closely followed his 1925 theory (Provine 1986, p. 235-237).[11]

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[10] Provine views this controversy as being of the highest significance: "Indeed, I would argue that many of the most fundamental issues now energizing modern evolutionary biologists are extensions of issues that were bones of contention between Wright and Fisher" (Provine 1986, p. 233).

[11] As Provine explains, for Wright, "natural populations must be subdivided into small-enough partially isolated subgroups to cause random drifting of genes, but large-enough subgroups to keep random drifting from leading directly to fixation of genes, for this was the road to degeneration and extinction" (1986, p. 236).

The received view in modern synthesis historiography states that Fisher's basic evolutionary ideas, as also expressed prior to the synthesis in his 1922 paper, "On the dominance ratio," stand in marked contrast to Wright's. In accordance with his biometrical training, Fisher believed evolution most effective in large populations where genetic variability was high. Deterministic selection acting on single genes was practically all-important, and, in Provine's words: "Among the negligible assumptions as to the accidental circumstances in evolutionary theory were the effects of genic interaction and random genetic drift." But, Provine adds, "Sewall Wright was to vigorously disagree with Fisher's judgement in these cases" (1986, p. 241).[12]

0.3. Preliminary Hardening of the Synthetic Theory: The Dismantling of the Old Evolutionary Synthesis and the Formation of a Two Tier Embryology.

Provine's perception that the synthetic works of Fisher, Haldane, and Wright, were "a crucial element in the vast narrowing of the controversies over the mechanisms of evolution in nature," has been taken a step further by Gould in his writings on the pan-adaptationist "hardening" of the later synthesis (Gould 1980, 1983). Provine, in broad agreement with Gould, stated regarding the shift towards adaptationism in Wright's later work: "The development of Wright's views in the period 1929-48 exemplifies nicely Gould's thesis about the 'hardening' of the evolutionary synthesis toward a more adaptationist view." In broader terms, Provine continues: "A corollary of Gould's thesis is that the selectionism/adaptationism of the later evolutionary synthesis went too far and that current evolutionary theory should provide a more balanced view, including nonadaptationist mechanisms of speciation" (Provine 1983, p. 67; see also Lewontin 1978, and Gould and Lewontin 1979).

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[12] Interactions between Mendelian factors in the production of the phenotype had been shown experimentally by the earliest Mendelians. Thus Bateson and Punnett demonstrated epistatic effects in domestic fowl as early as 1905 (Panchen 1993, pp. 107-109). Likewise, in the same year, Bateson Saunders and Punnett had shown incomplete dominance for coloration in the same organisms. Lewontin has thus maintained that genetic interactions were left out of Fisher's account, not because of their unimportance, but because of the difficulty of formally integrating them into the mathematics (Lewontin 1980, p. 62).

Hence in 1963, Mayr expressed the long-established orthodox view in his statement: "The proponents of the synthetic theory maintain that all evolution is due to the accumulation of small genetic changes, guided by natural selection, and that transpecific evolution is nothing but an extrapolation and magnification of the events that take place within populations and species" (Mayr 1963, p. 586; in Gould 1983, p. 73). The historical background to Mayr's proposition is, I believe, of great importance to any history concerned with the status and significance of modern synthesis developmentalism.

As proposed in section 0.1., the staunchly Mendelian-Hereditarian aspect of this doctrine had been in place since its inception in the early 1930s. What Gould calls the "pluralistic" synthesis of the early 1930s, nevertheless insisted that all evolution was caused by small-scale randomly occurring genetic changes within natural populations (Gould 1983, p. 75). Hence, although the selectionist aspect of the early synthetic theory had not yet sufficiently hardened to support the pan-adaptationism of the late 1940s and 1950s, nevertheless a preliminary hardening excluded all evolutionary mechanisms not strictly conformable to neo-Mendelian principles of heredity. This pre-hardening most radically excluded those ideas harking back to the evolutionary analogy with growth, particularly as expressed within the developmentalism of Haeckel's "old synthesis" (Gilbert 1994, p. 144; see my section 1.1.).

Thus in 1922, invertebrate morphologist and neo-Darwinian systematist Walter Garstang attempted a thorough and final discrediting of Haeckelian recapitulationism. For those late nineteenth and early twentieth century recapitulationists who had relativised Haeckel's original 1866 theory, ontogeny was the accelerated recapitulation of specifically adult organs and structures produced earlier in phylogeny (Gould 1977, p. 175). Thus a compressed, if rearranged, presentation of evolutionary history was made available simply by observing ontogeny in higher organisms. Garstang urged that neo-Mendelian hereditary principles of random variation, finally provided biology with a deductive disproof of what he called this "cramping and delusive" doctrine of Haeckel's "biogenetic law." Morgan's views represented for Garstang the basis of a "true" biogenetic law. Far from phylogeny being the direct mechanical cause of ontogeny--the aeteological doctrine of the biogenetic law--it was actually the passive result of the sequence of ontogenies, alterations within which were the chance result of random mutations.[13]

Embryologist and neo-Darwinist Gavin de Beer reinforced Garstang's supposed disproof of the old biogenetic law, and wrote what many historians, especially Gould, believe to be the first work of the neo-Darwinian synthesis (Gould 1977, pp. 221-222). De Beer followed Garstang in supporting Morgan's view of the very limited significance of recapitulated structures. He also elaborated seven additional heterochronic modes: other ways, besides acceleration, in which the normal time of appearance of organs and structures may be altered in ontogeny, although the legitimacy of six of these has since been questioned (de Beer 1930, 1940, and 1958; see Gould 1977, p. 228). De Beer also placed great emphasis on discrediting the neo-Lamarckian heredity which he saw as essential to the recapitulationism of the biogenetic law. In de Beer's view, Haeckel and Lamarck stood or fell together. Furthermore, they did not do so on the basis of the validity or invalidity of the historical arguments against Lamarckism. Rather, they did so precisely on the basis of whether or not external influences upon the organism, which during phylogeny may become necessary to development, could in de Beer's words "become internal" (de Beer, 1930, p. 15; see section 1.4. for a full discussion of this "internalisation"). Since, in de Beer's view, external factors could not become internalised, both the doctrines of Haeckelian recapitulation and neo-Lamarckian heredity necessarily fell. Also in 1930, Joseph Needham discredited Haeckelian recapitulation, on the basis of evidences from chemical embryology. Thus in the view of these neo-Darwinian morphologists and embryologists--though not in the view of other modern synthesis embryologists writing between 1939 and 1959 such as Waddington and Oppenheimer--the old synthesis had been completely dismantled.

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[13] Garstang believed Haeckel's law to be discredited by the synthesis of the Weismannian germ-line doctrine and neo-Mendelian heredity. Thus he opened his 1922 paper with a diagrammatic sketch of metazoan evolution, showing a closed and uni-directional flow of information running from zygote to adult. Furthermore, new germinal variations--for Garstang, Morgan's genetic micro-mutations--were not necessarily added sequentially to the adult terminus of ontogeny as Haeckel's (and Weismann's) recapitulationism required, but might be added at any point in the life-cycle. Thus, supporting Morgan's passive embryonic survival explanation of recapitulation, Garstang stated: "Morgan has already urged (1919), that recapitulation is merely the static aspect of inheritance, and that, in this respect, inheritance is not primarily the reproduction of adult characters, but the reproduction of the characters of each part of the whole life-cycle--the sequential expression of the full train of zygotic potencies [namely, Mendelian genes]" (Garstang 1922, p. 86).

Though neo-Darwinian, neither Garstang's nor de Beer's works ever mentioned natural selection and adaptation. Yet they very effectively cleared the way for a strong selectionist approach to the causes of adaptive evolution. Embryology had been rendered a neatly compartmentalised discipline. Firstly, in what de Beer called its "historical descriptive" aspect, embryological morphology complemented the work of palaeontological and comparative morphologists to describe the path of phylogenetic development. Secondly, in its "causal-analytic" aspect, chemical and experimental embryology could be subordinated to the transmission genetic and physiological genetic analysis of ontogenetic development (see the views of T. H. Morgan, in Hamburger 1980, pp. 100-101). However, these two aspects of embryology remained hermetically sealed apart, without one having any causal significance for the other: Haeckel's notion of phylogenetic causes, supported by neo-Lamarckian inheritance, was to be expunged from the synthesis without trace (de Beer 1938, pp. 76-77; in Churchill 1980, p. 120).

These preliminary events of the 1920s and 1930s greatly facilitated the synthetic neo-Darwinian theory's occupation of the explanatory high ground in adaptive evolution. Firstly, it's Mendelian-hereditarian core was apparently untouched in the confrontation with the hereditary basis of old synthesis evolutionary morphology. Secondly, a broad ground for the solitary action of natural selection had been opened up between the tiers of the now modernised two-tier embryology. To paraphrase a popular dictum: ontogenetic development (as explained in proximate causal terms by experimental embryology and developmental genetics) proposed, and natural selection disposed. Furthermore, Dobzhansky's famous 1937 description of evolution as essentially a change in gene frequencies, and his view that experimentally observable kinds of genetic mutations supplied the actual materials of evolution, became the ground level orthodoxy. Dobzhansky's view of the lowest-level hereditary causes of evolution, only needed the added support of an unimpeachable strong selectionist mechanism, to fully explain the hereditary fixation of adaptive variations--now understood by most (though as Huxley rued in 1942, not yet all) to coincide with Morgan's genetic micromutations. Nevertheless Dobzhansky, into the 1940s, expressed the belief that the persistent challenge from neo-Lamarckism meant the debate over the adequacy of selection to adaptive evolution was still an important issue (Dobzhansky 1937, 1941; see my section 2.1.). It was only by the 1951 third edition of *Genetics and the Origin* that Dobzhansky felt satisfied of selectionism's unimpeachable credentials.

Hence although ontogenetic development had long been understood--in fact, since the dawn of Mendelism--to be dependent upon a complex network of genetic and morphogenetic interactions, nevertheless the icon of Dobzhansky's definition of the essence of evolution meant that such complex issues could be sidelined, just as they had been sidelined in Fisher's and Wright's mathematics. As Gould relates, the early synthetic theory had "sought to render all of evolution by *known* genetic mechanisms that could be studied directly in field and laboratory" (1983, p. 74; author's emphasis). It was, he adds, "primarily a plea for knowability and operationalism, for a usable and workable evolutionary unity" (ibid.).

The selectionist adaptationism of key supporters of the synthetic theory then hardened significantly during the 1940s. Thus in 1937, Dobzhansky had pluralistically emphasised the importance of population size, in Gould's words, "*because* selection is not always in control" (1983, p. 78; author's emphasis). Yet, by the 1951 third edition of *Genetics and the Origin of Species*, Dobzhansky had radically reinterpreted Wright's "adaptive landscape" model to fit within a strict adaptationist framework (p. 79). Likewise, palaeontologist and systematist G. G. Simpson, saw as his primary aim the explanation of how all evolutionary change, including the discontinuous changes evident from the fossil record, was congruent with the principles of modern genetics (p. 80). Thus in the 1944 first edition of his *Tempo and Mode in Evolution*, Simpson realised that gradualist selection would not account for such discontinuity. He therefore applied Wright's non-adaptationist mechanism of genetic drift to what Simpson called "quantum evolution"; a mechanism he believed to be dominant in the production of higher taxa.[14] In Gould's terms, Simpson believed quantum evolution "carried his consistency argument to completion by showing that the genetical models of neontology could encompass the most resistant and mysterious of all evolutionary events" (p. 81).

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[14] Simpson's quantum evolution was conceived as an "all or nothing" reaction, carrying a small population across an "inadaptive phase" between two stable adaptive peaks, thereby producing a new family, order, or even class of organisms. Only random drift could effect this transition (Simpson 1944, p. 199; in Gould 1983, p. 81).

However, by the time of publishing *The Major Features of Evolution* in 1953, Simpson's selectionism had also considerably hardened. He decided that Wright's drift could no longer account for major evolutionary events, stating: "Genetic drift is certainly not involved in all or in most origins of higher categories, even of very high categories such as classes or phyla" (Simpson 1953, p. 355; in Gould 1983, p. 83). Simpson apparently went through his own transitional stage between pluralism and pan-selectionism. Hence he had emphasised the dominance of selection in his 1949 paper "Rates of evolution in animals," but not exclusively. However, as Gould confirms: "In 1953, quantum evolution merits only four pages in an enlarged final chapter on modes of evolution. More importantly, it has now become what Simpson explicitly denied before--merely a name for phyletic evolution when it proceeds at its most rapid rates, a style of evolution differing only in degree from the leisurely, gradual transformation of populations" (ibid.).

0.4. Further Hardening: New Synthesis Developmentalism and the Adaptationist s' Dilemma.

The gradual hardening of selectionism across disciplines, apparent as it had become among such key supporters of the synthetic theory as Mayr, Dobzhansky, and Simpson, was the catalyst to a phenomenon I have characterised as the adaptationists' dilemma. The re-emergence in the early 1940s, of late nineteenth century explanations of the hereditary fixation of adaptive modifications to the phenotype, posed a serious problem for the strong selectionism of the synthesis. That problem could be presented as a question: What degree of evolutionary significance could supporters of the synthetic theory afford to lend phenotype-genotype interactions, without re-legitimating developmentalist aspects of the Old Synthesis? Julian Huxley, Hardy, Ewer, Thorpe, and others insisted on the importance (with Hardy and Ewer arguing for the complete indispensability) of J. M. Baldwin's mechanism of organic selection, for explaining both adaptive evolution and speciation. Developed in the 1890s, during the period of Darwinism's lowest popularity among naturalists, to account for such fixations within a non-Lamarckian framework, organic selection was furthermore being claimed in the 1940s by Hardy in England, and Hovasse in France, as a kind of selection completely separate from classical Darwinian natural selection. Hardy even believed, subject to empirical investigation, that organic selection might prove more important to adaptive evolution than its classical forerunner.

Imparting such significance to organic selection was not acceptable to staunch defenders of the synthetic theory, and least of all to palaeontologists like Simpson, for several reasons (Simpson 1953a). Firstly, supporters of organic selection were traditionally sympathetic in some degree to Lamarckism, and particularly to the concept of use-inheritance in higher organisms. Thus palaeontologist and systematist H. F. Osborn, one of the co-founders of classical organic selection, had been a supporter of Lamarckian orthogenesis in explanation of trends in the fossil record, and of de Vriesian saltationism for explaining gaps in the same record. Neither explanation, of course, was acceptable to synthetic neo-Darwinism. Similarly, in the 1940s, Hardy revealed himself as deeply sympathetic to the doctrine of Lamarckian use-inheritance, and later decried his hard-line selectionist neo-Darwinian colleagues' seeming paranoia in their campaigning against neo-Lamarckism. Thus although classical organic selection lent itself easily to being "Mendelised," the resultant "neo-organic selectionism" necessarily had to concede the reality of many phenomena, long claimed by neo-Lamarckians as evidence for the inheritance of acquired characters. Furthermore, synthetisists like Dobzhansky, and most notably, Simpson, realised that neo-organic selection in fact merely highlighted the synthetic theory's dilemma. The movement towards pan-adaptationism within the synthetic theory had only brought the conflict between neo-Darwinism and neo-Lamarckism to a head, and over a very old and unresolved issue: namely, the overwhelming evidence for the hereditary fixation of highly specific adaptive modifications to the phenotype. Yet it would surely have strained the credulity of marginal supporters of the synthetic theory, to have hardened its selectionism to the point of excluding Baldwin and Lloyd Morgan's classic answer to neo-Lamarckism.

A central theme of the current thesis, then, is the view that the strategic defence against this reactionary adaptationist threat from within neo-Darwinism's own ranks, has been too easily accepted as unproblematic and successful. In particular, neither the current evolutionary orthodoxy, nor modern synthesis historiography, has either properly perceived, or fully accepted, the severe difficulties which this strategic defence of the synthetic theory ran into. Principally, Simpson's recourse to the phenogenetic principles of modern synthesis developmentalism, promoting them as an unproblematic extension of neo-Darwinian population genetics, necessitated an oversimplified representation (if not deliberate obfuscation), of the central tenets of the developmentalist tradition. Looking at the adaptationists' dilemma from the perspective of the established population genetics, we witness Dobzhanksy's overwhelming support for Soviet modern synthesis developmentalism over its Western counterpart: that is, his support for Schmalhausen's functionalist morphology in Moscow, over Waddington's developmental genetics in Edinburgh. Clearly this favouritism was stimulated, not only by partisanship and professional charity, but by Waddington's vociferous criticisms of mathematical population genetics (specifically, of its neglect of the adaptive significance of the selected phenotype), and his equally loud sponsorship of a genuine inheritance of acquired characters, underpinned by modern genetics. Although the principles on which Western and Soviet modern synthesis developmentalism were founded were largely identical and equally adaptationist, nevertheless Waddington's synthesis was more overtly based on experimental evidence from his own research in chemical embryology and genetics. Waddington's late 1930s embryology research and entire subsequent evolutionary thinking justifiably undermined, in the view of some modern synthesis embryologists, the basis the new synthesis had for rejecting at least one of the tenets of the old synthesis: namely, Haeckelian strong recapitulation.

Lastly, the exclusion of embryology and development from the synthesis has been made an issue in modern synthesis historiography (Mayr and Provine 1980; see also Hamburger and Churchill in the same volume). Perhaps, then, the fact of the exclusion of embryology from the synthetic theory was a genuine enigma, requiring closer investigation of the detailed history of the construction of the synthesis. On reflection it seems clear, however, that the central tenets of early 1930s synthetic neo-Darwinism--to many evolutionists still the very heart of the present day synthesis--necessitated the comprehensive discrediting of embryology's direct causal evolutionary significance. Embryology's relegation to the twin lesser roles described in section 0.2., and its subordination to the direct causal mechanism of population-genetical selection, was an absolute requirement for the success of the new orthodoxy. This position, combined with Hamburger's explanation that few experimental embryologists were even much concerned, between the 1890s and

1930s, with speculating over evolutionary mechanisms, provides quite sufficient explanation for embryology's evolutionary demise (Hamburger 1980, p. 99).

Charitably, then, some supporters of the synthetic theory with an interest in modern synthesis historiography, may be genuinely bemused by the exclusion of Darwin's greatest repository of evidence for his classical theory. Less charitably, some may continue to promote the search for explanations in this area as a means of perpetuating a myth of synthetic neo-Darwinism's potential inclusiveness. Such potential inclusiveness, combined with a radically contingent view of history, might find a hypothetical re-run of the period from 1920 to 1950 with embryology successfully integrated in an evolutionary causal role. In this context, the following passage from Bruce Wallace, with its open advertisement to the necessary supersession of evolutionary embryology by synthetic neo-Darwinism, is quite refreshingly honest. It also testifies to the efficiency with which the tenets of modern synthesis developmentalism have been rationally reconstructed into conformity with the new orthodoxy. Speaking of Hamburger's 1980 paper on embryology and the synthesis, where he suggested Waddington's 1957 *Strategy of the Genes* might be the synthesis' "missing chapter," Wallace states: "His account of Waddington's (1953) 'genetic assimilation' is largely responsible for the thrust of this article. It would appear that Hamburger (perhaps most embryologists) even now has little understanding of the genetic basis of Waddington's observations and, by inference, of neo-Darwinism. Evolutionary geneticists have the responsibility for explaining the origins and subsequent fates of the genetic programs which determine developmental programs; embryologists, on the contrary, need not explain how somatic development might affect the evolution of these developmental programs. Except for achieving success in reproduction, they do not" (Wallace 1986, p. 150).[15]

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[15] The theoretical basis for Wallace's last assertion, that somatic development can have no effect upon evolution, is again supported by the synthesis of Weismannism and neo-Mendelism central to the synthetic theory. He provides several diagrams, showing the adaptive interactions between environment and somatic cells, illustrated by large and small arrows depending upon their adaptive significance. These interactions are entirely causally independent of "arrows from the germ line to the soma [emphasising] that the program for normal development (including the concomitant interactions) exists in the germ line" (Wallace 1986, p. 154). Thus, except in very obvious cases of somatic cell-line selection in plants, Wallace rejects all epigenetic inheritance mechanisms (section 5.1). His views therefore represent a now uncommonly extreme neo-Darwinism (see my Chapter 5).

It is hoped that the following pages will shed fresh light on the historical causes which have led to the institution of such views as Wallace's, and fresh doubt upon the legitimacy of their extremism, in as much as it is still openly expressed within neo-Darwinism today. Supporters of the modern synthesis may yet argue that synthetic neo-Darwinism is a broad church, and indeed was so in the 1940s and 1950s. I nevertheless hope to provide evidence, regardless of many superficial differences, that the evolutionary insignificance of somatic changes as strictly dictated by Mendelian gene selectionism, and the historically closely related independence of ontogenesis upon phylogenesis, were doctrines essential to the synthesis' development, and have remained integral to its character. I believe these to be doctrines which, if pressured, all supporters of the synthetic theory would have assented, across all periods in the movement's history. Furthermore, the theoretical underpinning to this broad assent would always have been clear: namely, the synthesis of the Weismannian doctrine of the isolation of the germ plasm, with neo-Mendelian hard heredity.

Finally, Jablonka and Lamb have recently indicated how protracted, and, lately, how topical, these issues have become within evolutionary biology. Hence they have asserted, introducing molecular terms: "During the past fifty years there has been a gradual narrowing of the concept of heredity. Although this was probably important and necessary for the development of genetics as a discipline, it is now a handicap to evolutionary thinking. The trend needs to be reversed, because there is more to heredity than DNA, and DNA is not just a passive information carrier, it is also a response system" (Jablonka and Lamb 1995, pp. 1-2). Further discussion of the significance to developmentalism of this third, more universal mode of hardening within the modern synthetic theory, is given in my concluding Chapter 5.

Chapter 1.

The Reassessment of the Old Evolutionary Synthesis: Embryology, Genetics, and Recapitulation in the Early Modern Synthesis Years.

> Our brief survey has shown, I think, that the doctrine of recapitulation has had a rather curious history. This is largely because recapitulation has turned out to be something quite different from what it seemed to most of its adherents. We cannot regard it as a uniform expression of the mysterious creative forces of nature, as held by Kielmeyer, nor as a direct consequence of heredity, as maintained by Haeckel. We cannot consider it a manifestation of memory like the repetition of a tune, nor as a mechanically determined pushing back of embryonic characters, as postulated by Weismann. We may be justified in construing it as in part a function of the way in which germinal mutations fit into the physiology of development, but the appearance of recapitulation may also be merely an expression of the uniformities of relative growth. In the light of present knowledge, recapitulation represents no simple principle deducible from some more general law. It is rather a conglomerate effect of heterogeneous causes. We shall doubtless know more of at least some of these causes when the causal factors of embryonic development are better understood than they are today.[1]
>
> Samuel Jackson Holmes.

1.1. Recent Historiographical Trends in the Reassessment Of Recapitulation: Gould, Rasmussen, and Mendelian Gene Selectionist Explanation.

One reason why the synthetic theory of evolution was designated modern during the early 1940s, was simply because it supplanted older syntheses. Quite unlike the currently accepted orthodox theory, however, the most influential among older syntheses was explicitly developmentalist, and its foundations lay in the study of comparative embryology. The famous nineteenth century post-Darwinian synthesis of Haeckel, in Scott Gilbert's words, "saw a very close relationship between ontogeny and phylogeny." Gilbert has described Haeckel's "old synthesis" in very simple and accurate terms: Development took an embryo just so far, but by adding a

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[1] Holmes 1944, p. 330.

new step to ontogeny, it would, says Gilbert, "occasion the production of a new organism" (Gilbert 1994, p. 144). Descendent organisms would re-run, during their own embryonic development, the ontogenetic stages of development of their ancestors. Descendent ontogeny therefore recapitulated ancestral phylogeny. Post-Darwinian embryology was, by the 1870s, to become completely dominated by Haeckelian recapitulationism, as a powerful and simple method for constructing evolutionary lineages where palaeontological evidence was limiting. Such phylogenetic speculations were the infamous hallmark of late nineteenth century evolutionary morphology. Infamous particularly from the perspective of early twentieth century experimentalists, who later wrote of how they, along with evolutionary biology as a whole, had long suffered in this field of research.[2]

Nevertheless, there exists an enduring historiographical industry surrounding this simple doctrine, in which fascination has continued throughout the modern synthesis period until the present day. Recent reviews in the historiography of evolutionary theory have moved towards a working reassessment of recapitulation, and have focused on the doctrine as epitomised in Haeckel's famous dictum, "ontogeny recapitulates phylogeny.[3] Hence a number of historians of biology, beginning in the late 1970s, have paid the doctrine considerable attention. Gould, in his comprehensive 1977 survey *Ontogeny and Phylogeny*, found some support for, in

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[2] Garland Allen has described how, in the wake of the biogenetic law: "'Phylogenizing' came to be the dominant concern of many late nineteenth century morphologists. With overweening zeal these workers constructed family trees with abandon--from those of mollusks and worms to that of man. . . . The fact that the evidence for many such phylogenetic trees was circumstantial was not a matter of great concern to many morphologists" (Allen 1975, p. 4).

[3] This dictum, central to Haeckel's synthesis or "biogenetic law," was first described in his 1866 *Generelle Morphologie der Organismen*. Uschmann tells us that "*Generelle Morphologie* contained all the essential aspects of Haeckel's later work. After 1866 he change neither his methods nor his goal in any significant way" (Uschmann 1972, p. 8). Haeckel's biogenetic law had two essential aspects. Firstly, there was the historical-descriptive aspect which, according to Gould, was given on page 300, vol. 2 of the *Generelle Morphologie*, in the statement: "Ontogeny is the short and rapid recapitulation of phylogeny. . . . During its own rapid development . . . an individual repeats the most important changes in form evolved by its ancestors during their long and slow paleontological development." The second aspect is the aetiological one, a version of which is given on page 5 of Haeckel's 1874 *Anthropogenie*, where he stated that "phylogenesis is the mechanical cause of ontogenesis," and furthermore that "the connection between them is not of an external or superficial, but of a profound, intrinsic, and causal nature." In Gould's anti-recapitulationist opinion: "These strong words, reflecting the aggressively mechanistic attitude of Haeckel's time, have often been ridiculed in our more cynical age" (Gould 1977, pp. 77-78).

his words, the late nineteenth century's "almost unanimously upheld principle of recapitulation" within late twentieth century theories of genetics and morphology (Gould 1977, p. 229). In 1991, Rasmussen suggested that there existed a variety of non-Lamarckian supports for recapitulation, which "did not become substantially less tenable during the early twentieth century period of its decline" (Rasmussen 1991, p. 52). Most significantly, in 1994, Mayr stated that recapitulation's acceptance "documents the maturation of biology" and looked to developmental induction processes to provide support for, in his terms, a "somatic programme" explanation of recapitulation (Mayr 1994, p. 231).[4]

Looking more closely at these historians' writings, Rasmussen, in his 1991 paper "The decline of recapitulationism," was concerned with critically examining four of the most influential arguments against recapitulation, which had existed up to the early 1930s. These were Garstang's famous 1922 critique, de Beer's 1930 book, and T. H. Morgan's critiques of 1916 and 1932. In 1930, E. S. Russell's contention had been, said Rasmussen, that "no theory of heredity and development (including Morgan's Mendelism) could be considered adequate unless it accounted for the overwhelmingly recapitulatory nature of development" (Rasmussen 1991, pp. 60-61).[5] Urgent conflict over the doctrine continued to appear in the professional literature well into the 1940s, and was closely linked with the conflict over the neo-Lamarckian mechanism of heredity--that is, at least in this context, the developmentally sequential inheritance of acquired adaptive characters.[6] Although the

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[4] See footnote 16 below for Mayr's most recent (1997) explanation of his somatic programme concept.

[5] Russell also maintained, with relevance to the present chapter and to my Chapter 2, that the theory of the gene, as described by Morgan in 1926, "can by its very nature offer no explanation of the spatial and temporal harmony of development, nor of recapitulation, and it ignores completely the historical aspect of development." There was, Russell continued, "indeed in the writings of the Morgan school a distinct tendency to deny the validity of many of the concepts regarding adaptation and evolution which are commonly accepted by biologists--presumably because such concepts cannot find a place in the genetic scheme" (Russell 1930, p. 74).

[6] The close historical connection between Haeckelian recapitulation and Lamarckian heredity is readily explained within Bowler's account of Haeckel's progressivism: "The belief that acquired characters are normally adaptive was a part of Haeckel's optimistic philosophy of progressive evolution, in which Lamarckism was the primary force generating new characters to be tested by selection at the level of interspecies competition. The concept of variation by [Lamarckian] addition to growth was crucial in Haeckel's commitment to the recapitulation theory" (Bowler 1983, p. 68). Furthermore, as Gould stated: "Since Haeckel is so often cited as Darwin's apostle in Germany, it is generally assumed that he preached a Darwinian

infamous neo-Lamarckist and recapitulationist MacBride had, Rasmussen derided, "retained an unregenerate belief in such inheritance on the theory that heredity is analogous to memory," several non-Lamarckian theoretical supports for the biogenetic law existed in the early modern synthesis years (1991, p. 62). As the first of these theoretical supports, Rasmussen discussed J. A. Thomson's explanation of recapitulation, which suggested that somatic adaptations could become genetically fixed to the end of ontogeny (ibid.). When a pre-formed response to a constant environmental stimulus would be advantageous, genes promoting an earlier, and ultimately embryonic expression of this adaptation would be selected for.[7] The thoroughly inconclusive denouement for recapitulation and Haeckel's synthesis was, from Rasmussen's perspective, the rise of the new power base in evolutionary biology that was T. H. Morgan's genetics. Morgan claimed that the precision of genetics made it the foremost science of evolution. Unless, then, biologists gave evolution over to the exact science of genetics, evolution theory itself would be endangered by a lack of secure footing (1991, p. 84).

S. J. Gould, in his major 1977 work, sought to reassure his readers that the late nineteenth century embryological literature supporting recapitulation could be accounted for, in large part, by the merely apparently recapitulatory nature of

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interpretation of evolution. In fact, he was only evolution's apostle. Though Haeckel acclaimed Darwin, he ranked Goethe and Lamarck as his equals in the origination of evolutionary theory (vol. 2 of *Generelle Morphologie* is dedicated to them jointly). For Gould, then, "Haeckel's own view of evolution is a curious and inseparable mixture of all three, each in about the same proportion. To Lamarck, he owed his intense belief in the inheritance of acquired characters" (Gould 1977, p. 80).

[7] Rasmussen makes reference to two sections of Thomson's 1925 *Concerning Evolution*. However, of the 14 pages suggested by Rasmussen, only a single paragraph appears remotely similar to his version of Thomson's theory. Thomson began, on the previous page, by asking the neo-Lamarckian question of whether the effects of the surroundings, or use and disuse, can have a specific effect upon the germ cells such that those effects become inherited. He continued: "(1) No doubt advantageous modifications are always useful for the individual who acquires them, and conversely. (2) These useful modifications can be hammered on to each successive generation. (3) They may perhaps serve as a protective screen until, happily, similar germinal variations arise from within" (Thomson 1925, p. 150-151). Rasmussen fails to note, however, that in this explanation Thomson is invoking Lloyd Morgan's coincident selection (more commonly referred to as organic selection), and uses the screen metaphor in precisely the same way as J. M. Baldwin did in 1897 to define the concept of organic selection (see section 2.3., footnote 14). Bowler has viewed classical organic selectionism as an attempt, made by 1890s Darwinians under severe threat from a resurgent neo-Lamarckism, to repudiate the Lamarckist claim that Darwinism denied the role of purposeful behaviour in evolution (Bowler 1983, p. 81; see my Chapter 2 for an extensive investigation of organic selection).

development. In truth, said Gould, development was essentially von Baerian.[8] Nevertheless, he conceded, this could not be the whole picture. Within a discussion of what he called the "historical paradox of the supposed dominance of recapitulation," he summarised his position, stating that parallels between ontogeny and phylogeny were produced by heterochrony: "Heterochrony proceeds by acceleration or retardation. We have no a priori basis for assuming that one of these processes is more frequent than the other; their attendant results--recapitulation and paedomorphosis--should be equally common" (Gould 1977, pp. 228-9).[9] Yet, since the observational powers of the late nineteenth century embryologists and anatomists were indeed formidable, the fact that "almost to a man, they upheld a principle of universal recapitulation, under which paedomorphosis included only a minor class of exceptional cases," provided Gould with a dilemma. Surely, he appealed, "the *impression* of recapitulation's dominance has some basis in nature" (p. 229; author's emphasis). After asserting that "ironically, the evolutionary transformation of [von Baer's] laws guaranteed that recapitulation would seem to prevail where it does not exist at all" (p. 230), Gould reluctantly returned to what he called "the classic argument: recapitulation dominated because acceleration was more common than

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[8] The opening footnote to Rasmussen's 1991 paper serves well as annotation to Gould's assertion: "1) It will become important to distinguish [Haeckel's biogenetic law], today thought of as asserting specifically that adult ancestral stages are recapitulated, from the laws of Karl Ernst von Baer [von Baer, 1827], which assert the repetition only of ancestral *embryonic* stages. In the period of the biogenetic laws' ascendancy, von Baer was thought of as a forerunner of recapitulation by many adherents (e.g. Haeckel) and opponents (e.g. Morgan). Actually, the Darwinian interpretation of von Baer's laws, suggesting that early embryonic features of a modern organism resemble embryonic features of a more primitive ancestor, amount to the same thing as the biogenetic law to the degree that primitive adult organisms resemble their own embryos. . . . The concept that von Baer's laws were quite different did not become influential until late in the period of the biogenetic law's decline" (Rasmussen 1991, p. 5). However, rather than adopt Rasmussen's partial equation of von Baer's laws with the biogenetic law, which may cause confusion, I prefer Weber and Depew's distinction between "strong" (Haeckelian) and "weak" (von Baerian) recapitulation (Weber and Depew 1994, pp. 506-7).

[9] Paedomorphosis, described in the glossary to Gould's book as the "retention of ancestral juvenile characters by later ontogenetic stages of development" (1977, p. 484), was the term coined by Walter Garstang in his 1922 critique of the biogenetic law. It defined a process which was the antithesis of recapitulation, producing the "retention of [features] purely embryonic, not adult, in origin" (Garstang 1922, p. 97). Its cause was the retardation to later stages, rather than the acceleration to earlier stages, of the time of appearance of characters in ontogeny.

retardation."[10] At this point, Gould asked if any theoretical arguments could be cited to "justify the dominance of acceleration over retardation" (p. 232). He discussed two then recent theoretical arguments supporting this apparent dominance. The second argument was provided by marine zoologist Gosta Jagersten, and his embryological concept of "adultation."[11] Yet Gould remarked very reservedly that Jagersten's evidence was only significant if one was "inclined to feel friendly toward speculative phylogeny in the old tradition" (p. 233). Gould's first argument, however, came from genetics. This was Stebbins' notion of the "increasing precocity of gene action." In his 1974 *Flowering Plants: Evolution above the Species Level*, and within a chapter on recognising evolutionary trends, Stebbins included this principle as a major line of evidence from plant development for the existence of such trends, and elaborated upon it as follows:

> 1. Mutations that affect late stages of development are less likely to disturb harmonious interrelations between gene-controlled processes than are mutations that produce comparable effects on early stages. Hence we can

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[10] However, other inquirers, both before and after Gould, and not sharing his anti-progressivism, have accepted that the post Darwinian transformation of von Baer's laws vindicates belief in the frequent occurrence of recapitulation. Russell in his classic 1916 work considered that: "We might almost sum up the relation of the biogenetic law to the laws of von Baer [weak recapitulation] and Meckel-Serres [strong recapitulation] by saying that it was the Meckel-Serres law applied to the divergent differentiation upheld by von Baer instead of to the uniserial progression believed in by the transcendentalists" (Russell 1916, p. 256). Similarly Ospovat saw that "In von Baer's scheme, embryological development is divergent, and it is this that constitutes the most striking difference between [it] and the theory of recapitulation." However, with Haeckel after 1859, "the theory of recapitulation grafted onto a system of divergent development" (Ospovat 1976, p. 6; see also Ghiselin 1992, p. 499). More recently Lovtrup, also designating post-Darwinian recapitulation "von Baerian recapitulation," reaffirms the Haeckelian aetiology, stating: "in fact, *ontogeny recapitulates the historical as well as the creative aspects of phylogeny.*" Though Lovtrup eschews Allen's "phylogenizing" he adds: "Nevertheless, I venture to make the following assertion: *in the course of their ontogeny the members of a set of twin (sister) taxa follow the same course of von Baerian recapitulation up to the stage of their divergence into separate taxa*" (Lovtrup 1984, p. 169; author's emphasis). Gould offered some speculative calculations made by biologists in the 1960s: "Zimmerman [1967] has estimated the dominance of recapitulation over paedomorphosis at 80 percent in plants, while Remane [1962] estimates 80-90 percent for organs of higher animals in later stages of embryonic development, after differentiation from the primary germ layers. But these are mere guesses" (Gould 1977, p. 232).

[11] Through extensive research Jagersten had observed, in marine organisms which alternate between free-swimming (pelagic) and bottom-dwelling (benthic) lifecycles, a recapitulatory acceleration of benthic characters into the pelagic larva, thus facilitating metamorphosis. This process he referred to as "adultation." Jagersten early on completely generalises his version of recapitulation, saying: "A shifting of the initial development of the adult characters to the pelagic larva is in reality a very common phenomenon. . . . so common that *we can designate the phenomenon of adultation as a general principle among the metazoans*" (Jagersten 1974, p. 6; author's emphasis).

> expect that radical alterations of the morphogenetic pattern are likely to appear initially at relatively late stages of development. They can be shifted to successively earlier stages by the accumulation of modifying genes that increase the precocity of gene expression. 2. Mutations that affect early stages are most likely to be integrated into harmonious developmental patterns if their effects on these stages are relatively slight. They can, however, exert relatively strong effects upon the final pattern by altering the rate of a continuing process, so that their initial small effects at early stages are amplified into much larger effects at later stages. (Stebbins 1974, p. 128).

Appropriately enough for Gould's ideological purposes, Stebbins' third and final point also explicitly supported a von Baerian, or weak recapitulationist understanding of development. Thus Stebbins concluded: "The kinds of gene action mentioned in assumptions 1 and 2 would both result in embryonic similarity. Hence, the generalization that young stages in the development of a particular organ will resemble one another more than they do adult stages of the same organ will hold except for examples in which great divergence in development at an early stage has an adaptive or functional value" (ibid.).

It is interesting that Gould's own discussion of the accelerating action of modifier genes, directly employed C. H. Waddington's 1942 concept of canalisation. As Gould went on to say in Chapter 7 of *Ontogeny and Phylogeny*, "Stebbins agrees that the canalisation of development virtually precludes the introduction of major innovations at points other than at or near the end of ontogeny" (Gould 1977, p. 232). Yet surprisingly in a work that is otherwise very inclusive and conceptually detailed, Gould did not discuss the term canalisation--either with regard to his own, or Stebbins', or even Waddington's understanding of the term. Neither did he discuss anything of its detailed history in evolutionary theory.[12]

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[12] Hall has recently provided us with the following full account of Waddington's concept of canalisation, describing it as the property of developmental pathways to produce standard phenotypes despite environmental or genetic influences that would otherwise disrupt development. Hall continues: "It is the buffering of development against perturbations, whether of environmental or genetic origin. The latter is especially significant and was central to Waddington's thinking; the collective action of groups of genes can isolate a developmental event from perturbations arising from single or small numbers of genes. Such supragenomic organizational thinking is typically Waddingtonian. Essentially similar concepts were developed by Lerner (1954) as genetic homeostasis and Wright (1968) as universal pleiotropy. Canalization allows the build-up of genetic variability within the genotype, even though that variability is not expressed phenotypically. Such hidden genetic variability can be brought to light and subjected to selection through genetic assimilation" [see Hall 1992, p. 117] (Hall 1992, p. 116).

1.2. Ernst Mayr, and the Resurrection of Recapitulationist Historiography in the *Quarterly Review of Biology*.

Most important of all for the current historiography of recapitulation, has been a recent paper by Ernst Mayr. Writing in the June 1994 *Quarterly Review of Biology*, Mayr has sought to redress the balance of debate strongly in favour of Haeckelian recapitulation. As a founding figure in the history of the modern evolutionary synthesis, especially through his classic book of 1941, *Systematics and the Origin of Species*, Mayr's latter-day support of the Haeckelian doctrine is of particular interest, and warrants close analysis. It is, says Mayr, a matter for concern that "in spite of the disrepute into which Haeckel's claims had fallen owing to justified as well as unfair criticism, every embryologist knew that there was a valid aspect to the claim of recapitulation" (Mayr 1994, p. 227). He praises Rasmussen for "well describing the various factors responsible for the steady decline in the popularity of recapitulation, and how frequently proximate and evolutionary causations were confounded" (p. 226).

Mayr's paper channels the reassessment of recapitulation in two directions. Firstly, we can and should now accept that ontogenetic development--particularly in higher land vertebrates displaying direct rather than metamorphic development--can legitimately be interpreted as a series of recapitulations of "ancestral archetypes." He primes an attack against the "unfair and misleading" criticism of Haeckel's biogenetic law with an historical point of order. Regarding the *Naturphilosophe* J. F. Meckel as "the first consistent recapitulationist," Mayr seeks to persuade that the terms "higher" and "lower" in Meckel's 1821 formulation refer to "positions in the Great Chain of Being." Of course, Mayr states controversially, permanent stages to the idealist morphologists of the time meant the morphotypes.[13] Mayr believes, in his words,

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[13] Richards in his *The Meaning of Evolution* (1992) took a similar view of Meckel's recapitulationist credentials, saying that "Meckel provided the most sophisticated form of the recapitulation principle." Earlier, Meyer had suggested that if the concept of transmutation had "gained wider adherence," then Meckel "probably would have emphasised the idea of descent" (Meyer 1935, p. 384). Richards takes the stronger line that Meckel was a species transmutationist who had suggested, as had Lamarck, a mechanism of transmutation by gradual alteration from "one and the same urorganism." Thus, says Richards, Meckel's work "displayed the demonstrative power of comparative embryology for the theory of species evolution" (Richards 1992, p. 55).

that "it is straight whiggishness--and has led to a great deal of confusion--to translate 'permanent' stages into 'adult' stages." Mayr is quite satisfied that "Meckel knew perfectly well that the fish stage of the mammalian embryo did not look in the least like an adult fish, yet it did have some of the characteristic features of the fish archetype" (p. 223).[14]

Mayr's writings also imply that Meckel provided us with the earliest form of an important late nineteenth century relativisation of recapitulation; that is, with respect to individual structures and organs. In this context, Mayr paraphrases Meckel's 1821 *System der Vergleichenden Anatomie*, where Meckel stated that "as long as a certain organ [of an embryo] has the form that remains permanent in a lower class, this embryo of the higher animal evidently belongs to the lower class as far as this organ is concerned" (p. 224). Thus, as far as the phenomenon of the higher animals' recapitulatory ascent through lower classes is concerned, Meckel apparently believed this law of parallelism to be valid without exception for all organs. In Mayr's view, although Meckel is generally identified by historians as having referred to the whole embryo's being on lower or higher levels, nevertheless "all the evidence he cites refers to specific organs or structures" (ibid.).

It has been Mayr's further concern that Haeckel's statement of the biogenetic law, namely, "ontogeny is the short and rapid recapitulation of phylogeny," suffered a similar and equally confusing misrepresentation soon after its inception. In the period immediately after the publication of Darwin's *Origin of Species*, Mayr tells us, Haeckel's opponents unfairly altered his law to "ontogeny recapitulates the *adult stages* of their ancestors" (p. 225, emphasis added.). This of course allowed Haeckel to be too easily refuted, since it was quite obvious that no embryonic stage of, for example, a mammalian species was exactly like any adult fish or amphibian. Haeckel was, for Mayr, "far too experienced a biologist not to know that a mammalian embryo during its gill-arch stage did not look like an adult fish." Nevertheless,

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[14] Similar qualification for the acceptance of Meckel's 1821 writings (though notably without invoking the ideal morphologists' notion of archetypes), was voiced by T. H. Huxley in 1878: "If Meckel's proposition is so far qualified, that the comparison of adult with embryonic forms is restricted within the limits of one type of organization; and, if it is further recollected, that the resemblance between the permanent lower form and the embryonic stage of a higher form is not special but general, it is in entire accordance with modern embryology; although there is no branch of biology which has grown so largely, and improved its methods so much since Meckel's time, as this" (T. H. Huxley 1878, p. 750; in Richards 1992, p. 550).

Haeckel realised that sufficient vestiges of the ancestral morphology were left, to permit placing the adult at the correct phylogenetic position in the evolutionary tree (ibid.).

Mayr's clear intention has been to resurrect the legitimate aspects of evolutionary organ and structure recapitulation. We need only eliminate the late nineteenth century's embryological excesses--specifically its attempts at producing speculative ancestral forms--from the study of ontogeny. His explicit agenda, within this reassessment of the recapitulation doctrine, is to promote the search for the ultimate, evolutionary causes of the recapitulatory nature of development. Hence we must realise the total failure of proximate causes to provide an explanation of recapitulation. Mayr goes so far in Haeckel's defence as to argue that the aetiological aspect of the biogenetic law--where phylogenesis is described by Haeckel as the "mechanical cause of ontogenesis"--was a misrepresentation of evolutionary causes as proximate ones held merely "in order to placate the physicalists," then prevalent in German science, as exemplified by the pupils of Johannes Muller.

The same fallacy of "describing evolutionary causations as if they were proximate ones," says Mayr, was also fallen into by Haeckel's most successful twentieth century critics. These critics mistakenly relied on a revised conception of heterochrony to provide a universal explanation for all the forms of parallelism between ontogeny and phylogeny. Such criticisms of the biogenetic law as were made by Garstang (1922, 1928), de Beer (1930, 1958), and Gould (1977), focused upon such aspects of proximate causation.[15] But does this completely explain recapitulation? Mayr's answer is that it does not. How, he asks rhetorically, can the retention of seemingly useless ontogenetic stages be *explained* by heterochrony, when what is needed are, in his view, "Darwinian explanations of the ultimate causations?" What is, he asks, the selective advantage of retaining ancestral

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[15] In 1982, and in contrast to his later "somatic programme" notion, Mayr gave a particularly deterministic and gene-centred account of his proximate-ultimate distinction, saying: "The two biologies that are concerned with the two kinds of causations are remarkably self contained. Proximate causes relate to the functions of an organism and its parts as well as its development, from functional morphology down to biochemistry. Evolutionary, historical, or ultimate causes, on the other hand, attempt to explain why an organism is the way it is. Organisms, in contrast to inanimate objects, have two different sets of causes because organisms have a genetic program. Proximate causes have to do with the decoding of the program of a given individual; evolutionary causes have to do with the changes of genetic programs through time, and with the reasons for these changes" (Mayr 1982, p. 68).

ontogenetic stages? (1994, p. 228). Finally, in pointing towards the solution to the problem of the causes of recapitulatory development, Mayr suggests that some parts of the solution were found independently by experimental embryology and by genetics, "but have never been synthesised into a well rounded explanatory theory" (ibid.).[16]

Indeed, such critiques of recapitulationism as Garstang's in 1922, and de Beer's in 1930, depended heavily on the repeated and ceremonious refutation of Mayr's "unfairly altered" version of Haeckel's law. In 1922, Walter Garstang's openly stated goal had been the discovery and instatement of the "true biogenetic law" (Garstang 1922, p. 82). This true law would replace Haeckel's "delusive and cramping hypothesis" that had held zoology in its thrall for far too long (1922, p. 90).[17] Looking more closely at these critiques, it is important that for Garstang (and more particularly de Beer), periods of progressive recapitulatory evolution along specific lineages are far from rejected. On the contrary, they are to be expected as a necessary counterpart to the nevertheless evolutionarily more important rejuvenating

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[16] Mayr's solution, the "somatic programme" explanation given in the title of his 1994 paper, is further elucidated in his most recent book. In it, he questions: "Why does a mammal not develop the neck region directly instead of roundabout through the gill-arch stage? The answer is that the development of the phenotype is not strictly, exclusively, and directly controlled by genes but by the interaction between the genotype of the developing cells and their cellular environment. At any stage of ontogeny, the next stage of development is controlled both by the genetic programme of the genotype and by a 'somatic programme' consisting of the embryo at this stage. To apply this, for instance, to the gill arch problem, it means that the gill-arch system is the somatic programme [cf. organiser] for the subsequent development of the avian and mammalian neck region" (Mayr 1997, pp. 171-172). Yet historically, the somatic programme concept has not quite provided the resolution of the proximate versus ultimate explanation dispute within recapitulationism that Mayr currently hopes for. The original somatic programme theorists--chemical embryologists interested in organiser phenomena in the wake of Spemann's amphibian researches, rejected Haeckel's biogenetic law, and accepted Garstang's instead. They were strictly interested in recapitulated embryonic structures as proximate causes of ontogenetic development, completely denying them any phylogenetic or ultimate causal significance. Thus Needham wrote in his 1930 review of recapitulation: "For if ancestral ontogenetic stages are only recapitulated because they are useful, *and useful in a perfectly definite, almost endocrine, sense*, then the concept of embryonic development is one and the same for the morphologist as for the experimentalist. Future research will have to unravel the details of the action of the formative factors of the recapitulated structures, and it would be unwise to prejudge the issue" (Needham 1930, p. 150; emphasis added).

[17] Rasmussen makes the important point about Garstang's motivations: "Unlike Morgan, Garstang did not want to consign traditional morphology to the basement of a natural history museum. . . . Thus he represents a revisionist defender of the established morphology, interested very keenly in deducing laws of evolution from what Morgan considered mere 'circumstantial evidence'" (Rasmussen 1991, p. 76).

process of paedomorphic retardation.[18] Thus, immediately after a rousing passage debunking MacBride's naive recapitulationist interpretations of metamorphic development in marine organisms, Garstang quietly stated: "It is true that ontogeny could not exhibit its normal progressive differentiation of structure if evolution had always been of the type exhibited by these [metamorphoses]. Evolution within these groups to-day partakes mostly of the nature of an adaptive radiation of the various types, whereas the general lines of ontogeny correspond rather with that kind of evolution which involves morphological and physiological progress" (1922, p. 90).

However, Garstang very quickly denied any implied foothold for the recapitulationist in his views on progressive evolution. It was his conviction that the "slightest survey of vertebrate evolution shows a series of [adaptations] which has been based as much on the substitution of new for old organs as on the continuous elaboration of particular ones." Nevertheless, in the same paragraph, Garstang willingly conceded that cases of evolution via organ fusion and, more especially, via the apparent developmental dependence of new structures upon ancestral ones, "confers on vertebrate ontogeny its marked recapitulative character" (p. 91). But "recapitulative character" did not constitute support for Haeckelian recapitulation. Back-pedalling still further, Garstang thought it equally clear that such succession of organs and structures "is explicable without recourse to the theory of successive adult incorporations, and that the ontogenetic stages afford not the slightest evidence of the specially adult features of the ancestry" (ibid.). Talking of, amongst many other organs and structures, the notorious notochord and gill slits, Garstang was adamant: "No example can be adduced of any of these organs *arising* in an adult stage of ontogeny. Until that evidence is produced, it is idle to claim that recapitulation which involves any of these organs is a repetition of specifically adult ancestral features" (ibid.; author's emphasis).

Mayr's 1994 paper also resurrects a tradition in the *Quarterly Review of Biology* of historical reviews of the recapitulation doctrine, and appears to owe a

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[18] Garstang introduced the concept of "paedomorphosis" in 1922 as the antithesis of recapitulation; that is, as the incorporation of previously *juvenile* features into the *adult* stages of descendants. Gould tells us that many people have supposed paedomorphosis disproved recapitulation. In fact, says Gould, "recapitulationists had recognized this phenomenon from the beginning; they had discussed it at length, and had catalogued as many cases as Garstang ever knew" (Gould 1977, p. 177).

substantial debt to those earlier writings. In 1932, Shumway pre-empted much of what Mayr said in 1994, and felt then that objections to the biogenetic law were "more widespread than ever before" (Shumway 1932, p. 93). His paper initially focused on de Beer's argument that there are eight modes of heterochrony which may disturb the strictly palingenetic development of Haeckel. Shumway conceded that "in spite of these opportunities for misrepresentation the embryological record is often curiously reminiscent of ancestral history" (1932, p. 94). Following on from Lillie's 1908 attempted modification of the recapitulation theory (emphasising inheritance of the whole of ontogeny as a cause of recapitulation, rather than just the inheritance of the adult stage), Shumway concluded: "It was with this in mind that I stated (1927) that the theory of recapitulation 'is not applicable to the embryo as a whole, but only to individual organs or systems of organs.'"[19] Accepting, as had his contemporary de Beer, both Morgan's theory of the gene and "embryonic survival" theory of recapitulation, Shumway long anticipated Mayr's call for a somatic programme explanation for organ recapitulation. Hence he concluded with discussion of Spemann's "organizator theory" and stated, with respect to the work on amphibian primary induction, that "we have reason to believe that the dorsal lip of the blastopore in the amphibian egg exists, not as a reminiscence or recapitulation of the open blastopore of an invertebrate animal, but as an organizator necessary to later development." Furthermore, he added, "many of the so-called vestiges of embryology may prove to play leading roles in the development of the individual" (1932, p. 98).[20]

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[19] In the 1935 third edition of his *Introduction to Vertebrate Embryology*, Shumway only discussed organ recapitulation in passing: "There are evidences that the vertebrates do retain in development certain features which also appeared in the development of their ancestors. For example, clefts appear in the pharynx of the embryos of birds and mammals, opening to the exterior just as they do in the embryos of fish." Yet, he continued: "It has been very found very difficult, if not impossible, to draw up a genealogical tree of the vertebrates based solely on embryological data, and the recapitulation theory is not so widely accepted as in former times" (1935, p. 6).

[20] Interest in the causal significance of recapitulated embryonic structures to development had, in fact, long since been heralded by Needham, who accepted that "there are recapitulation phenomena and that they need explanation" (Needham 1930, p. 145). Such interest, focusing on the organiser concept, was the outcome of Needham's, and chemical embryology's, acceptance of Garstang's recapitulationism: namely, Garstang's so-called "true biogenetic law," which embodied a reversal of the Haeckelian aetiology. Thus for Garstang, stated Needham, "Phylogeny is anything but the 'mechanical cause,' as Haeckel called it, of ontogeny; on the contrary the latter creates the former" (p. 147). Needham confidently stated

In 1935, Meyer wrote a detailed historical review of the concept of recapitulation, beginning with its origins in the writings of Aristotle, Harvey, and John Hunter. The most important aspect of Meyer's paper was his analysis of the confusion over von Baer's supposed recapitulationism. Thus, he reflected, "I do not know who was originally or primarily responsible for the spread of the idea that von Baer formulated the 'law' of recapitulation or for the fact that various writers regard von Baer's 'law' and the theory of recapitulation as synonymous" (Meyer 1935, p. 385; see also Rasmussen 1991, p. 51). Meyer observed that many were so confused. For example Salesby, writing in *Academy* in 1903, expressly identified von Baer's law with Haeckel's dictum, ontogeny is the recapitulation of phylogeny. Even prominent biologists were implicated. Those who had fallen into error included Kellogg, E. B. Wilson, Woodruff, and even Joseph Needham, who, according to Meyer, "spoke of '. . . the recapitulation theory, which was first clearly formulated by von Baer. . . ,' and repeated this statement several times" (1935, p. 386). For Meyer, the fact that von Baer could not be regarded as the author of the theory of recapitulation was "shown clearly by his own words," in von Baer's 1828 *Uber Entwicklungsgescichte der Thiere* (ibid.).

Meyer saw his role far less as judge of the veracity of recapitulation, than as neutral chronicler of its history. Commenting upon J. A. Thomson's extreme application of the doctrine to child psychoses, Meyer added: "But this raises the question of the validity of the law and with that I am not concerned here" (p. 394). Meyer did, however, proffer the opinion that "Haeckel's formulation made recapitulation into a slogan but this could not make it a law, though his enthusiastic advocacy of it stimulated much work in embryology" (ibid.).

1.2.1. Searching for Causal Explanations at the Time of the Synthesis: Holmes, Goldschmidt, and the Genetic Explanation of Recapitulation.

A third paper, published in the 1944 *Quarterly Review* by Holmes, is most interesting with respect to the relationship between recapitulation, embryology, and the modern synthesis. In opening, Holmes stated that he was avoiding ground

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in his review: "Having now taken stock of the theory of recapitulation as it comes to us from the hands of the morphologists, it would appear as if they have brought it to just a position in which it could be incorporated into a chemical embryology" (p. 150; also see note 16 above on Mayr and the somatic programme explanation of recapitulation).

already covered by Shumway and Meyer, confining himself "mainly to the discussion of theories of the causes of recapitulation" (Holmes 1944, p. 319).[21] With respect to the history of these causes, Holmes tells us:

> The pre-Darwinian exponents of the doctrine of recapitulation developed no plausible explanation as to why recapitulation occurs. The doctrine that ontogeny summarizes phylogeny obviously implies that organisms have a phylogeny. But one who attempts to trace its early history is sometimes perplexed by the uncertainty as to whether or not certain writers regarded the forms of life as constituting a genetically connected series. The phraseology of several authors is indefinite on this subject and has undoubtedly misled a number of writers who have treated the history of evolutionary thought, including Ernst Haeckel and Henry Fairfield Osborn. This phraseology is all the more confusing because of the employment of "evolution" in different senses. (1944, p. 320).[22]

The recapitulation doctrine was therefore endorsed across a wide spectrum of opinion with respect to the idea of species transmutation. In Holmes' terms, then, the doctrine that "higher organisms in their embryonic development pass through the various stages of the taxonomic series was set forth by creationists, such as Agassiz, and by [transmutationist] evolutionists, such as Meckel (1821) and Serres (1824, 1842, 1859), and by some naturalists, such as Oken (1847), who held to the de novo origination of organisms out of primitive *Urschleim*" (ibid.). Despite this early confusion over the relationship between recapitulation and species evolution, Holmes felt that Kielmeyer's 1793 writings provided "the first statement of the doctrine of recapitulation and the first suggestion as to its causes." Kielmeyer, said Holmes, "treats of development not as a series of structural changes but as succession of forces or powers." Kielmeyer also appeared to accept the concept of an historical

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[21] A contemporary work also concerned with the causes of recapitulation was H. V. Wilson's 1941 review in *The American Naturalist.* Wilson discussed nineteenth century embryologist Oskar Hertwig's ideas, closely related to the somatic programme notion, saying: "It is for these resemblances of basic morphology between embryo and lower adult, marvellous enough, that we ask an explanation. Oskar Hertwig's [explanation] is that there are basic morphogenetic laws which bring about the facts as we see them. . . . Ontogenetic stages thus can not be eliminated if the end result, the adult condition, is to be reached. They provide the necessary conditions for the attainment of this objective" (Wilson 1941, p. 28).

[22] Robert Richards, in his 1992 book *The Meaning of Evolution*, engages this problem. He traces in his chapters 2 and 3, "several moments in the gradual alteration of the meaning of 'evolution,' namely: its initial use to describe the embryological condition; its transformation in the transcendental principle of recapitulation--the idea that the embryo of a higher organism passes through the adult forms of lower organisms; and its new life as a term for species change" (Richards 1992, p. 3).

phylogenetic series (1944, p. 321).[23] However, the doctrine was set out "much more explicitly by Meckel (1821) and most copiously by Serres." Yet, Holmes also asserted, recapitulation "as expounded by its adherents was intimately tied up with a lot of ill-grounded speculations that made the devastating criticisms by von Baer an easy task" (ibid.).

It was Charles Darwin who, in Holmes' view, salvaged what was legitimate within nineteenth century recapitulationism.[24] Holmes felt it "clear that Darwin regarded embryonic history as recapitulating in a general way the course of phylogeny" (1944, p. 323).[25] Thus, although Darwin believed that recapitulation of the adult stages of progenitors did occur in the embryos of their descendants, he "hastens to explain that recapitulation is not a universal law." This breakdown of universality was because of disruptions to palingenesis, caused by early ontogenetic adaptations in the progenitor organisms. Holmes' high regard for what he called Darwin's "masterly treatment of the subject" was explicit in his writing: "In striking contrast to some of his predecessors [Darwin] did not give free rein to his fancy, but tested the generalizations of von Baer by actual measurements on the young and adults of several species, carefully scrutinized his data for non-conformable facts, and came to conclusions, both as to why recapitulation sometimes occurs and also why it

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[23] The following is the passage from Kielmeyer which Holmes refers to as the first clear causal statement of the doctrine: "Since the distribution of powers in the series of organisms follows the same order as their distribution in the developmental conditions of the same individuals, it can be inferred that the power through which the production of the latter occurs, namely the reproductive power, agrees in its laws with the power through which the series of different organisms of the earth were called into being" (Kielmeyer 1793; in Holmes 1944, p. 321).

[24] Oppenheimer reminds us that "Darwin himself in the final edition [of *The Origin of Species*] withdrew some earlier reservations and stated categorically that: 'Several . . . highly competent judges insist that ancient animals resemble to a certain extent the embryos of recent animals belonging to the same classes; and that the geological succession of extinct forms is nearly parallel with the embryological development of existing forms. This view accords admirably well with our theory'" (Darwin 1872; in Oppenheimer 1973, p. 57).

[25] Richards 1992 book gives a colourful (if controversially strong and progressivist) account of Darwin's recapitulationism. Describing what he calls "the most creative and heated phase of his theory construction" in the period from December 1838, Richards wrote: "Darwin supposed that each of us during embryogenesis comes to 'pass through' the evolutionary history of our species. Thus at the core of his emerging theory of descent, which stands firmly fixed upon an embryological model of species change, and about which are layered conceptions of adaptation through terminal additions, progressive advance in the organic improvement of life, and natural selection as the law governing these processes--at the core of these ideas lies the venerable thesis of recapitulation" (1992, p. 98).

sometimes does not, which have anticipated a number of later hypotheses based on a much greater wealth of knowledge" (Ibid.).[26]

To conclude his discussion of Darwin's views, Holmes returned to his central theme of the history of attempts at causal explanation of recapitulation. Darwin's treatment, then, made "a great advance over previous discussions of recapitulation in soundness of judgement . . . and in resourcefulness in devising explanations of the phenomena in terms of heredity and selection" (ibid.). Haeckel, by contrast, was "uncritical, dogmatic, intolerant, a hard fighter who wielded a bludgeon, instead of a rapier like Huxley" (ibid.). Haeckel looked upon recapitulation, said Holmes, as a necessarily corollary of the fact of evolution, and was hence "naturally led to attempt a causal explanation of this relationship": to Haeckel, recapitulation was simply a consequence of heredity (p. 324). Commenting on Haeckel's 1866 statement that ontogeny "is immediately determined through the phylogeny or the development of the organic phylum to which it belongs," Holmes believed this sentence to express an old fashioned conception of heredity as the "derivation of an organism's characteristics from the corresponding characteristics of its parents, a process which is still implied in theories of Lamarckian inheritance." Holmes then added dismissively: "As might be inferred, Haeckel believed in the inheritance of acquired characters, and hence he believed that ontogenies could be molded through accumulating modifications contributed by ancestors, but his attempt at a mechanistic explanation of such transmission, embodied in a paper (1876) bearing the rather pedantic title of 'perigenesis of the plastidule,' is a fanciful production of little scientific value" (ibid.).

Given Holmes's incisive criticisms of Haeckel's neo-Lamarckist aetiology, his most interesting contribution was a sympathetic treatment of the recapitulation doctrine itself, made from the viewpoint of genetics during the modern synthesis

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[26] Lending support of Holmes's comments, Michael Ghiselin is severely critical of any imputation of an "ultra strong recapitulationism" to Darwin and Haeckel. Richards' assertion that "Darwin clearly viewed development of the embryo as comparable to a series of daguerreotypes" (Richards 1992, p. 172) is described by Ghiselin as "utterly preposterous," and adds: "Only if terminal addition were the exceptionless rule that Richards claims it is, in spite of the plain signification of the documents, would such an allegation make any sense." Ghiselin, in agreement with Holmes' views, adds that "Darwin's theory does explain the correspondences between ontogeny and phylogeny that occur when they do in fact occur" (Ghiselin 1992, p. 499).

period. Holmes commented in turn on the recapitulationism of the American neo-Lamarckists Hyatt (1889, 1893) and Cope (1904), Weismann's neo-Darwinian approach (1904), and the differing views of the morphologists Garstang (1922) and Severtsov (1931).[27] Ruing his inability to do justice to the great contributions of Severtsov from within comparative morphology, Holmes nevertheless looked forward to a new approach: "The writers thus far considered have viewed the problem of recapitulation chiefly from the standpoint of comparative anatomy, embryology, and paleontology. . . . In a few recent contributions the problem has been treated from the standpoint of modern genetics" (1944, p. 327).[28]

Holmes immediately focused on the application of Goldschmidt's rate-gene theory of heredity, first developed in his 1927 *Physiologische Theorie der Vererbung*, to the causes of recapitulation. As Goldschmidt said in 1940: "If macroevolutionary changes proceed by mutations affecting the rate of embryogenetic processes at a definite time in development, the ontogeny of all descendants of the

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[27] Churchill's close observations of Weismann's research, explain the deep connections between Weismannian strong (Haeckelian) recapitulationism, and his neo-Darwinian hard heredity. For Weismann (as for F. M. Balfour, Lankester, and many other recapitulationists), the biogenetic law was derivative upon the conception of heredity which, in the nineteenth century, stood for much more than inter-generational transmission. Rather, says Churchill, "It denoted the genetic connection between alternating generations in a complex life cycle [and] included the genetic connections between cell generations. . . . As a consequence, 'heredity' was as much a part of the developmental phenomena as it was a designation of transmission between traditional parents and offspring" (Churchill 1983, pp. 27-28; See also section 5.2., footnote 30 for an intriguingly parallel view of heredity expressed by Schmalhausen in 1960). Thus Weismannian hard heredity and strong recapitulation are intimately linked by a doctrine of strict transmission down specific cell lines. Weismann's rigid germ-line doctrine (and hence equally strict developmental distinction between blastogenic and somatogenic characters) resulted from his observations of the capacity of only certain cell lineages to produce the sex cells (ibid.). See my Chapter 5 for a historical discussion of the relations between Weismannian heredity, Lamarckian soft heredity, and modern synthesis notions of epigenetic inheritance.

[28] Holmes held Sewertzoff's ideas in the twentieth century in as high regard as he held Darwin's from the nineteenth. Thus, he lamented: "I am not able to do justice to the contributions which the researches of Sewertzoff have made to our problems. They constitute the most significant factual additions to our knowledge in this field in recent decades. They show that the relations of ontogeny and phylogeny cannot be expressed in terms of one simple principle" (p. 327). Ghiselin is again in agreement with Holmes, stating recently: "The best post-Darwinian analysis of the relationship between ontogeny and phylogeny remains that of Sewertzoff" (Ghiselin 1992, p. 498). However, in relation to the immediate concerns of this chapter Severtsov, according to Adams, showed no interest in the causes of evolution. Severtsov also wrote in his posthumously published work of 1939: "Despite the brilliant successes in hereditary theory, the results of genetic research have brought little to the solution of evolutionary questions" (Sewertzoff 1939; in Adams 1980, p. 218; see my section 4.1.).

mutant form must continue along ancestral lines up to the stage in development first affected by the mutant. . . . The presence of recapitulation shows positively that the original mutational change in the ancestors affected development after the stage which is recapitulated" (Goldschmidt 1940, p. 389). The timing of mutant action thus became important for detecting evidence of recapitulation, since early activity would tend to obliterate ancestral records by modifying all later changes. As Holmes observed, "recapitulation would be evident in proportion as gene mutations become active toward the end of ontogeny." Holmes significantly added the query, "One is naturally led to ask, therefore, whether mutations are unusually prone to appear at this time, and if so, why" (1944, p. 327). The answers he provided to this question differed very little in substance from Gould's appeal to canalisation processes, and Stebbins' notion of the increasing precocity of gene action, as discussed by Gould 33 years later. Yet unlike Gould's account, the (then recently published) concept of canalisation, and its foundations within embryology and genetics, were not mentioned by Holmes.

Having surveyed the historiography of the recapitulation doctrine from the early 1930s, it is clear that historians have neglected giving any account of highly relevant work, begun in the 1930s, attempting to synthesise chemical embryology and Morgan's genetics. This work is also of general importance to the history of embryology, in its relation to the modern evolutionary synthesis during the 1930s and 1940s. Thus between Rasmussen's Latourian concerns with interdisciplinary conflict, and Gould's scholarly, anti-progressivist critique, there is a missing history. This history would further inform Gould's critical account of early modern synthesis embryology, specifically, his successful reduction of de Beer's eight categories of heterochrony to two; namely, acceleration and retardation (1977, pp. 221-228). It would do so, by providing a selectionist account of the importance of embryology to adaptive evolution, both supportive of Gould's critique, and in direct opposition to de Beer's trenchant views on recapitulation. It would also have lent context and depth to Holmes' discussion of modern synthesis genetics--particularly his discussion of Goldschmidt's physiological genetics. Similarly, Mayr's recent (and Shumway's prior) call for experimental embryology and genetics to provide a "somatic programme" explanation, in support of the "resurrection" of recapitulation, would be given clearer historical focus. This missing history revolves around the development of the synthetic, embryo-genetical evolutionary theory of C. H. Waddington.

1.2.2. From Invertebrate Palaeontology to Embryology and Genetics: A Biographical Sketch of Conrad Hal Waddington.

It is not difficult on investigation to see the relevance of Conrad Waddington's work, both in chemical embryology and later in developmental genetics, to the history of the recapitulation doctrine in the twentieth century. In fact, from the very earliest stages of his scientific education, Waddington was intrigued by matters geological and palaeontological. Describing his pre-secondary school days at Sedgeberrow, he reminisced: "My uncle, who was a bit of a naturalist, had already given me a taste for collecting odd things, like fossils. I used to spend hours hunting for them in the gravel used for paths in that neighbourhood" (Robertson 1977, p. 576). Waddington's sister also described how their Quaker grandmother was "a notable naturalist" who would surely have "instilled 'observation' into Con, as she did to me" (1977, p. 577). The connection between Waddington's palaeontological interests, and his later fascination with the development of ancient spiral-shelled invertebrates, probably also had its origins in his early childhood experience. Thus he continues: "I also collected snails, land snails and water snails from the river. I used to love rolling off my tongue, as a form of swank, their resounding Latin names like *Cyclostoma elegans* and *Planorbis cornuta*" (ibid.). Waddington's earliest scientific experimentations also began at about this time, with the assistance of a book from his grandmother, described by Waddington himself as "a guide to 'indoor entertainments'" (p. 576).

An elderly gentleman of the Quaker meeting (though there was, apparently, no actual meeting house at Sedgeberrow) entitled Dr. Doeg, was the most inspirational of Waddington's elders. In Waddington's words, Dr. Doeg "was, I suppose, almost the last surviving real 100% scientist. By that I mean that he reckoned to deal with the whole of science. He could give one the name of a fossil, or show one microscopical preparations of bits of animals and plants; he made colour photographs by an early process which involved a lot of dyed starch grains; and he could explain about lenses and prisms and magnets" (ibid.). These influences led Waddington, at a tender age, to his first taste of scientific "institutional" administration. Hence, as his sister describes: "He was certainly encouraged and helped to have a miscellaneous collection of every sort of natural history, geological and archaeological object in what was known as "Con's museum" in one of the barns attached to our house, where he could also conduct his chemical experiments under the auspices of Grandpa Doeg" (p. 577).

Waddington eventually made it to Cambridge on a Scholarship, and not surprisingly took the Natural Sciences Tripos at Sydney Sussex College, with a First in Part II in geology, taken in 1926. According to Robertson, Waddington "seems to have held simultaneously an 1851 studentship in palaeontology and an Arnold Gerstenberg studentship in philosophy for a thesis entitled 'the vitalist-mechanist controversy'. This award is made for the encouragement of the study of philosophy amongst natural scientists" (p. 578). The connection between Waddington's philosophising and his more strictly biological interests, was given a high profile by Waddington himself throughout his career. In Waddington's self understanding, a dialectical approach to the very mechanist-vitalist debate addressed in his Gerstenberg thesis, served as the continuing foundation to his world view until his death in 1975. Thus in an autobiographical note, written in 1969, and entitled "The practical consequences of metaphysical beliefs on a biologist's work," Waddington made explicit the dependence of his theory of biological evolution upon the process philosophy of A. N. Whitehead; a complex metaphysical system of the world which, according to Reese, "abjured all mechanical models" (Reese 1980 p. 625).[29]

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[29] Passmore says of Whitehead's writings: "The shifts of opinion which are everywhere apparent, not only as between the diverse and substantial works which he produced in the course of his long life but even within the confines of a single chapter; the obscurity and looseness of expression which too often prevail; the elusiveness of his multitudinous references to science, to art, to society, to the history of philosophy; these together produce in the chronicler of contemporary thought a feeling of desperation." (Passmore 1968, p. 336). Passmore adds, "It is in *Process and Reality* (1929) that Whitehead's metaphysical impulse finds its most complete, if its most baffling, expression" (19 , p. 340). R. F. Atkinson makes similar criticisms to Passmore, and feels that "a vast expenditure of time is needed to come to terms with [Whitehead's] system. His opponents therefore ignore him instead of criticising him in detail" (Atkinson, *Twentieth Century Mind, 2*; in Waddington 1975b, p. 21). In response to Atkinson, Waddington retorted: "This is as though some one felt he was duty bound to assess the literary worth of James Joyce, and decided, after plunging into *Finnegan's Wake* for half an hour, that Joyce was not worth bothering about. One should approach *Finnegan's Wake* through *The Artist as a Young Man* and *Ulysses*; one should approach *Process and Reality* through *The Principles of Natural Knowledge*, *Symbolism, its Meaning and Effect* and others of Whitehead's earlier writings, including *Science and the Modern World* (recognising that, however, as being something of a popularisation). Although I took this course in both cases, I confess I never quite made the grade to a confident mastery of either of the two *magna opera*--

Waddington, therefore, whilst writing of his schooldays encounters with gnosticism (symbolised by what he described as "*the world egg*" metaphor), and holism (symbolised by "*the ouroboros*," or snake eating its own tail), introduces the apparently much more significant concepts of mechanism and anti-mechanism in materialist philosophy:

> Before these highly poetic metaphysics had any practical influence on my scientific work, there was added to them a large body of much more explicitly rationalized thinking; in the first place that of Whitehead, to whose writings I paid much more attention during the last two years of my undergraduate career than I did to the textbooks on the subjects in which I was going to take my exams. Later this was joined by some infusions of thought which claimed to be materialist--either 'fancy' (dialectical), which preceded Whitehead and seemed to me to be in the main left behind by him; or 'crude', the prime example being Morgan and his school, who insisted that the gene is not just a logical construct from Mendelian ratios . . . but is just a simple lump of stuff. But one was anyway surrounded by materialists, and the whole of science was dominated by essentially Newtonian conceptions of billiard-ball atoms existing at durationless instants in an otherwise empty three-dimensional space. It was, for me, Whitehead who suggested new lines of thought. (Waddington 1969a, pp. 74-75).[30]

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both a bit too big for their boots. I will go along with Atkinson that he is a difficult author, but that is more because his ideas are unfashionable and profound than on account of his readiness to redefine words to suit his own purpose" (ibid.).

[30] Waddington offered a five point summary, paraphrased below from Waddington's own words, of Whitehead's supposedly "new lines" of thought: 1. Science's raw material are "occasions of experience." 2. Such occasions have a duration "(cf. David Bohm, 'there are no things, only processes'"). 3. An occasion is "injured" by its (unfortunately necessary) analysis; the subject-object dichotomy of analysis is an "arbitrary and artificial" convenience. 4. The content of an occasion is "essentially infinite and indenumerable," otherwise denumeration would create "the experience itself'." 5. Nevertheless the experience, or "event," has definite characteristics which Whitehead described as "objects." These definite objects imply that although every event is related to every other event, past and present, "these relations are brought together and tied up with one another in some particular and specific way characteristic of that event." For this nexus, Whitehead used the term "concrescence," which Waddington has used in relation to the polygenic nature of canalisation processes (Waddington 1969, p. 75; see section 3.1.2.). With respect to Whitehead's strict event-object distinction, Passmore states: "Whitehead's Platonism is now full-blown . . . An event is unique; by its nature it can never recur. Events, we might say, are the stuff, the particularity, of Nature. 'objects', on the other hand, are what we *recognise* in Nature, its permanent features. Neither object nor event can exist in isolation; every event is of a certain character, i.e. an object has 'ingressed' into it, and every object characterizes some event" (Passmore 1957, p. 339). With respect to Whitehead's "fallacy of simple location," Passmore adds: "Nevertheless, according to Whitehead, although we can properly ascribe a specific 'situation' to an object, it is a great mistake to think of it as being 'simply located' in that region. We may say, for example, that a gale is situated in the Atlantic. So it is; but nervous passengers in England cancel their berths; the gale is in England, therefore, as well as in the Atlantic. 'An object is ingredient throughout its neighbourhood,' [Whitehead] writes, and its neighbourhood is indefinite" (ibid.).

It is doubtful, however, that Waddington had a very deep understanding of later Whiteheadian metaphysics (Waddington himself called his own understanding into question in his posthumously published *Nature* review, "Fifty years on"). What is more, Waddington's personal metaphysics appeared rather to be a hybrid of Whitehead's Platonism (where essential "objects"--the objects of science--were "ingressed" into the "occasions of experience," or "events"), and David Bohm's own eliminative process philosophy. By contrast with Whitehead's essential objects, Bohm believed, according to Waddington, that "there are no things, only processes" (1969a, p. 75). In any case, late in his career Waddington was adamant that his own process philosophy had been of genuine scientific significance: "I should like to argue," he remarked, "that a scientist's metaphysical beliefs are not mere epiphenomena, but have a definite and ascertainable influence on the work he produces, by reminiscing for a moment about my own career. I am quite sure that many of the two hundred or so experimental papers I produced have been definitely affected by consciously held metaphysical beliefs, both in the types of problems I set myself and the manner in which I tried to solve them" (p. 72).[31] Clearly, then, Waddington's career concept of canalisation--for him the prerequisite process leading

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[31] Not only did Waddington's process-philosophical approach apparently have a deep influence upon his laboratory researches, it also had a much wider influence upon his views of the very close relationship between genuine science, Marxist political philosophy, and the development of a humanist ethics founded in evolutionary biology (see also his 1961b "The Human Animal," in Julian Huxley's collection of humanist essays *The Humanist Frame*). Thus in his popular 1941 pamphlet, *The Scientific Attitude*, Waddington decried Marx and Engels' adoption of a crude dialecticism "characteristic of the Middle Ages, a technique which has been given a thousand-year trial and has produced practically no increase in Man's understanding of Nature" (Waddington 1948, p. 99). Waddington nonetheless applauded the Marxist emphasis on the primacy of process, "made by their insistence that change is an essential part of the world" (ibid.). In Waddington's view, "Much of the recent development of science seems to have been towards a view of this kind. As I understand it, the basic ideas of modern physics, quantum mechanics and the theory of relativity, do actually describe the world in terms of processes and not in terms of static things. *Certainly in biology . . . the process view* (what is called dialectical materialism as opposed to mechanical materialism) *is more or less unavoidable.* Living things are not mere machines; they are essentially developing and changing things, growing from the egg to infant to adult, and dying, and linked with others in a succession of individuals which show the long-range changes of evolution. These are incontrovertible facts; but I believe biology at present under-estimates their importance, and would be well advised to give them something more like the emphasis which the Marxists urge" (p. 100; emphasis added). Finally, with regard to the claimed scientificity of Marxism, Waddington concluded: "The basic notions of Marxist philosophy are then almost, if not quite, identical with these underlying the scientific approach to nature; there is certainly nothing in them which could cause scientists to reject the rest of the Marxist system out of hand" (ibid.; see also Abir Am 1987, and Werskey 1988, for discussion of Waddington's relationship to the fashionable and predominantly Marxist "biotheoretical gathering" in the 1930s).

to the eventual genetic assimilation of acquired adaptive characters--would necessarily have been so influenced (see section 3.1.2. for the relationship between Waddington's metaphysics and the Edinburgh controversy over canalisation in the 1950s). If, in fact, we accept Waddington's view, then all his evolutionary theorising may be portrayed as an attempt to resolve the dialectical antitheses of T. H. Morgan's atomistic and mechanistic materialist theory of the gene, and Waddington's own particular brand of anti-mechanism.

The direct relevance of process philosophy to his late 1920s research in the study of fossil marine invertebrates, is also made very clear by Waddington. Thus he states in his autobiography: "I began work as a palaeontologist, studying the evolution of certain groups of fossils, and I chose, as my main interest, a group which forces on one's attention the Whiteheadian point that the organisms undergoing the process of evolution are themselves processes. The Ammonites were cephalopods, related to squids and the Nautilus, which laid down spiral shells. . . . The whole developmental process is preserved so that one cannot avoid examining it. And the process is, of course, complex, with many facets" (1969a, p. 76). Waddington also explicitly stated this work's connection with recapitulationism. Whilst unfortunately misquoting Haeckel's 1866 formulation of the biogenetic law, Waddington stated: "These early exercises left me with the deeply ingrained conviction that the evolution of organisms must really be regarded as the evolution of developmental systems. . . . It is of course related to such old ideas as Haeckel's 'biogenetic law'--phylogeny repeats ontogeny [sic]--but I took it also as a guiding principle in population genetics" (pp. 77-78).

However, as Waddington himself suggested, his active career in palaeontology was curtailed, in no small part, because of the influence of genetics: "I studied geology simply because it seemed that becoming an oil geologist would be a good way of earning a living. But I gradually got interested in evolution, chiefly because of an excellent tutor, miss G. L. Elles. I then got interested in genetics, through friendship with Gregory Bateson, son of William Bateson, the introducer of genetics to Britain, and I did two years' research in systematics of fossil ammonites but decided I wanted to study 'live' biology rather than fossils and never presented my thesis" (p. 578).[32]

Waddington's introduction to embryology, which led into collaboration with Joseph and Dorothy Needham into the chemical nature of the vertebrate evocator substance, occurred according to Waddington in 1930. Some interesting events at the Cambridge Strangeways laboratories are recalled from that time by Dame Honor Fell:

> Somewhere in the early 1930s, one of my colleagues told me that she had met a young palaeontologist (with a scholarship in moral philosophy) who had been reading the works of Spemann. He wondered whether it would be possible to adapt our organ culture technique to the study if induction in warm-blooded animals. I thought it would be a long shot, but marvellous if it worked, so I said he could come along and try. This he did. I showed him the watch glass method that we were using at that time, he implanted his chick blastoderms and found that such preparations could be utilized very well for many types of embryological experiments including induction. (Ibid.; see sections 1.3.1. and 1.3.2. for an elaboration of Waddington's subsequent and important Strangeways research into the chemical nature of the evocator).

Waddington had by now begun to call for a unified approach to the study of physiological genetics, experimental embryology, and evolution under the general rubric of "diachronic biology." It was in his 1939 *An Introduction to Modern Genetics*, that he began publishing working on this synthesis. Thus he proclaimed in the preface: "The different kinds of biological cobblers have stuck too closely to their

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[32] Unfortunately, not only did Waddington fail to present his thesis, he also left no published (or otherwise accessible) indication of what he read or who supervised him in invertebrate paleontology, during the brief period of his research in the field from 1926 to 1928. As Bowler has recently stated of the period leading up to the anti-recapitulationist critiques of Garstang (1922), Needham (1930), and de Beer (1930): "Curiously, it was the [invertebrate] paleontologists who now remained the chief advocates of the recapitulation theory. . . . When the recapitulation theory came under strong attack in the 1890s, it was defended by Paleontologists such as Francis Bather and James Perrin Smith, while Hyatt's concept of racial senility was upheld by H. W. Shimer" (Bowler 1996, pp. 82-83). Though by the time of Waddington's semi-professional involvement in the mid 1920s, Bowler adds that "some paleontologists were looking for more naturalistic explanations of the decline of the ammonites," nevertheless in 1932 "J. B. S. Haldane still thought that Hyatt's evidence was difficult to explain in Darwinian terms" (1996, p. 83; see my section 1.4. for discussion of Waddington's acceptance [with reservations] of Hyatt's data on "programme evolution" in ammonites; and section 1.4., footnote 54, for invertebrate palaeontologist T. N. George's acid criticisms, as late as 1933, of the anti-recapitulationists' disparagement of the doctrine). We do, however, have ample record of Waddington's continuing enthusiasm for invertebrate fossil hunting at the time, since, as Robertson says, "Gregory Bateson recalls Waddington's skill and nimbleness in clambering over the Dorset cliffs in search of [fossil] ammonites" (Robertson 1977, p. 578).

lasts. I want to urge that the connection between genetics and other branches of biology such as cytology, embryology, the study of evolution and of the biochemical nature of cell constituents, is much closer than is often admitted, and that the boundaries between these subjects deserve less attention than is usually paid to them" (Waddington 1939, p. 8).[33]

1.2.3. Canalisation and Modern Synthesis Recapitulationism: Waddington's Elaboration of Goldschmidt's Synthesis.

Just prior to Holmes's writings on Goldschmidt's genetics, Waddington published an intriguing and very relevant critique of Goldschmidt's 1940 book, one year before publishing his own canalisation hypothesis. In his 1941 *Nature* paper, "Evolution of developmental systems," Waddington first stated deferentially:

> In recent times, Goldschmidt has been the most prominent biologist who has attempted to describe biological organisation in terms which are at once developmental and not too far removed from the genetical concepts employed by students of evolution. His great contribution to the topic was made by the publication in 1927 of his *Physiologische Theorie der Vererbung*. He pointed out that the development of an animal consists of a large number of correlated reactions proceeding at different relative velocities; and he suggested that genes act by altering the rates of one or more of the reactions. This fruitful idea was successful in directing the attention of many geneticists to developmental problems, and has been the stimulus to much valuable work. (Waddington 1941, p. 108).

Waddington described Goldschmidt's mechanism for the acceleration and retardation of developmental reactions, "which [Goldschmidt] suggested were caused by alteration in the quantity of gene material, which was thought of as acting in an enzyme-like way." He then made what must have been a unique criticism of Goldschmidt among evolutionists at the time of the synthesis. For, Waddington argued, "Interesting as this suggestion is, it is not quite to the point so far as evolution is concerned. What evolutionary theory requires is not so much a hypothesis of the ultimate physico-chemical mechanisms of development, but rather a

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[33] As Yoxen comments: "In 1938 Waddington completed his textbook on genetics, presumably before he left for America that autumn [culminating, at Pasadena, in an extensive genetic analysis of wing development in *Drosophila*]. In the preface he acknowledges that he is crossing a disciplinary boundary, although clearly he had been reading the genetics literature carefully for some while" (Yoxen 1985, p. 318). Before he left for the United States, Yoxen adds that "Waddington was thinking seriously about the complementarity of embryology and genetics and the kinds of genetical experiments that could throw light on the potentiality of development" (1985, p. 319).

picture of the possible kinds of interactions between developmental processes" (1941, p. 109).[34] Thus for Waddington, Goldschmidt's theory was too biochemical, mechanistic and reductionist: it took too little account of the processes of development which, to the minds of supporters of the new synthesis it must on the contrary have appeared too concerned with.[35]

Audaciously, Waddington proposed a 5 point "elaboration" of Goldschmidt's theory, intended to give it greater developmentalist and process-philosophical credibility. Paraphrased, these alterations ran as follows: "1. The course of a developmental reaction is the resultant of a large number of mutually interacting influences. . . . [This] follows directly from the experimental data concerning the effects of modifying genes, and of the genetic background. It also issues in the following generalization from experience." Waddington's generalization, constituting a basis for the yet unpublished canalisation doctrine in experimental embryology, ran: "2. In a normal animal, there are only a certain finite number of possible resultants of the interacting developmental processes. . . .This implies that during development there is a succession of 'branching points,' at each of which the

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[34] As Yoxen again points out, Waddington had already severely criticized Goldschmidt, within the write-up of his Pasedena work (Waddington 1940c). After discussing a section illustrative of Waddington's Whiteheadian epigenetic holism (1940c, p. 94), Yoxen adds: "He then goes on to a very detailed discussion of defects of wing formation, which are explained in structural and mechanical rather than physiological terms. The work of Richard Goldschmidt, who favoured physiological mechanisms, is repeatedly criticized, often for its sloppiness as well as explanatory inadequacy. Not surprisingly Goldschmidt was not pleased by the paper. Waddington was clearly unhappy with biochemical explanations and writes instead in the tradition of D'Arcy Thompson, whose work is cited, and James Gray. It is also a very empirical paper. Nowhere is the developmental landscape mentioned" (Yoxen 1985, p. 320).

[35] Waddington's attack is all the more intriguing in the light of Allen's evidence, linking Goldschmidt's views to a Whiteheadian, process-philosophical approach to genetics. Thus Allen writes of Whitehead's 1934 *Nature and Life*: "Whitehead clearly deduced his conclusions from the philosophical basis of antimechanism and came to conclusions similar to Goldschmidt's about genetic units. Although Goldschmidt wrote relatively little about his own philosophy of science, it is apparent that, like William Bateson and others, he rejected simple mechanical explanations (like the kinetic theory of gene function) as naive and misleading" (Allen 1974, p. 84). However, in light of Waddington's strong support for Morgan's genetics, Harwood illustrates a long-term divergence between Waddington and Goldschmidt. Writing to Julian Huxley on 27.5.20, Goldschmidt stated: "It is really too bad that Morgan and his students--who after all are unusually clever and experienced researchers--have got stuck in such a narrow interpretation of genetic phenomena and oppose at all costs any new idea, especially a physiological one which might invigorate an otherwise somewhat boring Mendelism. I have discussed this issue at some length with my dear friend Morgan, but he insists that a thing [phenotype] has been explained once one has mapped a corresponding Mendelian factor" (Huxley papers; in Harwood 1993, p. 50; interpolation Harwood's).

course of development can move in one or other of a few alternative paths" (ibid.). At this point in his remake of Goldschmidt's rate-gene theory, Waddington described the most important theoretical development to come out of his own 1930s work within chemical embryology--that is, within the search for the chemical nature of the evocator substance in vertebrate primary induction:

> 3. One of the difficulties of an embryological theory has been to find a characteristic of a tissue which is causally connected with its future development. The classical concept of a potency is unsatisfactory because it is non-causal. One can discover a characteristic of the required kind during a 'branch point'. At this time a tissue is in a state of indeterminacy between alternatives. This state, which I have called competence, is open to experimental investigation. It has the character of a readiness to react to certain stimuli (evocators), which may be applied either externally or, probably, from inside the cell. The future character of development depends directly on whether or not such a reaction occurs. (Ibid.).

Point 4 relates these, the empirical foundations of canalisation, to the concept's proposed significance for the synthetic theory of evolution, hence: "4. The definiteness of the alternative modes of development is a product of natural selection, and characterizes animals in the state of nature. It is lost, or partially obscured, in most mutant forms." Point 5 concerned the phenomenon of homoeotic mutants in *Drosophila*, as an example of crux genes that can cause major diversions from the normal pathway of development, at important branchpoints. The existence of such genes provided further empirical if circumstantial evidence for the reality of canalisation, and a perfect opportunity to remind the reader of the author's credentials as a geneticist. To Waddington, Goldschmidt's understanding of developmental genetics appeared a little less sophisticated since "some, at any rate, of these points are adumbrated in Goldschmidt's writings; but they have not been clearly recognised by him" (ibid.).

Returning to Goldschmidt's views on evolution, Waddington found that Goldschmidt's main criticism was directed "not at the theory of selection, but at the idea that macro-evolutionary change is dependent on genes" (p. 110). Yet this observation of Waddington's appears to be in direct contradiction of Goldschmidt's views, as discussed three years later by Holmes, on the genetic causes of both the presence and absence of recapitulatory development. Incongruously in the light of Goldschmidt's views in the very work under discussion (Goldschmidt 1940, p. 389), Waddington speculated that "One reason for Goldschmidt's distrust of genes as adequate building materials for species may be that his 'rate concept' of gene action allows no place for differences in kind in the organisms produced; alterations in rate are essentially continuously variable" (1941, p. 110).

Following these misrepresentations of Goldschmidt's views, Waddington provided his own explanation of macroevolution, with equally obvious implications for recapitulationism, from "the basis of the somewhat fuller theory given above" (ibid.). Representing the animal as "a set of branching developmental paths, along which a certain part of the egg moves during its development," two possible kinds of changes were envisaged. Firstly, there may be changes in the topological relations of these paths, so that novel regions of the embryo produce structures normally produced by other embryonic regions (giving, for example, homoeotic mutants). Secondly, there may be "alterations in the actual course of the paths, which would imply that the final tissues were changed." It was this second kind of change which had causal implications for recapitulation, although Waddington did not discuss the mechanism in recapitulationist terms (ibid.). Passing over the first kind of change as necessarily producing macro-variation, the second kind could also explain Goldschmidt's controversial macro-evolutionary theory of "systemic" variations, or so-called "unbridgeable gaps." Waddington essentially restated Goldschmidt's own genetic explanation, both of recapitulation and of divergence in early development, in terms of pathways. Thus, Waddington asserted, a gene which causes an "alteration in the course of a developmental path will, if it occurs early in development, shift the whole set of paths which afterwards branch from it; that is to say, there will be a change in the character of a large number of tissues" (ibid.). In Waddington's theory, however, the "unbridgeability" of the change followed necessarily as a consequence of canalising selection, although he appeared loath to use the term canalisation until its official publication in November 1942. Instead of canalisation, Waddington spoke of developmental paths having to be "equilibrated," and of natural selection building up a genetic background which "stabilizes each part at the optimum." He continued: "If, by an early-acting gene, a whole set of paths are thrown out of their old equilibria, a very considerable modification of the genetic background will be called for. Once accomplished, this will not be easily reversed or copied; and the new form will be effectively isolated from the old" (ibid.).

From this critique of Goldschmidt, we see how Stebbins' later idea of the "increasing precocity of gene action" and Waddington's evolutionary theory from the early 1940s show a marked similarity. Firstly, both required the concerted action of modifier genes to effect the alteration of canalised developmental pathways. It is the developmentally up-stream alteration of pre-existing canalised pathways, that is necessary to allow the accelerated development of structures--that is, recapitulation--to occur.[36] Secondly, both provided selectionist explanations for the occurrence of the proposed accelerations. Yet whereas Stebbins' account adopted an overtly orthodox Mendelian gene selectionism, Waddington's concentrated more on the selection of the phenotype; that is, on the process of canalising selection, leading to the eventual hereditary fixation of a new adaptive phenotype.[37] Though population genetical and selectionist, nevertheless Waddington's theory, for this and other reasons to be discussed, was later construed by some as a subversive attempt at re-introducing neo-Lamarckian inheritance. In fact, Waddington's theorising from the late 1930s and early 1940s could have provided Rasmussen with a far more rigorous and detailed "non-Lamarckian theoretical support" for recapitulation, than did J. A. Thomson's writings (Rasmussen 1991, p. 62). Thomson's purported mechanism, of fixing late occurring somatic adaptations via the selection of genes for their earlier (embryonic) expression, found detailed Darwinian and embryological explanation in Waddington's work.

As Gould showed in his 1977 book, and Holmes discussed in his 1944 paper, many nineteenth century Darwinians, particularly Fritz Muller, had suggested a selectionist approach to explaining the recapitulatory acceleration of structures. Muller was the first to resurrect recapitulation in Darwin's light, and wrote in his

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[36] By the same token, the downstream alteration of pre-existing canalised pathways facilitated Garstang's paedomorphosis--that is, ontogenetic retardation of the appearance of early formed structures. Waddington's epigenetic landscape metaphor might well be used to represent the recapitulation and paedomorphosis processes, respectively, by the upstream and downstream migration of previously fixed topographical landmarks, such as kinks in the channels of the landscape. Although Waddington did not represent recapitulation in this manner, he nevertheless applied a very similar visual technique in his 1957 *The Strategy of the Genes*, to represent the difference between his genetic assimilation and Simpson's Baldwin effect (Waddington 1957, p. 167).

[37] Stebbins' concept is therefore *prima facie* more acceptable to the synthetic theory, because its mechanism is dependant upon the advantageous phenotype of a single late-acting gene. In Waddington's "genetic assimilation," however, canalising selection for a polygenically determined adaptive character defined the initial process. For this reason, had Stebbins' theory been proffered in 1953, it would undoubtedly have been identified by Waddington with Simpson's "Baldwin effect," rather than with genetic assimilation.

1864 *Fur Darwin*: "In general it will be useful for an animal to express those advantages by which it sustains itself in the struggle for existence. A precocious appearance of features first acquired at a later period will usually be advantageous, their retarded appearance disadvantageous. The former when it appears by chance, will be preserved by natural selection" (Muller 1869, p. 250).[38] Waddington, then, at the time of consolidation of the synthetic theory, furnished this selectionist explanation of recapitulatory acceleration with a novel Mendelian genetic mechanism, for the fixation of environmentally produced adaptive modifications. Thus in his 1942 *Nature* paper, "Canalisation and the inheritance of acquired characteristics," and within a precursory account of his later named "genetic assimilation" theory, he stated: "Thus once a developmental response to an environmental stimulus has been canalized, it should not be too difficult to switch development into that track by mechanisms other than the original external stimulus, for example, by the internal mechanism of a genetic factor; and, as the canalization will only have been built up by natural selection if there is an advantage in the regular production of the optimum response, there will be a selective value in such a supersession of the environment by the even more regularly acting gene." Crucial to the mechanism, he asserted, was that such a gene "must always act before the normal time at which the environmental stimulus was applied, otherwise its work would already be done for it, and it would have no appreciable selective advantage" (Waddington 1942, p. 565).

Thus we see that the history of Waddington's genetic assimilation theory is particularly important to Holmes's, Gould's, and Rasmussen's purposes. Gould, perhaps had other reasons for not discussing Waddington, in his discussion of the problems posed by the canalisation of development. Hence the title of Waddington's paper to *Nature* in 1942, "Canalisation and the inheritance of acquired

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[38] Weismann made very clear Haeckel's immediate debt to Muller's Darwinist recapitulationism, saying : "A few years after the appearance of Fritz Muller's work *Fur Darwin*, Haeckel elaborated Muller's idea, and applied it in a much more comprehensive manner. He formulated it under he name of 'the fundamental biogenetic law,' and then he used this 'law' to deduce from the ontogeny of animals, and more particularly of Man, the paths of evolution along which our modern species have passed in the course of the earth's history." Yet in doing so, Weismann warned, "the greatest caution was necessary, since ontogeny is not an actual unaltered recapitulation of the phylogeny, but an 'abridged' and in most cases--in my own belief, in all cases--*a greatly modified recapitulation*" (Weismann 1904, p. 172; author's emphasis; see my section 5.1. for discussion of Weismann's and Balfour's relativised organ and structure recapitulationism).

characteristics," provides a strong clue to the historical neglect of his views on adaptive evolution--at least until the late 1980s. Published in the year of Huxley's *Evolution, The modern Synthesis*, the first paragraph of Waddington's paper set the tone. Discussing the long battle between naturalists and geneticists over the mechanism of evolution, he suggested that the "classical naturalist theory--the inheritance of acquired characters--has been very generally relegated to the background because in the 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."[39] Hence, in Waddington's view, the theory's long popularity was not based on positive evidence, but on its utility in accounting for "some of the most striking of the results of evolution." He added, controversially: "Naturalists cannot fail to be continually and deeply impressed by the adaptation of an organism to its surroundings. *These adaptive characters are inherited*, and some explanation for this must be provided" (1942, p. 563; emphasis added.). A sentence later, in an apparently open attack on the new orthodoxy of the synthetic theory, Waddington stated: "If we are deprived of the hypothesis of the inheritance of the effects of use and disuse, we seem thrown back on an exclusive reliance on the natural selection of mere chance mutations. It is doubtful, however, whether even the most statistically minded geneticists are entirely satisfied that nothing more is involved than the sorting out of random mutations by the natural selective filter" (ibid.). Such forthright language, fully supporting the inheritance of acquired characters, might hardly be expected to promote canalisation and genetic assimilation among supporters of the synthetic theory--least of all as a non-Lamarckian theoretical support for recapitulation.[40]

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[39] As discussed in section 5.1., many early twentieth century evolutionary biologists understood that it was, in fact, Weismann and the neo-Weismannian pan-selectionist, who required of neo-Lamarckian inheritance "a type of hereditary variation for the existence of which there was no adequate evidence."

[40] In fact, as Rasmussen has suggested, Darwin's own recapitulationism depended heavily upon Lamarckism and Geoffroyism. Hence "Darwin explained [the principle of late variation] mainly through the inheritance of acquired characteristics. Use and disuse of parts, as well as habituation to and direct effects of the environment, play an important role in causing variations. Embryos obviously tend to be active in, and exposed to, their habitats far less than adults; thus, embryonic forms should vary less" (Rasmussen 1991, p. 56).

Evidence for the rejection of Waddington's synthetic theory by the founders of the modern synthesis is discussed by Gilbert in his highly informative 1991 volume, *A Conceptual History of Modern Embryology.* In a footnote to his chapter on Waddington, Gilbert tells us that by the 1960s, two major supporters of the modern synthetic theory, Theodosius Dobzhansky and Ernst Mayr, had openly interpreted Waddington's genetic assimilation theory as "a failed attempt to support Lamarckian inheritance" (Gilbert 1991, p. 205). By 1959, Dobzhansky had come into conflict with Waddington for apparently rejecting canalising selection and genetic assimilation, and accepting Soviet morphologist and phenogeneticist Ivan Schmalhausen's very similar theory of "stabilising selection," in all his public discussions. De Beer, whose own highly influential and deeply anti-recapitulationist 1930 work attempted a synthesis between embryology, genetics and evolution, may be added to the list of those who dismissed genetic assimilation in this manner in the 1950s. On the face of it, only Simpson appeared to be less dismissive. Apparently accepting a limited role for genetic assimilation, he characterised it as a broader population genetic account of the "Baldwin effect," Simpson's phrase describing the neo-Mendelian version of Lloyd Morgan's and Baldwin's late nineteenth century concept of "organic selection" (Simpson 1953a, pp. 110-117). Gilbert, having written extensively on Waddington, fears that the term genetic assimilation was poorly chosen in that "it conveyed a notion that physiological responses could be genetically fixed in the genome" (ibid.). However Waddington's rhetoric, calling as he did for some explanation for Lamarckian phenomenology, was precisely chosen to convey this notion, thereby sealing his fate with respect to the orthodoxy in the early 1940s.[41]

Irrespective of his concerns over the existence of genetic assimilation, Mayr made considerable use of Waddington's epigenetic language in his own evolutionary

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[41] The necessity of mentioning Waddington's enthusiastic acceptance by Julian Huxley, is complicated by Huxley's equally enthusiastic support for, and Waddington's emphatic rejection of, neo-organic selectionism. In the early 1940s, a neo-Mendelian reinterpretation of Lloyd Morgan's organic selection emerged strongly as an explanation, conformable with a the central tenets of the synthetic theory, of the hereditary fixation of adaptive modifications. The complex relationship between Waddington and Huxley is therefore discussed within this context in my Chapter 2.

writings.[42] In his 1963 book, *Animals, Species, and Evolution* Mayr objected, in common with Waddington, to the reductionist conception that the modern synthesis was founded principally on the population genetical formalisms of Fisher, Haldane and Wright. Such a view falsely implied that the contributions of field naturalists and systematists, particularly in the areas of geographic variation and speciation, were of only secondary importance to those of the geneticists. Hence Mayr believed: "The contribution of genetics to the understanding of the process of evolution has not yet been evaluated objectively. . . . The assumption made by some geneticists, that it was quite impossible to have sensible ideas on evolution until the laws of inheritance had been worked out, is contradicted by the facts." (Mayr 1963, p. 10). After contrasting the "remarkably correct picture of speciation, adaptation, and the role of natural selection" held by many genetically uninformed naturalists, with the ideas of some geneticists which "misinterpreted just about every evolutionary phenomenon," Mayr concluded, in direct reference to Waddington's 1957 book: "It would be going too far to claim that it is immaterial whether one believes the source of genetic variation to be de Vriesian or Lamarckian, yet it is true that it is less important for the understanding of evolution to know how genetic variation is manufactured than to know how natural selection deals with it" (ibid.).

What, then, of the obvious significance of Waddington's research to Mayr's current programme for the resurrection of recapitulation? Recalling Mayr's second major purpose in reassessing the case for recapitulation--namely, the search for a

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[42] Hall provides us with a useful definition of epigenetics and the epigenotype, terms first used by Waddington in 1939: "Waddington repeatedly stressed the role of the organization that links the genotype to the phenotype. With the term epigenotype he sought to capture that linkage as the series of interrelated developmental pathways through which the genotype is manifest in the phenotype. It encompasses all the interactions among genes and between genetic and environmental signals that produce the final phenotype, or epiphenotype." Most importantly for the controversy over Waddington's leanings toward Mayr's "soft heredity" (see section 5.4., footnote 28), Hall adds: "Interaction, integration, and *heritability* of these stable interactions are the essential elements of the epigenotype. Epigenetics and epigenotype are often used interchangeably" (Hall 1992, p. 118; emphasis added). Four years after Waddington's death, his close friend Gregory Bateson offered some more general insights: "*Epigenesis* is the word preferred by Waddington for his central field of interest, whose old name was *embryology*. It stresses the fact that every embryological step is an act of *becoming* (Greek genesis) which must be built *upon* (Greek *epi*) the immediate status quo ante. Characteristically, Waddington was contemptuous of conventional information theory, which allowed nothing, as he saw it, for the 'new' information he felt was generated at each stage of epigenesis. Indeed, according to conventional theory, there is no new information in this case" (Bateson 1979, p. 52).

Darwinian formula for the ultimate causes of organ recapitulation, he told us that "experimental embryology and genetics . . . have never been synthesised into a well rounded explanatory theory" (Mayr 1994, p. 228). In other words, during the synthesis years since 1942, there has existed no synthetic embryo-genetical and selectionist theory of any significance. More to the point, no such synthesis has existed sufficient to the purpose of supporting a somatic programme explanation of Gilbert's "old synthesis;" that is, Haeckel's fundamental biogenetic law.

At least Mayr's first assumption would now be challenged by a significant number of historians of biology. In 1991, Gilbert discussed the synthesis currently being negotiated in developmental biology between genetics, evolution, and embryology (Gilbert 1991b, p. 135). In his introduction, Gilbert says that "although the synthesis is presently being worked out, ours is not the first attempt to do so." He points out that earlier in the century, Goldschmidt, Just, Dunn, and Julian Huxley, had each attempted to unite these disciplines into a single framework, but concludes that from 1936 to 1960, "the person who probably went furthest in forging such a synthesis was Conrad Hal Waddington" (ibid.). Other recently supportive commentators on Waddington's synthesis include Weber and Depew, who comment that "Waddington fought somewhat more successfully than Goldschmidt against the marginalization of developmental genetics in the modern synthesis and sought doggedly to introject embryology into the evolutionary theory" (Weber and Depew 1994, p. 415). Most recently, Jablonka and Lamb mention several evolutionary biologists, working during the 1940s, interested in the relation between developmentally and environmentally induced characters and inheritance. Hence they tell us that "notably Schmalhausen in the USSR . . . and Waddington in Great Britain, began to re-examine the significance of the interrelations between the genotype, phenotype, and the environment" (Jablonka and Lamb 1995, p. 31).

Clearly, then, there has been growing acceptance of the significance of Waddington's synthetic theory to the modern synthesis, although its significance to recapitulationism has not been mentioned at all. Jablonka and Lamb's contribution to the recent trend of reassessing Waddington's and Schmalhausen's similar developmentalist theories of evolution has been a significant one, in that their agenda is explicitly the validation of neo-Lamarckian phenomenology, as Waddington's had been in 1941. Nevertheless, they misleadingly describe Waddington and

Schmalhausen's syntheses as neo-Darwinian explanations of the inheritance of acquired characters (see section 5.2.).

In summary, the repeated discrediting of Haeckel's biogenetic law was highly successful in the 1920s and 1930s. It ensured that mere lip service was paid to embryological concerns by those involved in the development of the synthetic theory between 1930 and 1942. In the following sections, I suggest that Waddington, coming as he did from the classical recapitulationist's stronghold of invertebrate paleontology, and holding to a metaphysically entrenched view of phyletic evolution as an extension of the ontogenetic processes of development, responded to the anti-recapitulationist gauntlet thrown down by de Beer in 1930, and again in 1940. He did so by attempting to prove phylogeny's direct causal significance to ontogeny, in the terms that de Beer, and earlier Garstang, had demanded from the recapitulationist. In section 1.3., I look closely at the experimental embryological origins of Waddington's synthetic theory of evolution, touched on above within the discussion of Waddington's criticism of Goldschmidt's synthesis views. These origins are to be found in Joseph Needham's chemical embryology programme of the 1930s. Their history serves to underline the significance of Waddington's synthesis to the history of recapitulationism, at the time of that doctrine's apparent demise during the early modern synthesis years.

1.3. Synthesising Proximate and Ultimate Explanations: Waddington's Embryogenetical Evolutionary Theory.

The history of Waddington's significance to modern synthesis recapitulationism, and hence to the modern synthesis in general, begins with his choice to move the research field of invertebrate palaeontological systematics--a continuing out of disciplinary stronghold of recapitulation and neo-Lamarckism well into the new synthesis years--and into experimental embryology and genetics. As discussed in the previous section, Waddington did this under the influence of his close friend Gregory Bateson (Robertson 1977, p. 578). During the period between 1933 and 1936, Waddington collaborated, in particular, with Joseph and Dorothy Needham, on elaborations of Hans Spemann's experimental researches into amphibian neural induction.[43] His research in this area displayed, according to Waddington's self-understanding, an uncharacteristically reductionist attitude which he ruefully discussed much later in his career (Waddington 1969a, pp. 80-81).

After having appropriated tissue culture techniques at the Cambridge based Strangeways laboratories to perfect extremely difficult avian embryo manipulations, Waddington was invited by Goldschmidt to go to Germany. However, instead of accepting the offer of working with Goldschmidt, he went to Freiburg in Germany in 1932 to work under Mangold, Spemann's former postgraduate student and then collaborator. The purpose of this move was to learn yet more techniques, this time in the manipulation of amphibian organiser material, for the purposes of beginning his own investigations into the early embryonic induction of amphibian neural tissue (Gilbert 1991a, p. 189).

1.3.1. The Cambridge Research Programme and the Embryochemical Search for the True Evocator.

Once armed with all the techniques necessary to undertake an experimental analysis of vertebrate development, Waddington returned to Cambridge. There he launched upon a biochemical, and later genetic, dissection of the problem of embryonic induction. The experimental attack on development began in 1933 with the financially ill-fated collaboration (initially tentatively funded by the American Rockefeller Foundation) of Waddington, Joseph Needham, and Dorothy Needham to discover the chemical nature of the evocator.[44] [45] This investigation may, on the face

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[43] For a comprehensive discussion of Spemann's work on the amphibian neural organiser, see Horder and Weindling 1983, pp. 183-242.

[44] Rockefeller Foundation funding of research in the early 1930s was oriented strictly toward furthering their policy of "technology transfer" from the "hard" physico-chemical sciences toward the softer and "technically impoverished" biological sciences, of which experimental embryology was unfortunately seen as the softest. A prime reason for removal of Rockefeller support for the proposed "big project" of a positivistic "Institute of Mathematico-physico-chemical Morphology," to be located at the Cambridge Dunn Laboratories, was the uncertainty as to how much funding would be "wasted" by going directly into purely morphological research (Abir-Am 1987, p. 23).

[45] Hall, who has made extensive study of Waddingtonian neologisms, writes that evocation described simply "the induction of differentiation," and adds that: "King and Stansfield (1985) define evocation as 'the morphogenetic effect produced by an evocator,' an evocator as 'the morphogenetically active chemical emitted by an organizer,' the organizer in turn being 'a part of an embryo which exerts a morphogenetic stimulus upon another part, bringing about its

of it, appear a strange research project for a graduate geologist, and postgraduate palaeontologist turned experimental embryologist, to undertake. Joseph Needham was having enough difficulty convincing the chemistry and biology communities, to use Abir-Am's phrase, that "biochemistry's ideal of explanation" (namely, Hopkins' "extrapolation from the chemistry of the dead to that of the living"), was of any benefit to either field (Abir-Am 1991, p. 163). A chair in biochemistry had only been established at the Cambridge Dunn laboratories since 1925. Needham, in his letters to J. H. Woodger, described ninety nine percent of embryologists as "depressingly morphological and static" in their approach. Hence to apply the methods of chemistry to such an area of biology, led to deepening suspicions over the blatantly cross disciplinary research Needham undertook (Abir-Am 1991, p. 169).

The main stimulus for Waddington's involvement in the evocator investigations--a landmark paper by Holtfreter describing the ability of the dead organiser to induce neural tissue--had on the contrary caused Spemann himself, according to Saha, to become "disillusioned and effectively cease active research" (Saha 1991, p. 105). As Waddington related: "It was not till the end of 1932 that it was unequivocally shown that the organiser would still induce after being killed. The discovery was announced jointly by Spemann, Bautzmann, Holtfreter and Mangold, working on the newt in Germany," and was "immediately confirmed" by Waddington himself (Waddington 1940, p. 20). A flurry of papers on the "evocatory" activity of various solvent extracted organiser fractions, and other unrelated chemical species, were published between 1933 and 1936. Evocation was one of many new terms coined by Waddington in embryology. It distinguished between the truly organ forming capacities of intact blastopore dorsal lip tissue (the location of the organiser), from the capacity of extracts of this tissue to induce neural tissue formation.[46] In 1934, after three years of technical problems getting chick organiser to adhere to the

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determination and morphological differentiation.' These definitions are essentially those introduced by Waddington in the 1930s and 1940s (Hall 1992, p. 117).

[46] Waddington, in a short communication to *Nature* in 1933, described how "Holtfreter has been by far the most successful of the newer workers; he reports large and typical inductions by organisers dried at 60 C., or heated to 100 C, or frozen, acting upon either isolated pieces of presumptive epidermis or on the same tissue in its normal place in the embryo. Bautzmann describes two structures, induced by organisers which had been heated to about 60 C. . . . Spemann has obtained one induction by an organiser killed in 96 per cent alcohol, and Mangold reports some doubtful cases which raise the possibility that that the inducing agent can diffuse into agar blocks" (Waddington 1933, p. 275).

presumptive ectoderm in embryo, Waddington said triumphantly that the "number of successful experiments is very small, but the fact of induction by dead organisers can be taken as proved" (Waddington 1934, p. 220). Work on the chemical nature of the evocator culminated in a paper of 1936 by Waddington, J. Needham, and Brachet, maintaining that the highest activity was to be found in sterol containing ether extracts (Waddington 1940, p. 24).

The emergence of evidence that many very improbable substances, including ordinary mechanical irritants, in fact had significant evocatory power, led Robertson to comment that the whole avenue of research "eventually became disembodied like a will-o-the-wisp" (Robertson 1977, p. 590). But in fact the research did not become insignificant, and to ignore it would mislead us from its historical and evolutionary significance, with respect to the development of Waddington's own evolutionary theory. Waddington's eventual hypothesis--the so called "masked evocator" (a chemical species thought to be constituted of a loose association between the active evocator, and some unknown deactivating ligand), appeared to fit the facts well but fell foul of lack of experimental evidence (1940, p. 28). Other substances could be acting as secondary evocators, unmasking the masked evocator in the target tissues, whilst the real mechanism for unmasking this "true" evocator remained obscure (p. 39).

The most significant event for understanding the developmental pathway followed by Waddington's own theorising, occurs amidst the resulting dilemma of having to decide between the opposing theories of evocator specificity and non-specificity. If non-specificity were accepted, the hope of isolating the "actual" evocator substance for the primary induction process under investigation, would become lost amongst the multiplicity of chemical candidates. As Waddington himself said, "non-specific chemical stimuli do not seem to be at all commonly employed by animals in their physiological systems. It is difficult to think of any example of a stimulus which is normally chemical and which is at the same time non-specific" (p. 25).

As the story was told by Waddington in 1940, it appears that in the theoretical battle between evocatory specificity and non-specificity, evocator specificity won. This was the outcome, not least, because the assumption of evocator specificity allowed work to continue on an hypothesis of masked evocator activation, along with further research into a resurrected "true" evocator substance. Also Joseph Needham's much-defended mechanistic and reductionist methodology--the "only one workable in modern science"--remained intact in this context (Abir-Am 1991, p. 166). As Waddington explained: "We have seen in practice several different classes of compounds can bring about evocation. The mere elaboration of the hypothesis that evocation is none the less a response to a specific stimulus, or to one of a small group of stimuli does not enable us to decide which of these compounds is the specific evocator. No amount of hypothesis can make the experimental data more definite than they are." Nevertheless, Waddington added in seemingly relieved tone, by adopting this hypothesis "the question of the identification of the evocator becomes meaningful and important and requires discussion" (Waddington 1940, p. 30).[47]

Here, then, we arrive at a critical point of conceptual transition: a "developmental branch point," we might say, which was to lead to the deeply canalised pathway of Waddington's subsequent epigenetic evolutionary thinking. Thus, he continued: "The hypothesis of the activation of the evocator, to which we have been led by a consideration of the experimental data, is only a particular instance of a more general theory which we might have been led to on *a priori* grounds. This theory is that during the passage from competent ectoderm to determined neural tissue, a series of reactions is involved in a complicated system of reactants and that development may be switched into a neural channel by affecting different steps of the reacting sequence" (1940, p. 29). Two such steps were the liberation of the evocator, and its action on the competent ectoderm (neither of which was anything

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[47] Saxen and Toivonen have described this period of primary embryonic induction research as "the confusing thirties," and characterise it using the three apparent schools regarding the true evocator (or, to use their term, the "inductor"). Hence they state: "In brief, three schools could soon be distinguished in this competitive effort to find the 'inductor': the Cambridge school with Needham and Waddington collaborating with Bracket [sic.], the German school with Lehmann, Wehmeier and Fischer, and Barth with his students. The Cambridge group reported results suggesting that the active compound might be a *sterol*, while the German school obtained inductions with various acidic preparations, including nucleic acid, oleic acid, and linoleic acid, and ended with the '*acidic stimulus theory*'. Barth, on the other hand, reached the conclusion that the normal inductor in the blastoporal lip might possess features of a *protein*." Similarly to Robertson, the authors observe that "This multitude of active compounds, together with the many controversial views and observations of the investigators, naturally had to result in great confusion and a gradual fading of interest in the entire complex problem" (Saxen and Toivonen 1986, p. 267; author's emphasis throughout; see also Brachet 1986, pp. 253-256 in the same volume).

known about). The biochemical complexity of evocation was, therefore, very significant: neural tissue development could be "switched into" at one of any number of points on the pathway to full neural determination. Hence, to Waddington's understanding, "in discussing evocation we are really attempting to determine the conditions under which a complex mixture sets out on one rather than another course of reactions; and these reactions themselves are by no means simple, but involve a co-ordinated set of syntheses of different proteins as well as the histological arrangement of these substances" (pp. 29-30).

These problems appear, if we are to accept the author's rational reconstruction of events, to have led Waddington to the most important development in his evolutionary thinking. All else in his evolutionary conceptual scheme followed from his decision, at some stage during the hunt for the true evocator, to resolve the antitheses of evocator specificity versus non-specificity by adopting a belief in *reacting tissue* specificity. This significant decision occurred amidst the emerging problems of a full-blown reductionist methodology: namely, the elusiveness of characterising a single biochemical, responsible for triggering very complex chemical processes of embryological induction. Nevertheless, Chapter 5 of *Organisers and Genes* now appears in retrospect as an unelaborated statement of Waddington's entire evolutionary hypothesis.[48] In Waddington's terms, "the whole process of development may therefore be considered as resulting from an unstable configuration of substances, which leads the embryo to change to a more stable state." Competencies are seen as secondary instabilities with "the choice between them depending on outside conditions (the presence or absence of the appropriate organiser)" (1940, p. 45).

1.3.2. The Emergence of the Concept of Genetic Assimilation from the Search for the True Evocator.

Once evocator substances and the primary products of genes have been identified with each other, as they were in Chapter 7 of *Organisers and Genes*,

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[48] Victor Hamburger, who worked alongside Waddington in Spemann's lab in 1932, sees Waddington's 1957 *The Strategy of the Genes* as the West's "missing chapter" of the modern synthesis (Hamburger 1980, p. 108). I see it more literally as Chapter 5 of *Organisers and Genes*.

Waddington's conceptual framework becomes fully apparent. What he came to describe as "genetic assimilation" in 1953, was simply an evolutionary and population genetical application of his investigations into evocation and competence in avian and amphibian embryos. Waddington incorporated these embryological phenomena within an evolutionary scheme, unified by the assumption of the natural selection of greater and greater "competence efficiencies."[49] His illustrative examples of the scheme included the much discussed data on ostriches from Duerden's research.[50] The following two paragraphs, taken along with the functional identification of genes with vertebrate evocators, encapsulate Waddington's synthetic evolutionary theory of the early 1940s:

> The most remarkable fact which has been discovered in this connection is the occurrence of what is known as dopelte sicherung or "double assurance". In *Rana esculenta* the eye cup can induce lenses in non-presumptive lens ectoderm and therefore presumably can affect the ectoderm which normally forms the lens; but if the eye cup is removed, a lens nevertheless forms, so that the inductive action of the eye cup is unnecessary. If this is thought of simply in terms of the capacity for self differentiation or the necessity of inductive stimulus, it seems a somewhat mysterious and complicated arrangement. But if the reaction of competent tissue always consists in the resolution of a state of instability in one of two or more possible ways, it is only to be expected that the decision can be produced by an action much less prolonged than that which the organiser actually provides in normal development, so that the tissue becomes self-differentiating at a time when the organiser is still active.
>
> In fact, one would expect that in general, the more highly developed the competence, that is to say the more sharply the alternatives are contrasted, the smaller the external stimulus which will be necessary to decide between them. The evolution of a really efficient competence may therefore be expected to reduce the importance of the evocator, which will probably tend to disappear; and we may expect to find cases in which the functions of the evocator are taken over by minor variations in conditions which are very difficult to identify. Phenomena of this kind may lead to the evolution of a mosaic kind of development from a regulative; and they may also help to explain cases such as that of the callosities of the ostrich, in

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[49] For Waddington's definition of the concept of cellular competence, see part 3 of his restatement of Goldschmidt's rate-genetical evolutionary synthesis, as discussed in my section 1.2.2. above, and in Waddington 1941, p. 109.

[50] Duerden's Ostrich data was also used in 1930 by de Beer, as a prime example of apparent but misleading evidences brought in support of neo-Lamarckian use-inheritance and the doctrine of recapitulation. However, de Beer only referred to Duerden's unillustrated 1924 *Science Progress* paper, where the neo-Lamarckian explanation is much less extensively and less forcefully applied than in his 1920 *American Naturalist* paper. Duerden's 1920 data and illustrations were used by Waddington, to illustrate Waddington's concept of the genetic assimilation of acquired characters in the early 1950s.

> which structures which are apparently adaptive responses to external stimuli actually develop before the stimuli can be present. (1940, p.49).[51]

Every important evolutionary notion Waddington expounded between 1939 and 1942, and elaborated upon in the early 1950s, may be extrapolated from these two paragraphs. The entire conceptual scheme was also visually represented by Waddington within an overtly teleological, if not mystical, graphic of the temporal and spatial forces that guided development toward future states. This was to become the "epigenetic landscape," a now familiar piece of iconography to developmental biologists, first depicted by the painting of John Piper on the frontispiece of *Organisers and Genes.* The landscape also made explicit the relationship Waddington saw existing between ontogeny and phylogeny: thus it represented both the ramifications of tissue differentiation in ontogenesis, and the parallel ramifications of organismic differentiation in phylogenesis, resulting from the single process of canalisation, and expressed within a single visual metaphor.[52]

Returning, then, to the possibility of extrapolating Waddington's later adaptive evolutionary terminology from the above 1940 passage: for "the evolution of a really

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[51] In the phenomenon of double assurance, whereas a developmental pathway in one species may require an evocatory stimulus from an organiser, in a very closely related species its continued action has become superfluous. This is because in the absence of the organiser, self (autoregulated) differentiation occurs. Thus the development of the structure produced by entering the pathway has become "doubly assured." The history of the phenomenon is related by Horder and Weindling: "In 1907 Spemann found a way to reconcile the conflicts in evidence from different species and indeed to capitalise on them. He invoked the phenomenon of 'double assurance', introduced one year previously by his friend Hermann Braus, as a result of his discovery that the opening of the operculum covering the limb bud of the frog larva, which is normally associated with the outgrowth of the limb itself, still occurs after the early removal of the limb bud rudiment" (Horder and Weindling 1983, p. 191; see also Saha 1991, p.101).

[52] Waddington described the meaning of the landscape metaphor (first alluded to in his 1939 *Introduction to Modern Genetics*), in the 1940 monograph *Organisers and Genes*: "The whole process of development may therefore be considered as resulting from an unstable configuration of substances which leads the embryonic tissue to change toward a more stable state; and the periods of competence are secondary instabilities. When there are two or more alternative modes of progression towards stability, the choice between them depending on outside conditions (the presence or absence of the appropriate organiser) one can compare a piece of developing tissue to a ball running down a system of valleys which branches downwards, like a delta. . . . The tissue, like the ball . . . must move downhill, but at some point there are two downhill paths open to it. At such branching points, it may sometimes require a definite external stimulus, such as an evocator substance, to push the tissue into one of the developmental paths; in such a case, competences which occur late along this path will only be developed if the evocator has acted. In other cases, a certain path may be followed merely because an evocator has failed to be present, and then the subsequent competences may appear to develop autonomously" (Waddington 1940a, p. 45).

efficient competence," we may substitute the term "canalisation," which first appeared in the literature in 1942. For "functions of the evocator being taken over by minor variations in conditions" read, from the same 1942 paper, "for example by the internal mechanism of a genetic factor" (1942, p. 565). After the claimed experimental verification of genetic assimilation by Waddington in 1953, this became: "We may say that the acquired character has been 'assimilated' by the genotype"--hence read "genetic assimilation," a process Waddington saw as responsible for both micro and macro-evolutionary processes (Waddington 1953d, p. 138; see section 3.1.3. for genetic assimilation's proposed macro-evolutionary significance).[53] Again, Waddington's statement in the above quotation that the more highly developed the competence, the smaller the external stimulus required "leading to a mosaic type of development from a regulative," was in the early 1950s the focus of some new terminology, but no new concepts. Thus his 1953 description of the shift, due to canalisation, from the "exogenous" through to the "pseudo-exogenous" (or assimilated) form of an adaptation, described precisely the same process in adaptationist terms (Waddington 1953d, pp. 134-135).[54]

Duerden's discussions regarding callosities in the Ostrich had been published in 1930, and again in 1940, by Gavin de Beer. Intriguingly, de Beer had used them as a

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[53] The concepts of "homeorhesis" and "creode"--Waddington's apparently new ideas appearing in his 1950s writings--were simply teleological terms expressing the principles embedded in the epigenetic landscape.

[54] In 1953 Waddington distinguished three types of adaptations. Firstly, *exogenous* (e.g. muscular hypertrophy): "a category in which an animal living under particular circumstances, or behaving in a particular way, itself becomes modified so as to be better fitted for its special circumstances" (1953d, p. 134). "Secondly, *pseudo-exogenous* (e.g. callosities in the ostrich): "in which the animal exhibits characteristics similar to effects which can be called forth as direct exogenous adaptations, but which on investigation are shown to be hereditary, and independent of any particular environmental influence." These, said Waddington, "pose one of the most striking problems to be solved" (ibid.). Thirdly, *endogenous* (for example, modifications of the epidermal cells to secrete sweat, and the development of the transparent cornea): "a very large class of adaptations, which . . . are characterised by the fact that the adaptive feature is of a kind which one cannot imagine as having ever been produced in direct response to the environmental conditions or mode of life of the animal" (ibid.). The connection of the first two classes of adaptation with Waddington's 1930s work is unproblematic. However, Waddington felt, "It is in connection with the third type of adaptation that we can as yet make the least progress beyond the current hypothesis, which is content to rely upon the chance occurrence of suitable mutations" (p. 135). Nevertheless, Waddington invoked an organiser-type explanation, believing "we shall often find that the various parts concerned in such endogenous adaptations are involved with one another not only during their functioning in the adult animal, but during their development in the embryo" (ibid.).

prime example of apparent but misleading evidence in support of the neo-Lamarckian inheritance and phylogenetic acceleration--that is, Haeckelian recapitulation--of acquired adaptive characters (de Beer 1930, p. 85). As might be expected from a field zoologist writing in 1920, Duerden's own views suggested sympathy with the Lamarckian viewpoint. Hence he asserted:

> "The main facts presented seem capable of interpretation in only one of two ways: *(a) An acquired character which represents a structural response to stimuli resulting from the activities of the organism may become transmissible. (b) A character may arise germinally of a form and nature exactly similar to one which would otherwise be acquired independently from the known activities of the organism and the established responsive nature of its structural parts.* In adopting the first interpretation we depart from the generally accepted opinion of biologists of the present day and admit that an acquired character may become transmissible; in maintaining the second we are exercising a credulity unjustified by biological experience. (Duerden 1920, p. 301, author's emphasis).

Three pages earlier, Duerden had spelled out the degree of credulity called for, saying: "If we are not prepared to admit that the callosities first arose as somatic adaptations and then became hereditary, we have to face the alternative that at some time in the history of the ostrich a change took place in its germ plasm of such a nature as to give rise to a directly adaptive character, altogether similar to what could be somatically acquired" (1920, p. 298). Significantly, Duerden's research was later used again by Waddington in the early 1950s, to illustrate his by then fully elaborated concept of the genetic assimilation of acquired characters. Waddington's choice of illustrative examples, therefore, suggested both a call for credence to be given to the inheritance of acquired characters, and positive support for the doctrine of recapitulation.

1.4. Waddington, De Beer and the Haeckelian Aetiology: Evidence for Recapitulation in Modern Synthesis Embryology.

There is a great deal of evidence, some of which has already been described in the biographical sketch of section 1.2.2., to suggest that Waddington saw his attempted synthesis between embryology, genetics, and evolution as providing the mechanism for Haeckelian recapitulation. Two years of palaeontological research in the systematics of fossil ammonites between 1926 and 1928 had, he maintained in later life, left him with the "deeply ingrained conviction" that the study of evolution was essentially the study of developmental systems (Waddington 1969, p.78). Unfortunately, as we have noted, Waddington misquoted Haeckel as he spoke of the close relationship between his developmentalist convictions, and the "old evolutionary synthesis" of the biogenetic law. It was the invertebrate morphologist Garstang, who very aptly reminded us in his 1922 critique of the biogenetic law: "It is the paleontologists who are the real defenders of the biogenetic stronghold. For them it is a faith that inspires to deeds" (Garstang 1922, p. 92).

Waddington quite openly carried the faith with him, in his move from the world of invertebrate palaeontological systematics, into the world of evolutionary genetics. Thus, in a somewhat unlikely chapter of his 1939 *Introduction to Modern Genetics*, Waddington discussed in detail the palaeontological evidence for palingenetic--that is, purely recapitulatory--trend and programme evolutionary processes, both in vertebrates and invertebrates. Whilst introducing the chapter, he explained that though much evidence for evolution exists, "facts which give some evidence for the genetic mechanisms involved are much fewer" (Waddington 1939, p. 241). For Waddington, the most important class of such facts was provided by "those fossils whose evolution can be followed in a continuous series through some considerable period of time [giving] conclusive evidence that evolutionary change can be by gradual transitions which, moreover, progress in a single direction" (ibid.). Waddington's main example of trend evolution was provided by the Lamellibranch genus *Gryphaea*.[55] Conceding that the apparently recapitulatory trends of spiral

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[55] Waddington's *Gryphaea* diagrams were reproduced directly from George (1933). Waddington's use of George's work is significant, since in his opening paragraph, George remarked acidly of Garstang's and de Beer's reversal of Haeckel's aetiology: "Such a consideration, if true, would not merely violate the cherished faith of complacent paleontologists : it would have a far more practical effect in shattering innumerable supposed phylogenies and lineages based on a Haeckelian foundation, and would entail the replacement of what is now considered to be in many instances (and ideally always) a genetic classification of fossils by a classification based upon comparative morphology, with its attendant dangers" (George 1933, p. 8). Similarly, in defence of a genuine palingenesis, against those who wished to completely relativise the Haeckelian doctrine because of frequent interpolations in development, George concluded: "These various divergences [principally caenogeneses, or Haeckel's exceptions to palingenesis, produced by heterochrony .(temporal displacement), heterotropy (spatial displacement), or larval adaptation (Gould 1977, p. 480)] from a complete recapitulation may result in ontogeny bearing little resemblance to phylogeny. But recapitulation is of too general occurrence to be explained merely by relegation to the incidental ; and although no satisfactory causal relationship between ontogeny and phylogeny has so far been determined, yet it would appear that when ontogeny departs from phylogeny, a profound recapitulation has been modified, rather than when ontogeny mirrors phylogeny, a superficial recapitulation has been imposed" (1933, p. 134).

growth and spiral tightening in these shells were in fact "heterogonic," rather than purely palingenetic, he continued: "Not all trends concern heterogonic growth. A very beautiful example may be taken from the chalk Micrasters, which were echinoderms rather like the modern heart urchin. We find several slow continuous processes of evolutionary change affecting different parts of the shell; the general outline, the position of the mouth and apical disc, the depth of the anterior groove and the cross-sectional shape, granulation and suturing of the umbulacral grooves all change slowly in definite directions. Many other examples could be given" (1939, p. 244).[56] Whilst noting that one of the most famous examples is "that of the reduction of toes in the horse," Waddington adds emphatically that it is marine invertebrates that "provide the most critical evidence" (ibid.). Though more sceptical of examples of supposed long-range or programme evolution, such as Hyatt's infamous fossil ammonites, Waddington nevertheless gave his complete support to the recapitulatory "small scale undoubted trends." Meanwhile, he cautioned, "the geneticist should note the alleged phenomenon of programme evolution as one which may require his attention; at present genetics has very little to say about evolution over such long periods of time" (p. 248).

What little genetics did have to say about orthogenetic and recapitulatory trends had, by 1930, been interpreted by de Beer to provide a viewpoint directly antagonistic to Waddington's. Furthermore, the precise examples chosen by de Beer in his 1930 book, and again in the second edition of 1940, as part of his rhetorical armoury against the biogenetic law, were chosen by Waddington as paradigm cases of the recapitulatory acceleration of adult characters, via the mechanism of genetic assimilation. In 1977, Gould described de Beer's 1930 *Embryology and Evolution* as being the "first in a series of remarkable books that established the synthetic theory of evolution." For Gould, then, de Beer "brought embryology into the developing orthodoxy by attacking Haeckel's theory of recapitulation as inconsistent with modern evolutionary theory" (Gould 1977, pp. 221-222). In this first book of the series, de Beer attempted his own synthesis between evolution, development and

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[56] Waddington's definition of heterogony, derived from Julian Huxley's 1932 *Problems of Relative Growth*, stated: "In heterogonic growth, two organs or parts of an animal grow at different rates (measured by increase relative to the mass which is already present). But their growth rates remain in a constant ratio to one another" (Waddington 1939, p. 243).

heredity. The foundations of this synthesis were supported by Garstang's crucial reversal of the Haeckelian aetiology: ontogeny becoming the cause and not the effect, of phylogeny. De Beer's synthesis also rested upon a developmental genetic, and specifically "rate-genetic" explanation for all the possible effects of heterochrony in phylogeny.[57] For de Beer, support for Garstang's aetiological reversal came from experimental embryology which showed us that, in de Beer's words, "Internal factors which were inherited from the parents are *not* sufficient to account for development" (1930, p. 13; author's emphasis). Thus, in his Chapter 2, he stated that the question being asked was how far heredity is responsible for the sequence of ontogenetic processes. Furthermore, de Beer added, " since phylogeny can only be related to ontogeny through heredity, we are testing the validity of Haeckel's statement that phylogeny is the mechanical cause of ontogeny" (ibid.).

For this aspect of his attack on recapitulationism, de Beer's own analysis required him to show that the "internal factors" of heredity--namely, Mendelian genes--were necessary, but by no means sufficient, for the production of adaptive structures during successive ontogenies. The work of his Oxford tutor, Goodrich (1924), and also of Child (1915), had already suggested this conclusion to de Beer. Thus he spoke of the organism's "exquisitely delicate adjustments," such as splinters of bone developing exactly where required, and tendon fibres lying along lines of strain, having to be made afresh during each ontogeny in response to external factors (1930, p. 15).[58] The student of genetics need never have worried over the question of a neo-Lamarckian explanation--which to the early new synthesis Weismannian

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[57] There is some doubt, in the historiography of embryology and the modern synthesis, over whether de Beer adhered to his Oxford colleague Julian Huxley's Mendelian notion of discrete "*rate genes*, or genes which determine that rate of a developmental process" (Huxley 1932, p. 229; author's emphasis): or to Goldschmidt's notion of genes as rate-determining enzyme activities, giving, in Goldschmidt's words, "an *explanation* of gene action via rates of developmental processes" (Goldschmidt 1938, pp. 52; emphasis added). Though Huxley and de Beer collaborated on much work in embryology, their divergence over the nature of the gene signalled, according to Churchill, "the diverging aspirations of the two Oxford-trained embryologists" (Churchill 1980, p. 118).

[58] De Beer also showed his epigenesist views in his 1934 *Experimental Embryology*, stating: "That a frog's egg should develop into no other animal than a frog is in part due to the presence of certain inherited factors which determine the first processes of the normal line of development characteristic of frogs. . . .On the other hand, it has been conclusively shown that all the factors of development are not present as such in the egg, but that they are constantly arising as a result of mutual interaction of parts, of the effects of previous factors, and of the relation of the organism to its environment" (de Beer 1934, p. 132).

would have required proof of "somatic induction" for the inheritance of acquired characters. On the contrary, these wondrous facts were for *Entwicklungsmechanik* to explain, since for de Beer, and from the point of view of the genetics of development, "all that is required is the transmission by internal factors of the capacity to react in these ways to new stimuli, which evoke one response after another" (p. 17). Hence characters were "due to responses and have to be made anew at each generation," internal factors being insufficient to development (p. 15). Furthermore, and as Garstang took pains to elaborate, the developmental powers invested in the zygote by the internal hereditary factors act autonomously within each separate ontogeny, hermetically sealed away from any phylogenetic causal agency. Ontogeny is then the necessary cause of phylogeny, and not vice versa.[59]

However, this line of attack led de Beer into an extreme position. It led to his demanding that external stimuli were directly necessary to all developmental processes in ontogeny. The consequences of de Beer's extreme anti-hereditarian view of development become clearer as he continues: "It is the very pressure in the tissues which causes the cells along the lines of stress to produce splinters of bone, and that is why these splinters are in the 'right place'; it is the very pull exerted on the tissues by the muscles which determines the production of the tendon with its fibres oriented along the lines of strain. . . . All that is required is the transmission by internal factors of the capacity to react in these ways to new stimuli which evoke one response after another" (pp. 16-17). De Beer clearly felt that experimental embryology vindicated this position. It supported his argument against a strong genetic determinism which, in his understanding, would be required for any post-Mendelian support of Haeckel's biogenetic law to be tenable. Hence he concluded:

> It is obvious on looking back over the subject matter of this chapter that ontogeny cannot be regarded simply as an extrapolation onto the future of a

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[59] De Beer's attack on strong recapitulationism, questioning how far heredity was responsible for the "sequence of processes which constitute ontogeny," and insisting that germinal factors were not sufficient to account for development, was thus also unwittingly an attack upon Weismann. As discussed above (footnote 27), Weismann's strong organ and structure recapitulationism, and doctrine of hard hereditary determinants, were intimately linked by his observations of strict hereditary transmission of characters down specific cell lines. (Churchill 1983, pp. 27-28). Furthermore, the Weismannian mechanism of heredity only allowed for the terminal addition of determinants during phylogeny, facilitating recapitulation. In Rasmussen's words, "For Weismann . . . ontogeny recapitulates phylogeny because evolution builds up an increasingly long series of physically interlocking ontogenetic actions (Rasmussen 1991, p. 59).

> chain of events which happened in the past. Each ontogeny is a fresh creation to which the past contributes only the internal factors by means of heredity. The action of the internal factors is to ensure that if the external factors are normal and do evoke any response in development and produce an animal at all, that animal will develop along the same lines as its parent. The internal factors are only a partial cause of ontogeny. (P. 18).

However, such a suggested impotence of the genes to produce morphological structures *ab initio* contradicted the embryological facts: namely, the definite appearance of such structures in ontogeny before any of the external stimuli described by de Beer could possibly have acted to produce them. Just where, to deal with one obvious example, might the fluid-borne foetus find "the very pressure to produce splinters of bone in the 'right' place?" In any case, de Beer's refutation of recapitulationism was still incomplete. Next he needed to refute any claims that the necessary external causes of ontogenetic development could become internalised. Thus, in de Beer's words, the Haeckelian aetiology can only stand "in old terminology, in so far as acquired characters can become inherited!" [sic] (p. 19). In de Beer's view, this second part of his argument was "all important." It was as significant to the dismantling of the neo-Lamarckian doctrine of the inheritance of acquired characters (for de Beer the source of the "old terminology"), as it was to discrediting Haeckelian recapitulation, and served to show how both doctrines stood or fell together (pp. 18-19). Thus, he continued, "the question--'are acquired characters inherited?'--has no meaning, and what the questioners really mean is--can external factors become internal" (p. 15). Now the old terminology of which de Beer spoke centred upon the nineteenth century pan-selectionist versus neo-Lamarckist debate over the inheritance of acquired characters, significantly narrowed down by Weismann himself to a debate over the issue of somatic induction. Hence, de Beer appeared to be requesting a shift away from the old (and, as the writings of Dendy and Delage and Goldsmith had shown, very ambiguous) debate over the existence of such a mechanism, to the simple question of the possibility of internalisation. In other words, de Beer appeared to want to address the broader question of whether or not the necessary external causes of ontogenetic development may become fully dependent upon, and thence become a functional part of, the internal hereditary architecture of the organism (p. 18; see also section 5.1.). And yet, de Beer immediately reverted to the old terminology in his critique, devoting much of his chapter on ontogeny to trying to disprove the existence of somatic induction. Thus somatic induction in his words would necessarily, if it existed, consist in "a change in the internal factors produced by a change in the structure of the body which latter change was itself produced by external factors." It was precisely this chain of causes which, de Beer asserted in strict neo-Weismannian fashion, "constitute the kernel of the Lamarckian point of view" (p. 19).

De Beer therefore clearly saw that the only way Garstang's deductive argument against the biogenetic law could be refuted was if the external factors, acting within ancestral ontogenies, could play a direct causal role in establishing the internal factors present within descendant ontogenies (p. 19). Once again, such a causal connection could only be conceived by invoking discredited neo-Lamarckian inheritance; that is, in 1930s terms, somatic induction. Assured of the inadmissibility of this neo-Lamarckist mechanism, de Beer clearly perceived his position to be completely unassailable. Hence within a section of his book concerned with supposedly rare cases of the recapitulation of structures, he dismissed such purported examples as, in his view, merely apparent cases of the inheritance and acceleration of somatic adaptations. Such cases, in de Beer's words, served only in "illustrating the care which is required in interpreting such evidence" (1930, p. 85). He discussed Kukenthal's discovery that "in the early unborn embryo of the Dugong the grinding teeth have unworn cusps, as one would expect. But in a later embryo, still unborn, [Kukenthal] found that the teeth showed flat surfaces, as if they had been worn down by friction" (ibid.). Similarly, Duerden's studies of Ostrich development were presented, showing that hatchlings "possess a number of callosities already developed" in functional positions (p. 87). Such apparent cases of Lamarckian somatic induction provided considerable rhetorical support for de Beer's deductive argument, when in the same section he challenged the reader: "Can anyone suppose that the friction in the adult has anything to do with the origin of the internal factor which controls the resorption of the tooth in the unborn embryo?" (ibid.).

In his 1942 paper to *Nature*, "Canalization and the inheritance of acquired characters," Waddington apparently accepted de Beer's challenge. That challenge had been reissued verbatim only two years previously in de Beer's 1940 second edition--now retitled *Embryos and Ancestors*, in line with de Beer's vision of embryology's new subordinate role in evolutionary causation (de Beer 1938, 1940, p. 76; see section 0.2.). Waddington did so by once again using Duerden's Ostrich data as illustration of "the supersession of an environmental stimulus by a genetic one," as he had in *Organisers and Genes* in 1940 (Waddington 1942, p. 565). This was the first detailed explication of his synthetic evolution theory, developed as it had been from the Strangeways evocator research in chemical embryology, and translated into developmental genetic and selectionist terms. Waddington's starting point was the notion, central to both his and de Beer's syntheses, that in Waddington's terminology, "the capacity to respond to an external stimulus by some developmental reaction such as formation of a callosity, must itself be under genetic control" (1942, p. 563). Waddington's second assumption was that "developmental reactions are in general canalized." That was to say, he explained, "they are adjusted so as to bring about one definite end-result regardless of minor variations in conditions during the course of the reaction" (ibid.). Thirdly, canalisation of an adaptive character can be increased by selection for its optimum level of development, "irrespective of the exact extent of the stimulus which it has met in its early life" (p. 565). Fourthly, selection for ever deeper canalisation of characters reduces the action of external stimulus to a switch, ensuring regular production of the optimum response. Lastly, and crucially with respect to the question phrased within de Beer's "new terminology," the external stimulus may eventually be superseded by the internal stimulus of an epigenetic factor--which in the case of an evocator substance, may in fact be a primary gene product. Hence the process was later called "genetic assimilation."[60] Also, and importantly for the question of the evolutionary or ultimate causes of recapitulation, Waddington stated that such a gene must always act precociously in ontogeny, otherwise it could have no appreciable selective advantage.[61] Thus the

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[60] It is important, given the anti-recapitulationist context of de Beer's challenge, that Waddington's superseding stimulus is understood to be acting at some point along the same developmental pathway towards callus formation as the original external stimulus is acting (cf. Waddington's discussions of reacting tissue specificity, and the possibility of multiple points of entry into the developmental pathway leading to vertebrate neural development; section 1.3.1.). This is also important for understanding later criticisms, made by Waddington, of various theories accepted by supporters of the modern synthetic orthodoxy, and purported to be empirically equivalent to genetic assimilation. These included (the first controversially) the classical organic selection of Lloyd Morgan; all forms of Western and Soviet neo-organic selectionism, including Simpson's 'Baldwin effect,' Medawar's genocopy selection, and (also controversially) Schmalhausen's stabilising selection, all of which will be discussed in my chapters 2, 3, and 4.

[61] This last aspect of Waddington's theory itself recapitulated, as discussed in section 1.2.3., many selectionist arguments for acceleration; for example J. A. Thomson's (1925), F. M. Balfour's

notion, in the morphologist Goodrich's words, that "no single character is completely acquired or due to inheritance alone," was put to work in precisely antagonistic directions, with respect to the recapitulation debate, by Waddington and de Beer (Goodrich 1924, p.61).

Regarding any public interaction over the status of embryology within the modern synthesis--especially over its diminished role within the mechanism of adaptive evolution--there was a remarkable silence from each regarding the other's views, at least prior to 1958. Then de Beer responded negatively to Waddington for the first time, in the third edition of his renamed *Embryos and Ancestors*. This belated critique of Waddington's work, a full 16 years after its first publication, may well have been provoked by a paper of Waddington's in 1953 in which he copied de Beer's use of Duerden's and Kukenthal's researches in combination. Waddington clearly alluded to de Beer's writings by reproducing the very same diagram of embryonic Dugong's teeth used by de Beer in every edition of his book ever since 1930 (Waddington 1953d).[62] The negative response from de Beer towards Waddington's synthesis is very probably what prompted Jane Oppenheimer's remarks, when she wrote in 1959 after publication of the final edition of *Embryos and Ancestors*: "De Beer's study does not however take full cognizance of the contributions of modern developmental genetics toward the support or the modification of the old recapitulation theory, and it is to be hoped that soon a new synthesis which goes beyond de Beer's will incorporate this relevant new material" (Oppenheimer 1959, p. 207).

It is evident that in the final edition of 1958, *Embryos and Ancestors* underwent a comprehensive restructuring, specifically to cope with Waddington's response to the 1930 and 1940 challenges over the internalisation of the external causes of development. Kukenthal's and Duerden's researches were brought forward, in truly recapitulatory fashion, from their first appearance in a later chapter on acceleration

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(1880), and most notably Fritz Muller's (1864). It is clearly echoed in the modern synthesis writer Stebbins' theory, of the "increasing precocity of gene action," so favoured by Gould as a genetic explanation of recapitulation.

[62] Waddington remarked, with regard to Kukenthal's observations of embryonic Dugong's teeth: "It certainly seems very far-fetched to attempt to explain such phenomena without bringing in the fact that the environment might be expected to produce similar results" (Waddington 1953d, p. 136).

into an earlier chapter on ontogeny. De Beer apparently hoped that Waddington's interpretations could be thwarted by a theoretical reinterpretation of the genetic assimilation mechanism. Thus he represented Waddington's notion as the production of a "genocopy," by the orthodox neo-Darwinian processes of gene mutation plus natural selection.[63] Medawar's 1951 genocopy concept, appeared to be nothing other than the second stage of palaeontologist G. G. Simpson's "Baldwin effect" by another name; the latter being a suggested adaptive evolutionary mechanism which Waddington vehemently challenged in 1953.

This manoeuvre of identifying Waddington's and Medawar's concepts performed several important functions in defence of de Beer's synthesis. Firstly, it reinforced the Mendelian genetic and strong selectionist mechanism of the then long established synthetic theory, and maintained its separation from the causal analysis of individual development--the latter being properly studied within modern experimental embryology. Secondly, it upheld strictly neo-Darwinian heredity in adaptive evolution, with its rigid separation of Weismannian "somatogenic" and "blastogenic" characters, in the face of any arguments for neo-Lamarckian heredity (Dendy 1923, p. 201; see section 5.1.). Lastly, it protected the anti-Haeckelian phylogenetic aetiology developed by Garstang in 1922, by denying the internalisation of external factors, and thereby denying the existence of any phylogenetic causes in ontogeny.

Thus the exclusion of embryology from any direct causal role in the synthetic theory's mechanism of adaptive evolution--a crucially important departure of the new synthesis from the old synthesis--was apparently secured. Far from the hereditary fixation and ontogenetic acceleration of adaptive modifications having any non-

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[63] Medawar's concept of the "genocopy," provides a perfect illustration of the classic Mendelian gene selectionists' reply to the neo-Lamarckian's suggested mechanisms for the hereditary fixation of adaptive modifications: that is, for the production of Medawar's "Class B", and Waddington's "pseudo-exogenous" adaptations. Thus Medawar stated: "It is in Class B adaptations that the Lamarckists claim a proprietary interest, for with Class B adaptations there is an overwhelmingly strong case for supposing that the functional change anticipated the genetical -- the prerequisite of Lamarckist theory. . . . So much can be readily admitted; but in the classical Lamarckist argument, it is then said to follow that a modification acquired by the habit of use in a series of individual lifetimes becomes directly imprinted upon the genetic mechanism. In a certain sense, of course, the Darwinist admits that it does: natural selection establishes in the population what (by analogy with phenocopy) might be called a *genocopy*, genetic imitation, of the acquired phenotypic change. There is not the slightest reason why more or less faithful genocopies should not appear among the other genetic variants, or, conversely, why genetic variation, though random in its origin, should not produce a pre-adaptive change" (Medawar 1951, p. 16).

orthodox causes, as far as de Beer was concerned: "We can say no more and no less about the origin of genocopies than we can about the cause of any other hereditary variations: they are due to mutations and recombinations of genes, preserved by natural selection" (de Beer 1958, p. 20).[64]

At this landmark in the history of biology, namely, the approaching centenary of the publication of *The Origin of Species*, de Beer was clearly very keen to re-establish his and Oxford Zoology's neo-Darwinian credentials. Describing genetic assimilation as essentially identical to the fully orthodox process of genocopying clearly forwarded this cause, as well as providing support for his anti-recapitulationism. Somewhat incongruously de Beer was able, at least by 1958, to accept many of Waddington's concepts: for example canalising selection, and the superseding of external stimuli in the production of ontogenetic structures by (randomly produced) internal genetic ones. Nevertheless, although these notions were central to Waddington's understanding of the genetic assimilation theory, de Beer insisted that such a transition in the causes of development was still fully explained by the random production of genocopies: that is, by the known processes of genetic mutation plus natural selection, fully accounted for within synthetic neo-Darwinism.

De Beer's strenuous efforts, over a period of twenty eight years, to undermine recapitulationism fully explain his dismissive treatment of Waddington's synthetic theory, and any direct causal role for embryology within the neo-Darwinian

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[64] In 1944, Holmes provided an intriguing selectionist commentary on de Beer's anti-Lamarckian and anti-Haeckelian arguments against external factors becoming phylogenetic causes of evolutionary change. Referring to the 1940 second edition of *Embryos and Ancestors*, Holmes observed in puzzlement: "De Beer concedes that modifications due to external factors might affect ontogeny if acquired characters are inherited. But since this is regarded as a very doubtful hypothesis, 'it cannot be stated that phylogeny plays any part in ontogeny at all'. If, however, external factors influence the kinds of variations that survive, as they demonstrably do, and if these variations influence the kinds of ontogenies that occur in the offspring, I cannot see, so far as our problem is concerned, that it makes any difference whether these conditions operate through the transmission of acquired characters, or by means of natural selection. In either case the events that form a part of the phylogenetic history play a role in shaping the course of ontogeny. In fact, this conclusion is inevitable if we accord to phylogeny any sort of status as a real series of events." (Holmes 1944, p. 329). In other words, de Beer's criteria for rejecting phylogenetic causes in ontogeny are far too strong. Neo-Lamarckian heredity cannot exhaust the causal connections between external factors, and the internal factors present in descendent ontogenies; for example, internal factors are themselves acquired from the previous generation and, the external factor of natural selection permitting, will necessarily be inherited by descendent generations.

mechanism of adaptive evolution. Churchill reminds us that experimental embryology for de Beer was purely (in Mayr's proximate sense of the term) a "cause-directed field which explained the mechanics, physiology, and chemistry of form," to be contrasted with the study of phylogeny, which was "a historical and descriptive endeavour that produced lineages" (Churchill 1980, p. 120).[65] Haeckel's great mistake had lain in trying to provide, in Mayr's alternate sense, an ultimate causational explanation of adaptive evolution by synthesising two domains of science which, in de Beer's eyes at least, were entirely separate in causal terms.

Finally, we may see that this entire thesis of de Beer's was made unmistakably clear, in the closing paragraph of his 1938 paper in honour of his teacher, E. S. Goodrich. Thus de Beer proclaimed:

> The events of ontogeny may be said to bear on the problem of evolution in so far as phylogeny is the result of successive ontogenies. But even a complete knowledge of the causes determining the succession of form changes in ontogeny would still fail to provide an explanation of why ontogenies themselves have been modified so as to give evolution. Similarly, a complete knowledge of the phylogenetic history of an organism does not explain the causal connexions between the events of its ontogeny. As Huxley has pointed out, a living organism must be studied from two distinct aspects. One of these is the causal-analytic aspect which is so fruitfully applicable to ontogeny. The other is the historical descriptive aspect which is unravelling lines of phylogeny with ever-increasing precision. Each of these aspects may make suggestions concerning the possible significance of events seen under the other, but does not explain or translate them into similar terms. (De Beer 1938, pp. 76-77).

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[65] De Beer was a consummate embryologist, appreciating all the branches of this complex set of disciplines and research traditions; morphological descriptive, experimental, and chemical. Yet like T. H. Morgan, his was a synthesis of coexistence rather than logical entailment and causal interdependence. Viktor Hamburger tells us of the heuristic isolation of experimental embryology, genetics, and evolution theory at the time of de Beer's writings on ontogeny and phylogeny: "By the 1920s and 1930s experimental embryology and genetics both had accomplished a major breakthrough, experimental embryology through the achievements of Harrison and Spemann and their schools, and genetics through the Morgan school. Both fields were deeply absorbed in their own problems and took little notice of each other. The embryologists were involved in the study of epigenetic mechanisms, such as induction, gradient fields, and morphogenetic movements. Evolutionary considerations turned up rarely" (Hamburger 1980, p. 99).

Chapter 2.

Conflicting Explanations of Adaptive Evolutionary Change. Neo-Organic Selectionism and the Adaptationist Dilemma.

> There seem to be three major fields in which further inquiry is called for. One is the problem of adaptation. Is it really sufficient to suppose that the extraordinarily precise fitting of an animal into it ecological niche is due solely to the selection of random variations ? We know of many cases in which the environment of a particular locality--for instance a mountain range or a swamp--will produce in individuals from some other region non-hereditary modifications which are strikingly similar to aberrant forms which in the local population have become genetically determined. Are we to suppose that such parallelism is completely beside the point, and that evolution of a local genetically fixed ecotype has been based on mutations which have occurred at random and are thus quite unconnected with the direct developmental effects of the environment ?[1]
>
> C. H. Waddington.

2.1. Adaptation, Adaptive Modification, and the Modern Evolutionary Synthesis.

There existed a considerable amount of disagreement, and some considerable confusion, amongst the leading proponents of the modern synthetic theory over the significance to be accorded to processes of adaptive modification in organisms. This state of confusion can best be investigated in relation to the suspicions, of some evolutionists, that the whole concept of adaptation held grave difficulty for evolutionary biology. In the 1937 first edition and again in the second edition of *Genetics and the Origin of Species*, Theodosious Dobzhansky made the point within an historical review of natural selection: "In its essence, the theory of natural selection is primarily an attempt to give an account of the probable mechanism of the origin of the adaptations of the organisms to their environment. . . . Some modern biologists seem to believe that the word 'adaptation' has teleological connotations and should therefore be expunged from the scientists lexicon" (Dobzhansky 1937, p. 150; 1941, p. 187). Dobzhansky "emphatically disagreed" with this view, believing

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[1] Waddington 1953c, pp. 187-188.

the fact that adaptations exist "so evident as to be almost a truism." He concluded, with apparent indignation, that a biologist "has no right to close his eyes to the fact that the precarious balance between a living being and its environment must be preserved by some mechanism or mechanisms if life is to endure. Furthermore, he added: "No coherent attempts to account for the origin of adaptations other than the theory of natural selection and the theory of the inheritance of acquired characteristics have ever been proposed. Whether or not these theories are adequate for the purpose just stated is a real issue" (ibid.).[2]

In his 1942 classic *Evolution, The Modern Synthesis*, Julian Huxley also discussed the problem. In Huxley's view, it had for some time been the fashion among certain schools of biological thought, "to decry the study, or even to deny the fact of, adaptation." Huxley saw that its "alleged teleological flavour is supposed to debar it from orthodox scientific consideration, and its study is assumed to prevent the biologist from paying attention to the proper business of mechanistic analysis." But to Huxley, both these strictures were unjustified, for "the teleology of adaptation is pseudo-teleology," and adaptations were simply biological facts that it was the business of biologists to study (Huxley 1942, p. 412).[3]

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[2] Whilst Dobzhansky fought the strong selectionism versus neo-Lamarckism issue throughout the 1940s, Fisher rallied against the twin enemies of saltationism and orthogenesis in the 1950s. Hence, in the context of discussing the difficulties of imagining the intermediate stages in the evolution of the bat's wing, Fisher stated: "In considering such a series of stages it becomes apparent that it is the theory of evolution by continuous adaptation, amid the extraordinary diversity of the expedients which are in fact useful to different animals, which makes such transitions possible. What would be incredible in such a case would be a non-adaptive orthogenetic urge leading straight from the fore-limb of an insectivore to the wing of a bat through some thousands of generations of intermediate types encumbered with useless appendages; or, to allude to a rival absurdity, the appearance of the bat's wing by a *saltation* among a litter of primitive insectivorous mammals" (Fisher 1958, pp. 89-90; author's emphasis).

[3] Huxley's particularly marked adaptationism is evident in his synthesis writings of the early 1950s. Thus in *Evolution in Action*, he stated: "To take only animals, there are species which feed entirely on flesh, on wood, on excrement, on nectar, on feathers, on the contents of others' intestines, on one particular kind of fruit or leaf. And each and every species is adapted, often in the most astonishing fashion, to its environment and its way of life. . . . There is no need to multiply examples: every animal and plant is from one aspect an organized bundle of adaptations--of structure, physiology and behaviour; and the organization of the whole bundle is itself an adaptation" (1953, p. 18). Again, in a paper first published in 1954 entitled "The evolutionary process," Huxley wrote: "In the first place, a single mechanism underlies the whole of organic evolution--Darwinian natural selection acting on the genetic mechanism. . . . In the second place, all evolution takes place in relation to the environment, including the biological environment and its changes. There is a universal process of adaptation, though this

Simpson, however, was apparently less than fully supportive of a pan-adaptationist approach to evolution in his 1944 synthesis work *Tempo and Mode in Evolution*. Thus, in discussing his view that evolution of higher taxa occurs in the phyletic mode; that is, by the progressive transformation of populations in lineages, and not by splitting of those populations, Simpson wrote: "It is within this [phyletic] mode that evolution tends to be most strictly adaptive. Hence the overgeneralization, e.g. of Osborn, that all evolution is adaptive" (Simpson 1944, p. 203; in Gould 1980, p. 162). Nevertheless, Simpson in the 1940s was in complete support of adaptation as a universal principle, and dismissive of misgivings over teleology. Hence earlier in the same work he had declared: "It is a truism that all organisms can live under the conditions under which they do live and that they could not live under other sets of conditions that exist. To this degree, at least, and without any teleological implications, adaptation is universal" (Simpson 1944, p. 180).[4]

As Bowler reminds us, it was the new breed of laboratory biologists, many of them ardent and outspoken experimentalists, who in the 1920s and 1930s "enabled natural selection to re-emerge as a viable mechanism of adaptive evolution" (Bowler 1989, p. 308). In 1943, Mather had made a similar but somewhat broader observation, in his discussions of the emerging study of genetic interaction in the 1920s and 1930s, and its significance for evolutionary theory in the 1940s. Referring particularly to the experimental work of Bridges (1922), and Muller (1932), Mather stated: "This change of ideas concerning the relation between gene and expression has had a profound effect on the attitude of geneticists towards evolutionary change,

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may take very various forms, from material adjustment of the parts of the gene-complex to the development of elaborate organs serving particular biological ends" (Huxley 1958, p. 2).

[4] In fact, Simpson identified a twin role for natural selection in the production of adaptive changes: "Thus natural selection usually operates in favor either of increased adaptation to a given way of life, organism-environment integration, or of such change as will bring about adaptation to another, accessible way of life. Natural selection thus orients evolutionary change in the direction of one or another of these two sorts of adaptation" (Simpson 1950, pp. 220-221). Thus the strength of adaptationism within the later synthesis is further illustrated by support for a notion of pre-emptive selection for adaptive structures. Simpson even claimed in 1953 that such "preadaptation" was "practically universal." He added: "As prospective adaptation, it is to be recognised as a general rather than a special feature of the adaptive process" (Simpson 1953, p. 189). In his 1958 discussion of multiple evolutionary pathways, ornithologist W. J. Bock concurred with Simpson's beliefs, saying: "My feeling is that the latter view is correct; in fact it would be reasonable to postulate that the evolution of most, if not all, new structures involved old structures which were preadapted for the new function" (Bock 1958, p. 200).

as recent writings have shown. Ford, Muller and Huxley have especially developed the application of this new outlook to the better understanding of adaptation and evolution. It is not without significance that the rise of the idea of the dependent action of genes has progressed side by side with a return to Darwinism and the abandonment of the mutation theory" (Mather 1943a, 68).[5] Yet before 1920, laboratory geneticists had been convinced that mutation was the only source of novel organismic characters in evolution. As Bowler again points out, "laboratory biologists were only too willing to ignore the pressures that might affect an organism living in the wild state." Thus adaptation was played down, as they focused upon processes such as mutation which could be studied in the laboratory (Bowler 1989, p. 308).[6]

2.1.1. Anti-Adaptationism from the Experimentalist Perspective: The Reactionary Views of Lancelot Hogben.

Nevertheless it was clear, at least to Julian Huxley, that the negative attitude of many experimentalists toward adaptationism in the early century, had lingered on too long into the later synthesis period. Hence in 1940, Huxley felt able to make the decidedly pointed observation that "There still is a widespread reluctance, especially among some of the younger experimental biologists, to recognise the prevalence of adaptation and the power of selection. This is doubtless in large part a reaction against the facile arm-chair reasoning of a certain school of earlier evolutionists. It is also, however, due to a failure to come to grips with the general principles of the subject" (Huxley 1940, p. 2). In contrast to this swingeing criticism of the mutationist school in evolutionary genetics (and, apparently, the neo-Darwinian school of biometricians) it was the population geneticists, at the heart of the modern

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[5] Mather went on to laud Waddington's elaboration of the consequences of the new genetics of interactions, in that they "permitted a more coordinated response of the organism to its environment" in the production and selection of adaptive modifications to the phenotype. (See my section 3.2. for the interaction between Mather and Waddington over Waddington's concept of canalisation. See also section 3.2. footnote 39 for a discussion of the relationship of Wright's work on genetic drift and interaction systems, to Waddington's claims for support for canalisation in the genetics literature of the 1930s).

[6] See also Mayr (1980), and my Introduction, on early twentieth century neo-Mendelian macro-mutationism as a mechanism of evolutionary change, in competition with Darwinian selectionism and neo-Lamarckism.

synthetic theory, who were responsible for underwriting its adaptationist credentials. Thus Huxley immediately continued: "Men like Fisher (1930), Haldane (1932), and Sewall Wright (1931, 1939) have recently done great service by pointing out that selection may take many different forms and achieve very different results according to the conditions under which it operates" (ibid.).

However, the continuing concerns regarding adaptation, still felt by some within the growing experimentalists' ranks, were forcefully and eloquently represented by the staunch experimentalist, population geneticist and biological polymath Lancelot Hogben. In 1932, Hogben had collaborated with the Edinburgh geneticist Crew (the force behind the institution of the Edinburgh Chair of Genetics in 1928, which Crew himself occupied), population geneticist and colleague J. B. S. Haldane (who held the Genetics Chair at University College London), and Julian Huxley, in establishing a Society for Experimental Biology. Werskey tells us that "the SEB's founders were determined to make their discipline a more exacting, hard edged and experimental one; compared to the more descriptive, taxonomic and historical approaches of the pre-war era" (Werskey 1988, p. 102). Also involved in the 1930s with the reductionist Biotheoretical Gathering, Hogben is believed by Werskey to be "firmly in the vanguard of those who would ultimately change the direction of British biology."[7] Werskey, in comparing Hogben's essays to those of Haldane, describes them as "markedly more hard hitting, closely argued, and serious" (ibid.). In just such an essay entitled "The concept of adaptation," Hogben, within the context of the vitalist-mechanist debate, vividly described the "outright interdisciplinary confusion" that existed over the concept of adaptation itself. To the physiologist, he argued, the term refers to "the self-regulating characteristic of the body." However, "the evolutionary biologist--who today is a physiologist in the broader sense of the term--is usually thinking of 'a change in the structure, and by implication also in the habits of an animal which render it better fitted' for life" (Hogben 1930, p. 104). Further

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[7] Provine shares Werskey's opinion over the importance of Hogben, and writes: "Sewall Wright and R. A. Fisher, together with J. B. S. Haldane, Lancelot Hogben, Sergei Chetverikov, and other quantitative evolutionists, have had an important impact upon modern evolutionary biology. They introduced the quantitative analysis and modelling of the evolutionary process" (Provine 1986, p. 232). However, Provine's statement in the next sentence that: "All the mathematical population geneticists agreed upon . . . the immense power of selection to change gene frequencies in a surprising small number of generations," does not sit well with Hogben's obviously vehement anti-adaptationism (ibid.).

on, he stated that "of the two ways in which the word adaptation is used in biological discussion, that which implies the notion of self-regulation is most fundamental" (ibid.).

Hogben's materialist-experimentalist agenda led him almost inevitably to indict evolutionary morphology over the abuse of adaptation as a concept. Hence, he asserted: "Adaptation in the morphological sense really includes two ideas which to some extent coalesce, and are therefore all the more readily confused. At times the word implies nothing more than viability." This sense of the term was, for Hogben, simply a restatement of the obvious evolutionary requirement for survival in a given environment. Yet on other occasions, as he explained, and as Julian Huxley later exemplified in his writings, "adaptation is extended to mean an essential unity in every detail of the structure of an organism." This he thought to be "a mischievous implication which, as will be seen later, has hindered a clear conception of the evolutionary process" (1932, p. 112).[8] Such extreme adaptationism, for a geneticist writing at the inception of the new synthesis, was an aberration inherited from nineteenth century evolutionary morphologists who, in Hogben's words, "regarded adaptation as a principle, like the principle of the conservation of matter, one of universal validity" (p. 116). The "morphological" theories of Darwin and Lamarck were, in Hogben's terms, equally in error by having "assumed that the differences between species, in the traditional Linnaean sense, are mainly utilitarian." Rather than accepting these adaptationist dogmas, we should now realise, Hogben suggested, that "from the modern standpoint, analysis of the species problem does not demand a recognition that specific differences are even in the main utilitarian."[9]

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[8] Burian claims that confusion over Darwin's notion of relative adaptiveness was also propagated by the synthetic theory: "Darwin first employed two distinct notions of 'absolute' or 'perfect' adaptedness . . . in the period from 1838-1854 and then, only after considerable difficulty, arrived at a version of the notion of relative adaptedness employed in the *Origin* sometime in 1857. . . . Ospovat is surely right that the notion of relative adaptedness developed by Darwin is of crucial importance to evolutionary theory" (Burian 1983, p. 288). However, Burian adds, the synthetic theory "obscured the importance" of Darwin's notions by conflating them with "two quite un-Darwinian notions, both of which pass under the label of 'Darwinian fitness'" (1983, p. 289).

[9] An intermediate position between Darwin's and Haeckel's extreme adaptationism, and Hogben's extreme anti-adaptationism (and in this context, anti-utilitarianism) may be represented by the views of T. H. Morgan in the Preface to his 1908 *Evolution and Adaptation*. Thus Morgan stated, in partial support of those who criticised the Darwinian doctrine: "But let us not, therefore, too hastily conclude that Darwin's theory is without value in relation to one side of

Because of the vast subject area involved, Hogben conceded that a discussion of the Lamarckian and Darwinian theories must be postponed to a later essay, adding bluntly that "here it is significant to point out that both, more particularly the latter, had a peculiarly sterilising influence on the growth of experimental biology" (pp. 116-117). Extending his attack to the evils of post-Darwinian evolutionary morphology, he exclaimed: "Obsessed with the principle of universal adaptation which natural selection had secularised, Zoology, from the publication of the *Origin of Species* to the rediscovery of Mendel's laws, wandered for forty years in a wilderness of phylogenetic speculation" (p. 117). Four pages later, speculation reached a crescendo within the biogenetic law as Hogben proposed, with evident disgust, that the "idea that a problem can be solved by invoking the principle of adaptation assumes its most grotesque form in Haeckel's discussion of recapitulation" (p. 121). Thus for Hogben, Haeckel's *Biogenetische Grundgesetz* fully epitomised the adaptationists' dilemma, and showed "the way in which the modern geneticist offers a striking contrast to the attitude of Haeckel and a generation of zoologists unduly preoccupied with the concept of adaptation" (p. 122).

2.2. Experimental Embryology and Adaptive Evolution: Gavin de Beer's New Synthesis Embryology and the Adaptationists' Dilemma.

Reflecting upon the geneticist Hogben's vehemently anti-adaptationist (and especially anti-morphological and anti-Haeckelian) writings from the early synthesis period, there are significant parallels with the contemporaneous views of Oxford embryologist and neo-Darwinist Gavin de Beer. De Beer obviously shared Hogben's anti-Haeckelian sentiments--as we have seen from the extent of de Beer's efforts to

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the problem of adaptation; for, while we can profitably reject, as I believe, much of the theory of natural selection, and more especially the idea that adaptations have arisen because of their usefulness, yet the fact that living things must be adapted more or less well to their environment in order to remain in existence may, after all, account for the widespread *occurrence* of adaptation in animals and plants" (Morgan 1908, p. ix). In other words, and as Allen explains, "To Morgan natural selection was only a negative factor in the origin of adaptive characters; it could select out the unfit but could not generate the new variations from which new adaptations could be derived" (Allen 1980, p. 363). For Morgan's consequent rejection of the evolutionary significance of adaptive modification (and hence of organic selection), see my Section 2.3.4.

discredit both the biogenetic law, and Waddington's subsequent attempts to causally reconnect phylogeny to ontogeny. Furthermore, de Beer's experimentalist approach viewed the whole field of embryology, including Needham's biochemical researches, as a unified front against Hogben's hated morphological explanations of evolutionary change (Churchill 1980, p. 120).

Yet it is equally obvious that de Beer most emphatically did not share Hogben's anti-Darwinian sentiments. As Waisbren has recently observed, de Beer, like Goodrich and Huxley, frequently used morphological evidences to support mechanisms of evolution in keeping with synthetic neo-Darwinian principles, "even though not all his published works focused directly on these mechanisms" (Waisbren 1988, p. 324). For instance, Waisbren continues, de Beer's "*Development of the Vertebrate Skull* [1927] had little information on natural selection. *Vertebrate Zoology* [1959], on the other hand, is filled with information on mechanisms. The last chapter of the volume, entitled 'Evolutionary morphology,' details how selection pressures have changed the morphology of chordates, amphibia, reptiles, birds, mammals, primates, and man. . . . Thus, de Beer both supported natural selection and defended its gradualness" (ibid.). Consequently, Waisbren argues, whilst Huxley had a broad interest in very many disciplines that *applied* morphology, "de Beer kept his focus mostly on morphology and its adaptationist significance" (Waisbren 1988, p. 329).

Waisbren's reply to Coleman's view that morphology was of little significance to the selectionist modern synthesis, also serves to highlight fact that at no place in de Beer's influential *Embryology and Evolution* series of books are the terms natural selection or adaptation to be found. This might seem strange from the work of a staunch neo-Darwinian ostensibly attempting a new synthesis of embryology and evolution to replace the old biogenetic law. Yet unlike Waddington de Beer did not see modern embryology, in any direct causal sense, as contributing to Dobzhansky's selectionist "mechanisms of the origin of adaptations of organisms." Rather, for de Beer, experimental embryology simply dealt with the mechanics, physiology, and chemistry of ontogeny in isolation from selection (Churchill 1980, p. 120). In terms of Mayr's categories of causation, experimental embryology for de Beer was concerned only with the proximate causes that unfold within each separate ontogeny.

It was not concerned with ultimate (that is, adaptationist) causes, and most emphatically not with any phylogenetic ones.

Thus in the early 1930s, de Beer was generally viewed to have finally and successfully discredited Haeckel's "old synthesis." As described in section 1.4., for supporters of the modern synthetic theory, the natural selection of random hereditary variations henceforth provided the sufficient causal mechanism for adaptive evolution. De Beer's work cleared the way for the later strong selectionist hardening of the synthetic theory (Gould 1980, 1983). By the time this of this hardening of the synthesis in the early 1940s, questions of development were simply left aside as environmentally contingent processes, entirely peripheral to forwarding the new and precisely hereditarian study of adaptive evolutionary change. Hence evolution, in Dobzhansky's view, was fully reducible to the quantitative study of changes in Mendelian gene frequencies.[10] The strong selectionists of the 1940s and 1950s therefore viewed anything that augured a return to outdated ideas, such as Lamarckian concepts of heredity, and specifically neo-Lamarckian inheritance mechanisms such as somatic induction, as threatening the return of morphological and developmentalist approaches to adaptive evolution.

Nevertheless, for some eminent later modern synthesis writers, the neo-Darwinian versus neo-Lamarckian debate over the true mechanism of evolutionary adaptation (Dobzhansky's "real issue"), was still the most important one. As the staunch progressivist and adaptationist Huxley optimistically wrote in 1942: "Thus the study of adaptation seems destined to take a new turn. The first stage concerned itself with the fact of adaptation--is such-and-such character an adaptation, or is it not? In the next stage, biologists were interested in the mechanism of adaptation--do adaptations arise through natural selection, by Lamarckian means, or in what other way ? Today the emphasis is on the analysis of adaptation itself" (Huxley 1942, p. 449). Yet although de Beer's genetically informed embryological study of the modes of ontogenetic variation may, for many selectionists, have facilitated graduation to Huxley's stage three, many others seemed permanently bogged down on the battlefields of stage two, well into the late 1950s and early 1960s. The cause for

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[10] In 1937, Dobzhansky famously asserted: "Since evolution is a change in the genetic composition of populations, the mechanisms of evolution constitute problems of population genetics" (Dobzhansky 1937, pp. 11-12).

their long delay was undoubtedly the entrenchment of some neo-Darwinians, clearly less enamoured of the synthetic theory's hardening selectionism, over the evolutionary significance of adaptive modifications to the phenotype.

2.3. The Evolutionary Significance of Adaptive Modification: Organic Selection, or the "Baldwin Effect?"

In June 1953, the journal *Evolution* published a detailed review paper by new synthesis palaeontologist G. G. Simpson entitled simply "The Baldwin effect." Simpson described, in the opening paragraph, the essence of the evolutionary phenomenon to be discussed: "Characters individually acquired by members of a group of organisms may eventually, under the influence of selection, be reinforced or replaced by similar hereditary characters" (Simpson 1953a, p. 110). Simpson's informative review attempted an assessment, in the light of the modern synthesis, of the experimental and theoretical writings of workers concerned with the evolutionary significance of adaptive modification in organisms. The first full and clear exposition of what Simpson believed to be the core phenomenon was J. M. Baldwin's notion of "organic selection."

The questions of authorship and priority surrounding the original concept of organic selection are quite complex. Huxley in 1942, for example, quoted Baldwin as the first to have published the idea in his two-part 1896 paper "A new factor in evolution" (Baldwin 1896, 441-451; 536-553).[11] This theoretical summary of Baldwin's was then followed in 1897 by H. F. Osborn's paper, "The limits of organic

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[11] In this summary paper, Baldwin discussed the terms "ontogenetic variation," and "phylogenetic variation," as corresponding to Lloyd Morgan's suggested terms "modification" and "variation" respectively (1896, p. 442). Three sorts of "ontogenic" agencies (Osborn's term) bring about ontogenetic variation: 1. "Physico-genetic"; physical agents producing "'fortuitous' or accidental changes." 2. "Neuro-genetic"; arising from "the spontaneous activities of the organism." 3. "Psycho-genetic"; secured by intelligent or "conscious agency" (p. 443). Baldwin seemed also to anticipate a later narrowing of the meaning of "Organic Selection" to describe processes of ontogenetic variation only (stage 1 of Simpson's Baldwin effect). Hence, said Baldwin, "we may simply . . . claim the law of use and disuse, as applicable in ontogenetic development, and apply the phrase, "Organic Selection," to the organism's behaviour in acquiring new modes or modifications of adaptive function with its influence of structure" (p. 444).

selection" (Osborn 1897, 944-951).[12] Osborn, according to Huxley, was himself followed three years later by Lloyd Morgan's 1900 book *Animal Behaviour.* Simpson however, had all three authors publishing "independently and almost simultaneously" and referred additionally to Morgan's 1896 book *Habit and Instinct*, along with a paper by Osborn, also published in 1896.[13] Hardy both disagreed with Huxley and added detail to Simpson's account, suggesting that "Baldwin and Osborn briefly put forward their views in a discussion which followed a lecture given by Lloyd Morgan to the New York Academy of Sciences on January 31st 1896, and then, later in the year, published papers on them" (Hardy 1965, p. 164). Hardy also described a resume of Morgan's views, which Morgan published in 1896, and went on to describe five sources not mentioned by either Simpson or Huxley in their reviews.[14] Thus Hardy tells us enthusiastically: "There was a most illuminating series

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[12] Osborn offered the view that the terms "natural selection of coincident variations," or "coincident selection," were more fully descriptive of the classically studied phenomenon than "Organic Selection." He continued, in near agreement with Baldwin's exegesis: "The hypothesis, as it appears to myself is, briefly, that *ontogenic adaptation . . . enables animals and plants to survive very critical changes in their environment. Thus all the individuals of a race are similarly modified over such long periods of time that, very gradually, congenital variations which happen to coincide with the ontogenic adaptive modifications are collected and become phylogenic. Thus there would result an apparent but not real transmission of acquired characters*" (ibid.). However, Osborn's writings were ambiguous, and these words seem to be at odds with his views on the previous page, where he asserts that "what are primarily *ontogenic variations* become slowly apparent as *phylogenic variations* or congenital characters of the race," suggesting an actual, rather than merely apparent, inheritance of acquired characters more in line with his long-time Lamarckist sympathies (1897, p. 945; author's emphasis throughout).

[13] This was Osborn's 1896 oddly named paper, "A mode of evolution requiring neither natural selection nor the inheritance of acquired characters," *Trans. New York Acad. Sci.*, 15 (1896), 141-142; 148; as cited in Hardy 1965, p. 164. Clearly, however, natural selection is at the very heart of coincident selection.

[14] One such reference constituted a brief clarifying letter from Baldwin to *Nature*. However, in the letter Baldwin suggests that the hypothesis "seems in some degree to mediate between the two rival theories of heredity," whilst providing the following anti-Lamarckian exegesis: "The point of view taken in these publications is briefly this:--assuming the operation of natural selection as currently held, and assuming also that individual organisms through adaptation acquire modifications or new characters, then the latter will exercise a directive influence on the former quite independently of any direct inheritance of acquired characters. For organisms which survive through adaptive modification will hand on to the next generation any 'coincident variations' (*i.e.* congenital variations in the same direction as adaptive modification) which they may chance to have, and also allow further variations in the same direction. In any given series of generations, the individuals of which survive through their susceptibility to modification, there will be a gradual and cumulative development of coincident variations under the action of natural selection." Importantly, Baldwin implied that modification and coincident variation were completely developmentally unconnected: "The

of articles discussing the whole conception of Organic Selection [sic] in the American journals *Science* and *The American Naturalist* for 1896 and '97; from a study of these it is seen that the germ of the idea was also present in some of the writings of both Weismann and Alfred Russel Wallace" (1965, pp. 164-165).[15] [16] Interest in organic selection and closely related concepts remained fairly dormant until the middle of the 1930s. In Simpson's words: "After general acceptance of Mendelism and before clear statement of the modern synthesis of evolutionary theory, the

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adaptive modification acts, in short, as a screen to perpetuate and develop congenital variations and correlate groups of them" (Baldwin 1897, p. 558; author's italics).

[15] Hardy's suggestion that Weismann anticipated Baldwin's organic selection is, I believe, deeply misleading. Hardy failed to recognise that Weismann's "intra-selection" deliberately dismissed the coincident selection process central to Baldwin and Lloyd Morgan's hypothesis. Weismann wished to circumvent any suggestion of orthogenetic forces being responsible for the supposed "coincidence" (namely, the morphological similarity) of his assumed causally independent "somatogenic" (modificational and non-hereditary) and "blastogenic" (germinal and hereditary) characters. In fact, intra-selection was merely the coadaptive modification, "due to innate plasticity," of the parts of an organism in response to previous germinal variations (Weismann 1894; in Lloyd Morgan 1896, p. 343). Thus, in Weismann's example of the coadaptation of other structures to a germinal increase in antler size in the deer, he stated: "It is by no means necessary that all the parts concerned--skull, muscles, and ligaments of the neck, cervical vertebrae, bones of the four limbs, etc.--should simultaneously adapt themselves *by variation of the germ* to the increase of the size of the antlers ; for in each separate individual the necessary adaptation will be temporarily accomplished by intra-selection" (ibid.). For Weismann, then, adaptive modification *followed* germinal variation, and not vice versa. Hence, as Lloyd Morgan observed: "So far [in Weismann] there is no direct relation between specific modifications and variations. Individual accommodation, as a factor in survival, affords time . . . for the occurrence of *any* variations of an adaptive nature" (Lloyd Morgan 1896; in Baldwin 1902, p. 348; author's emphasis). Whilst Lloyd Morgan tried to elaborate on Weismann's scheme by suggesting that Morgan's *coincident* selection, occurring after intra-selection, would give the organism "an added chance of survival," Weismann nevertheless ignored the idea (ibid.).

[16] The following is part of a passage, reprinted by Osborn, from Wallace's review of Lloyd Morgan's 1896 book published in *Natural Science* (1897): "Modification of the individual by the environment, whether in the direction of structure or of habits, is universal and of considerable amount, and it is almost always, under the conditions, a beneficial modification. But every kind of modification is also being constantly effected through variation and natural selection, so that the beautifully perfect adaptations we see in nature are the result of a double process, being partly congenital, partly acquired. . . . [I]n Professor Lloyd Morgan's words: 'modification *as such* is not inherited, but is the condition under which congenital variations are favored and given time to get a hold on the organism, and are thus enabled by degrees to reach the fully adaptive level.' The same result will be produced by Professor Weismann's recent suggestion of 'germinal selection,' so that *it now appears as if all the theoretical objections to the 'adequacy of natural selection' have been theoretically answered*" (Osborn 1897, pp. 948-949; Osborn's emphasis).

Baldwin effect was seldom discussed in detail, although it continued to be mentioned under various names in reviews of evolutionary theory" (Simpson 1953a, p. 110).[17]

However, an explosion of interest in organic selection began during the mid 1930s, initially in the Soviet Union (Kirpichnikov 1947, pp. 164-175). According to Simpson, the causes of this Soviet development were forces parallel to those which had existed in the West between neo-Darwinians and neo-Lamarckians in the 1890s. Soviet students independently thought of the Baldwin effect as a result of the conflict, in Simpson's words, "between Mendelism and Michurinism" (Simpson 1953a, p. 111; for a brief account of Michurin's support of Lysenkoist neo-Lamarckism, see Graham 1993, p. 132). The significances of Simpson's paper are manifold. Most importantly, it is in this paper that we find the fullest appreciation of the importance to the new synthesis of the debate concerning organic selection.[18] Simpson expressly understood organic selection's relevance, both to the neo-Darwinism versus neo-Lamarckism and Mendelism versus Michurinism debates, as part of the broader materialist versus finalist argument regarding teleology in evolution. Thus he commented: "Adaptation seems to be purposeful. The finalist's view is that it is purposeful, in fact, but materialists generally rule out purpose as a possible factor in evolution. There are several possible materialistic explanations for seemingly purposeful adaptation. Among them is the Baldwin effect" (ibid.). Because of the highly abstract and often arbitrary nature of the historical debate over organic selection, it is useful to review a range of actual laboratory and constructed natural historical examples, provided by the proponents themselves, of the hypothetical process in action.

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[17] Simpson mentions, among others, Delage and Goldsmith (1912) and Lull (1917). Delage and Goldsmith illustrate the confusion over terminology, stating that the "organic selection" theory was "also known as the theory of ontogenetic selection, of orthoplasis [sic], of coincident selection or of coincident variations." There was, at that time, general agreement among evolutionists with Delage's and Goldsmith's belief that the "last designation is certainly the most fitting, as it describes very accurately its characteristic features, but controversy over their suggestion that it "is what we might call a compromise between Darwinism and Lamarckism" (Delage and Goldsmith 1912, p. 276). Lull, for example, described "Osborn's theory of coincident selection" as a defence against Cope's acceptance of the inheritance of acquired characters; that is, against Cope's neo-Lamarckist doctrine of "kinetogenesis" (the law of use and disuse) as a "potent factor" in evolution (Lull 1917, p. 188).

[18] That is, organic selection as Simpson understood the term's original meaning from Baldwin's writings; namely, the hypothetical set of processes leading up to, and including, the natural selection of coincident variations.

2.3.1. Some Purported Examples of the Organic Selection Process.

In 1942, Huxley presented the reader with what he described as a "beautiful special case of the principle of organic selection" (Huxley 1942, p. 304). Such was the work of Thorpe on olfactory conditioning in *Drosophila melanogaster*, published in 1939. This work provided a good example of the concept of organic selection in its altered and narrower sense: that is, to use Osborn's phrase, "the process by which individual adaptation leads and guides evolution" (Osborn 1897, p. 946). Huxley described the relevant experimental results as follows:

> Whereas adult fruit flies are normally repelled by the smell of peppermint, those which have been reared on a synthetic medium to which peppermint essence has been added are markedly attracted by the smell [when] tested in an olfactometer. Further, this response is not abolished (though it is somewhat reduced) by washing the fully fed larvae or newly-formed puparia free of all traces of the medium and of the peppermint essence, thus proving that influences operative only during the larval phase can influence adult behaviour. If not reinforced, the influence gradually disappears and becomes extinct after about a week. (Huxley 1942, p. 303).

In this passage, Huxley describes the production of the initial ontogenetic variation, or adaptive modification. Thorpe also found, as evidence of the modifying power of environmental changes at this stage of the process, that "exposure of the adult insects only, immediately after emergence, to the smell of peppermint brings about positive conditioning even if the smell is not associated with any favourable aspect of the environment--the mere fact of the occurrence of the stimulus at this time brings about subsequent attraction to media containing the same substance" (ibid.).[19] In any event, for Huxley this was a prime example of "the principle of organic selection" in its first phase of action, "according to which modifications repeated for a number of generations may serve as the first step in evolutionary change, not by becoming impressed upon the germ plasm, but by holding the strain in an environment where mutations tending in the same direction will be selected and incorporated into the constitution." Crucially important, then, was the fact that this next (and perhaps long to be awaited) mutational step in the process "simulates

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[19] According to Huxley, Thorpe's own belief was that the conditioning effect would provide, in Thorpe's words, "a non-hereditary barrier which may serve as the first stage in evolutionary divergence" (Huxley 1942, p. 304).

Lamarckism, but actually consists in the replacement of modifications by mutations" (ibid.).

A most entertaining hypothetical example of organic selection acting in higher organisms was provided in 1900 by Conn. The interesting aspect of this example, was its suggestion that hereditary morphological changes are effected by intelligent behaviour in higher organisms, via the agency of organic selection. As Conn explained at some length:

> Perhaps a concrete case may make this obscure theory a little clearer. Imagine for example that some change in conditions forced an early monkey-like animal, that lived on the ground, to escape from its enemies by climbing trees. This arboreal habit was so useful to him that he continued it during his life, and his offspring, being from birth kept in the trees, acquired the same habit. Now it would be sure to follow that the new method of using their muscles would soon adapt them more closely to the duty of climbing. Changes in the development of different parts of the body would inevitably occur as the direct result of the new environment, and they would all be acquired characters. The children would develop the same muscles, tendons, and bones, since they too lived in the trees and had the same influences acting upon them. Such acquired characters would enable the animals to live in the trees, and would thus determine which animals should survive in the struggle for existence, for these modified animals would clearly have the advantage over those that stayed on the ground, or did not become properly adapted to arboreal life by acquired habits. All this would take place without any necessity for a congenital variation or the inheritance of any character which especially adapted the monkey for life in the trees.
>
> But, in the monkeys thus preserved, congenital variations would be ever appearing in all directions. It would be sure to follow that after a time there might be some congenital variation that affected the shape of the hands and feet. These would not be produced as the result of the use of the organs or as acquired variations, but simply from variations in the germ plasm. There might be thousands of other variations in other parts of the body in the meantime. The miscellaneous variations, however, would not persist. But as soon as variations appeared which affected the shape of the hands and the feet, the fact that the animal had continued to climb trees would make these variations of value, and therefore subject to natural selection. Selection would follow, and thus in time the monkeys might be expected to inherit hands and feet well adapted for climbing. The acquired variations, in such a case, had nothing to do with *producing* the changes directly, but they did shield the animal from destruction until congenital variations appeared. (Conn 1900, pp. 310-312; emphasis author's).[20]

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[20] This example was reprinted verbatim by Baldwin in an appendix to *Development and Evolution* (Baldwin 1902, pp. 367-368). Also, an abbreviated version was reprinted by Hardy, who thought it particularly confluent with his own ideas on the power of behavioural changes to effect evolutionary morphological ones (Hardy 1965, p. 179).

This lengthy scenario illustrated an important variation on the principle, the significance of which will become clear below. Here, then, subsequent hereditary variations are not necessarily providing hereditary *simulacra* of some modified habit form or morphological structure: they are merely endorsing new habits of use and disuse, via the germinal production of novel structures made adaptive by the organism's new behaviour patterns.

However, despite the obvious enthusiasm of the Oxford zoologists Julian Huxley and Alister Hardy, Simpson expressed extreme caution over embracing the principle, and his position remained in marked contrast to the viewpoint of his fellow new synthesis supporter Huxley. In 1942, Huxley had given a very positive account of "Organic Selection" in the sense expressed by Conn's hypothetical example. This he did within the context of subsidiary historical restrictions upon the direction taken by natural selection in the production of evolutionary trends. Huxley wrote that a "special case of subsidiary historical restriction" was provided by the "Baldwin and Lloyd Morgan principle of Organic Selection." Under this principle, Huxley continued, "an organism may in the first instance become adapted to an ecological niche merely by behaviour (whether genetic or purely habitual) and any consequent non-heritable modifications, after which mutations for the kind of structural change suitable to the particular mode of life will have a better chance of being selected." Again, where modifications were extensive, Huxley believed that "the process of their replacements by mutations may closely simulate Lamarckism." For Huxley, then, the principle was certainly "an important one which would appear to have been unduly neglected by recent evolutionists." (Huxley 1942, p. 524).

In 1952, Simpson only briefly acknowledged Huxley's enthusiasm for organic selection, and emphasised that Huxley's acceptance of it was only "as a subsidiary factor." Simpson also accepted that it was "so recognised by most followers of the synthetic theory (e.g. Mayr 1951)." Yet Dobzhansky's views on the matter were not discussed, and no mention of organic selection is to be found in the first or second editions of *Genetics and the Origin of Species*. However, a brief entry, and possible warning against support for the exponents of organic selectionism, is found in Dobzhansky's 1940 second edition in the form of an attack on Osborn. The passage relates to Osborn's well known denial of the importance of mutation as a factor in the process of adaptive evolution which, for Dobzhansky, revealed a serious lack of understanding of the role of genes evolution.[21]

2.3.2. Simpson's Three-Part Definition of the Baldwin effect.

An interesting aspect of Simpson's paper is its unmistakably rearguard tone. Having constructed his own definition of organic selection from a personal study of the literature, and having accepted the possibility (in fact probability) of such a series of events occurring, he nevertheless denied the existence of any evidence for the actual agency of the effect in particular cases. Simpson's offered a three part definition of the Baldwin effect as follows:

> The effect may be analysed as involving three distinct but partially simultaneous steps:
>
> 1) Individual organisms interact with the environment in such a way as systematically to produce in them behavioural physiological or structural modifications that are not hereditary as such but that are advantageous for survival, *i.e.* are adaptive for the individuals having them.
>
> 2) There occur in the population genetic factors producing hereditary characteristics similar to the individual modifications referred to in 1), or having the same sorts of adaptive advantages.
>
> 3)The genetic factors of 2) are favoured by natural selection and tend to spread in the population over the course of generations. The net result is that adaptation originally individual and non-hereditary becomes hereditary. (1953a, p. 112; author's italics).

Simpson was adamant that each process necessary for the Baldwin effect did in fact occur in nature, and that there was "no reason to doubt that they could occur together, in the stated sequence, and so produce the Baldwin effect." There was, he felt, "even some probability that they must have produced that effect sometimes." Nevertheless, for Simpson, two points remained highly questionable: namely, "whether the Baldwin effect does in fact explain particular instances of evolutionary change, and the extent to which this effect has been involved in evolution or can explain the general phenomenon of adaptation" (p. 113). Thus Simpson suggested

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[21] Dobzhansky describes Osborn's position over mutation and evolution, and quotes from the final words (originally in italics) of Osborn's 1927 paper "The origin of species, V: speciation and mutation," as follows: "Osborn (1927) denied the importance of mutation in evolution on different grounds: 'speciation is a normal and continuous process; it governs the greater part of the origin of species; it is apparently always adaptive. Mutation is an abnormal and irregular mode of origin, which while not infrequently occurring in nature is not essentially an adaptive process; it is, rather, a disturbance of the regular course of speciation'. Variations of this statement have been made into professions of faith by a number of writers. The source of the difficulty here is a profound misunderstanding of the genetic conception of the mechanisms of evolution" (Dobzhansky 1941, p. 52).

that in each proposed example, "direct evidence" that the effect was indeed the agent of evolutionary change seemed to be lacking--even, in Simpson's words, in the "impressive example of birdsong already discussed at length by Lloyd Morgan" (ibid.).[22]

However, in the final section of Simpson's paper on the Baldwin effect in evolutionary theory, the weakness with which he adhered to this sceptical position became more apparent. As Simpson said of the effect: "It probably has occurred, but there is singularly little concrete ground for the view that it is a frequent and important element in adaptation" (p. 115). Thus Simpson could not so his way to joining his co-new synthesis supporters, notably Huxley and Mayr, in openly accepting Huxley's "unduly neglected" principle as a welcome neo-Darwinian explanation of neo-Lamarckist phenomenology. In Simpson's far more cautious view, the Baldwin effect did not provide an unambiguous resolution to the dispute. Hence he contended that: "As an alternative to neo-Lamarckism or Michurinism, the Baldwin effect supposes that accommodation (adaptive somation) is paralleled by genetic changes with similar results. Actually this is no alternative at all and still leaves the basic decision to be made" (ibid.). Thus for Simpson, the decision still to be made was whether adaptive modification--Simpson's "adaptive somation"--is merely paralleled by genetic changes with similar results, or whether it may in fact sometimes directly cause the appearance of precisely similar adaptive hereditary variations. As a consequence, Huxley's "second stage" of the study of adaptation, far from being answered at all emphatically by "Baldwin and Lloyd Morgan's unduly neglected principle," was in fact questionmarked by it more profoundly than ever before. As Simpson explained ever more alarmingly for the synthetic neo-Darwinist: "If the Baldwin effect occurs, either there is or is not a causal connection between an individual accommodation and subsequent genetic change in a population. If there is a causal connection, the neo-Lamarckian argument is as much supported as supplanted. Indeed, the claim (as by Hovasse) that the Baldwin effect is usual in adaptive evolution could be taken as an argument in favour of neo-Lamarckism:

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[22] Simpson refers sceptically to an example provided by Lloyd Morgan in *Habit and Instinct*, yet added, "but that hypothesis has been accepted by Huxley among others" (ibid.).

frequent coincidence of somation and mutation might suggest that one causes the other" (ibid.).

Here, then, Simpson may have sensed all the slumbering monsters of neo-Lamarckism and late nineteenth century developmentalism--including Haeckelian recapitulation--beginning to stir. The question of a causal connection in the direction from phylogeny to ontogeny inevitably arises, once a causal connection is suggested between individual phenotypic modification and hereditary change. All the good works of the early modern synthesis embryologists such as Garstang, de Beer, and Joseph Needham, stood in jeopardy at any such suggestion of the legitimacy of neo-Lamarckist "somatic induction." Finally, Simpson warned, the position was not at all improved with regard to the broader concerns of biologists over the role of adaptation within the mechanist-vitalist debate. Hence, he remonstrated: "Nor is the Baldwin effect an adequate answer to the arguments of the finalists, who can as readily see directive purpose in somation as in mutation" (ibid.). Anti-adaptationists such as Hogben, might well have perceived Simpson's obvious concern as the just deserts of Simpson's, and the synthetic theory's, hardening selectionism during the 1940s and 1950s; neo-Darwinism having been, in Hogben's view, a "peculiarly sterilising influence on the growth of experimental biology."[23]

Simpson evidently saw organic selection as potentially playing into the hands of the neo-Lamarckians. He was therefore anxious to promote the strict empirical limitation of any principle that might possibly advance the phylogenetic significance of "non-heritable" adaptive changes, whilst fully supporting the strong selectionist-adaptationism of the synthesis. Simpson's strategy closely resembled de Beer's arbitrary limitation of the extent of recapitulation in modern embryology. De Beer had always accepted that the factual existence of recapitulation presented the anti-

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[23] Simpson's minimal enthusiasm (especially when compared with Huxley's) for organic selection, and his evident distrust of a mechanism which might at least diminish the role of classical selection in adaptive evolution, is placed in broader context by Gould's observations of Simpson's important 1953 book *The Major Features of Evolution*: "In particular, increasingly exclusive reliance on selection-toward-adaptation (for Simpson, in the gradual, phyletic mode), coupled with a greater willingness to reject alternatives more firmly than the evidence warranted, marks both Simpson's new book and the growing confidence of the synthetic theory in general. . . . Major Features, in numerous statements both subtle and explicit, and in general tenor as well, takes a much harder, much less generous, much more uncompromising line than its [1944] predecessor on the domination of evolutionary pattern by selection-toward-adaptation in the phyletic mode" (Gould 1980, p. 166).

recapitulationist with a problem. The uncontested fact of recapitulation--that is, the accelerated repetition of specific organs or structures of ancestral adult organisms, to appear in the embryonic stages of descendant organisms--indeed faced anti-recapitulationists with a difficult dilemma. In Chapter 13 of de Beer's 1958 *Embryology and Evolution* concerned with evidence for such accelerations, de Beer accepted that should the empirical evidence be plentiful, "the conditions for Haeckel's theory of recapitulation will then be fulfilled." Indeed, the number of accepted examples of acceleration appeared to have increased over the 28 years since publication of *Embryology and Evolution*, and de Beer finally felt it necessary to add a brief concluding paragraph not found in the previous two editions, stating: "If Haeckel's theory of recapitulation had been correct, this chapter would be the longest and most important in the book. Instead, only a few scrappy instances can be found, and this [heterochronic] mode has played only a minor part in evolution" (de Beer 1958, p. 110).[24]

Both de Beer and Simpson, as evolutionary morphologists struggling to legitimate a neo-Darwinian approach to their respective disciplines, felt very keenly the legacy of nineteenth century developmentalism in its various forms. To start with, as Hull relates, Simpson argued for a minority view in palaeontology with his neo-Darwinian phyletic gradualism, as expressed in the classic new synthesis work *Tempo and Mode in Evolution* (1944). In holding this position Simpson stood against the leading idealist morphologists of the 1920s, and most notably against Schindewolf. Furthermore, since both the directed evolution of orthogenesis and the neo-Lamarckian inheritance of acquired characters were especially popular among palaeontological systematists, Simpson was forced to combat these theories as well

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[24] In fact, the examples provided by de Beer in 1958 provided quite extensive evidence in support of recapitulation. They included the early development of the heart in the chick, mesodermic coelomoducts in diploblastic marine metazoa, the appearance of horns in the embryos of the late-evolving titanotheres, worn teeth (as though from adult use) in the embryonic Dugong, and the appearance of callosities in the embryo of the Ostrich. In any case, there are good reasons for questioning such a strategy of limitation. Gould has stated emphatically that "natural history does not refute its theories by cataloguing empirical exceptions to them . . . with millions of potential examples in a discipline second to none for its superabundance of empirical information, how can a catalogue of counter-cases ever refute a theory ?" The strategy, says Gould, is made all the more futile since "proponents can always furnish their lists as well. And since each list must include a ridiculously small percentage of all possible cases, how can a theory of natural history be rejected by simple enumeration ?" (Gould 1977, p. 168).

(Hull 1988, p. 69). Hence the palaeontologist Osborn's own tendencies towards classical Lamarckian orthogenesis, would clearly have provided a large part of Simpson's motivation to limit Huxley's resurrection of organic selection. Palaeontology's ubiquitous trends were traditionally linked to non-Darwinian mechanisms, in which adaptation to the environment nevertheless frequently figured. In Hull's words, "Simpson argued, regardless of the opinions of all these authorities, that the fossil record is totally compatible with the synthetic theory of evolution" (ibid.).[25]

2.3.3. Simpson and Huxley on Historical Restriction: Orthoselection or Orthogenesis?

By 1953, then, Simpson had clearly become very wary of Huxley's enthusiastic support for neo-organic selection. Simpson's personal concern was to limit the influence, within palaeontology, of explanations for long-term trend and programme evolutionary processes that bore any relation to, or provided any support for, orthogenesis. It would therefore surely have been recognised by him that Huxley's category of "dominant historical restriction" (identified by Huxley with Plate's "orthoselection") could be causally related to the Baldwin effect: organic selection being, for Huxley, a special and neglected example of "subsidiary historical restriction" upon the direction of natural selection. Since the extremists among supporters of organic selection (such as Hardy and Hovasse) were actively campaigning for its acceptance as *the* dominant influence upon the direction of

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[25] Gould, himself a palaeontologist, gives an interesting overview of these issues in a comment on the status of early modern synthesis paleontology: "As the synthesis dawned, very few paleontologists took an active interest in evolutionary theory, and even fewer followed the progress of genetics. I know of only one pre-Simpsonian attempt to base the phenomena of paleontology explicitly upon genetical theory--the anti-Darwinian work of Schindewolf (1936) with its invocation of de Vriesian saltation as an explanation for discontinuities and episodic pulsations in the fossil record. Most paleontologists adopted one of two attitudes toward the evolutionary theory of geneticists and other 'neontologists.' Some, like Simpson's teacher Richard S. Lull at Yale [also a keen supporter of organic selectionism] adopted an eclectic attitude and adduced paleontological support for a range of evolutionary phenomena often associated with contradictory theories--from selection to internal trends outside the control of selection (Lull, 1924). Others, like Henry Fairfield Osborn, searched the paleontological record for inductive generalizations and concluded that no neontological theory could encompass the regularities. He therefore argued that some special process must operate at scales of time longer than those available to genetics to study" (Gould 1980, p. 155). Clearly for Osborn, Baldwin and Lloyd Morgan's orthoplasy defined some part (if not all) of that process.

natural selection, and since Plate's neo-Darwinist credentials were very dubious (since he also accepted Lamarckian orthogenesis), it is important to investigate what Huxley understood in 1942 to be the distinction between orthoselection and orthogenesis.

The term orthogenesis had been popularised in 1898 by Eimer, author of the provocatively entitled, *On Orthogenesis and the Impotence of Natural Selection and Species Formation.*[26] Bowler relates that the term "came to be used in the context of regular evolutionary trends described by palaeontologists of the American school" (Bowler 1989, p. 268). Eimer characterised orthogenesis as a principle, strongly founded on empirical facts, "according to which the modification [including hereditary variation] of organisms takes place not accidentally, but in a few perfectly determinate directions" (Eimer 1898, p. 2). He maintained that "like facts have also been established in America by prof. Alpheus Hyatt with reference to the transformation of Ammonites." For Eimer, then, "Definitely directed evolution, orthogenesis, is a universally valid law" (ibid.). Huxley in 1942 broached the question of the (for him merely apparent) evolutionary evidence for such law-governed internal forces, by discussing the basic principles of the historical restriction of natural selection. Thus, says Huxley, "once a trend has begun, much greater changes will be necessary to switch the stock over to some other mode of life than to improve the arrangements for the existing mode of life" (Huxley 1942, p. 498). Huxley believed T. H. Morgan to have put the point very clearly, and provided the reader with the following quotation from Morgan's evolutionary writings: "Whenever a variation in a new direction becomes established, the chance for further advance in

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[26] The depth of Eimer's anti-adaptationism was seemingly matched only by the depth of his personal dislike for Weismann. Thus he wrote in defence of his "definitely directed evolution" [orthogenesis]: "*Everything is not adapted.* This is proved by the fact that the young, the females, and the aged individuals of animals, particularly butterflies [show] accurately determined patterns of markings which can only be attributed to a definite, law-conforming transformation, of which they are the expression" (Eimer 1898, p. 9). Weismann's rhetorical appeal to the "*discouraging circumstance* that we can assert in scarcely a single actual instance in nature whether an observed variation is useful or not" (Weismann 1893; in Eimer 1898, p. 8; Eimer's emphasis), was sternly denounced: "Our practised dialectician attempts by this exaggerated phrasing of a well-grounded criticism of Darwin's, to repudiate all the countless facts which go to show that the omnipotent natural selection propounded by him is a chimera. The "discouraging circumstance which the Freiburg zoologist adduces is rather a self-saving invention, a way of escape from the narrow corner into which the facts established by me and others regarding definitely directed evolution perforce have driven him" (ibid.; see also Bowler 1983, p. 153).

the same direction is increased. An increase in the number of individuals possessing a particular character has an influence on the future course of evolution, not because the new type is likely to mutate again in the same direction, but because a mutation in the same direction has a better chance of producing a further advance" (Morgan 1925, p. 148; in Huxley 1942, p. 499).[27]

Intriguingly, within his own explanation of the phenomena of dominant historical restriction, Huxley adopted a metaphor analogous to Waddington's canalisation, and proposed that "a specialised line thus finds itself on the bottom of a groove cut for it by selection." Here Huxley informed the reader that Plate, "who reaches very similar conclusions proposes the term *orthoselection* for selection promoting continuance of an adaptive trend" (Huxley 1942, p. 500; author's emphasis).[28] Twenty pages on, Huxley nevertheless defined "true" orthogenesis, and made a final judgement concerning the relative importance of these two forms of restriction upon hereditary variation, stating: "True orthogenetic restriction depends on a restriction of the type and quantity of genetic variation. When dominant it prescribes the direction of evolution: when subsidiary it merely limits its possibilities." Ending this section on the restriction of variation, Huxley concluded: "To sum up,

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[27] Morgan then immediately revealed his uniquely extreme view of the absolute evolutionary insignificance of adaptive modification. Strictly separating evolutionary adaptation from any response of the organism to its environment, he asserted: "The fitness of the animal or plant to an environment that it finds existing, gives the false impression that its relation to the environment, its adaptation, has come about through a response to the environment. The central idea of natural selection, as understood at the present time, is that the relation is purely fortuitous. The organism has been produced by one series of events, the environment by another; the relation of the two is secondary" (Morgan 1925, p. 151). Thus, at a time when so many other evolutionists had given accounts of organic selection as a compromise between Lamarckism and neo-Darwinism, Morgan made no mention of the principle or its adherents.

[28] Huxley referred favourably to Plate's orthoselection, and cited his *Selektionsprinzip und Probleme der Artbildung* (Plate 1913). Yet in 1907, Kellogg had provided an interesting account of Plate's dubious neo-Darwinian status, remarking: "Darwin himself included part of Lamarckism as a minor factor or influence in his explanation of adaptation and species forming, and Plate, in the recent most notable critical discussion of Darwinism, takes nearly exactly the old ground of Darwin, namely an acceptance of the inheritance, in some degree and under some conditions, of acquired characters, and the consequent possibility of a certain amount of Lamarckian orthogenesis, *i.e.*, an orthogenesis due to the inheritance of the results of use, disuse, and functional stimuli. It is only the neo-Darwinism (of Weismann, Wallace, and others) and neo-Lamarckism (of Spencer, Packard, and others) that are so radically opposed, so mutually exclusive" (Kellogg 1907, p. 264). Harwood has recently commented on Plate's neo-Lamarckian concept of the *Erbstock*, to which chromosomal genes were subordinated, and which responded directly to the shaping forces of the environment (Harwood 1993, p. 107). See my Chapter 5 for further discussion of Weismannian heredity and the development of the synthesis.

the only important agency restricting the direction of evolutionary change is the historical one, leading to a purely apparent orthogenesis" (1942, p. 524). However, as proponents of orthogenesis might have asked: What is the nature of the action of Huxley's orthoselective "groove" upon natural selection, if not at least to limit the possibilities of future variation? By the same token, between 1942 and 1963 Huxley openly praised Waddington's staunchly selectionist evolutionary writings. Yet Waddington's canalisation was an internal, epigenetic restriction upon the phenotypic expression of hereditary variations, and thus in Huxley's terms, might also be viewed as a subsidiary form of orthogenesis.

Given that such detailed obscurity covered the whole hypothetical area of restrictions upon hereditary variation, it would surely have occurred to Simpson that Huxley's dominant and subsidiary forms of historical restriction upon selection, might be reclaimed by evolutionary palaeontologists as evidence of orthogenesis. There is no doubt that Waddington saw the processes he himself was investigating experimentally in the 1950s as closely related to the concept of orthogenesis.[29] Huxley still claimed that whilst "dominant historical restriction is common, dominant orthogenetic restriction is very rare, if indeed it exists at all." Nonetheless, he went on significantly to add that "subsidiary orthogenetic restriction is probably frequent, but we are not yet able to be sure in most cases whether a limitation of variation as actually found in a group is due to a limitation in the supply of mutations or to selection or to other causes" (1942, p. 524).

Just as worrying for Simpson, those originally involved in promoting organic selection had also seen the process as closely related to orthogenesis. Most notably, fellow palaeontologist Osborn, in his 1897 *Science* paper "Organic Selection," remarked: "The evidence for definite or determinate variation [Eimer's definitely directed evolution] has always been my chief difficulty with the natural selection theory, and my chief reason for giving a measure of support to the Lamarckian

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[29] In a private letter written by Waddington to Dobzhansky in 1959, Waddington made the following remarks about an impending project: "I am starting another experiment which may interest you. Selecting *Drosophila* for small body size, which usually reduces fitness; but I shall select simultaneously for good larval survival in competition with a tester stock. . . . This is, of course designed to demonstrate a mechanism which makes it easier for selection to continue for long periods in the same direction, as in the lineages one used to call 'orthogenetic'" (Waddington 1975, p. 97).

theory. This evidence has steadily accumulated in botanical and zoological as well as paleontological researches, until it has come to a degree of demonstration where it must be reckoned with" (Osborn 1897; in Baldwin 1902, p. 337).[30] Baldwin and Lloyd Morgan were clearly not quite as keen for some evolutionary role to be given to orthogenesis. Nevertheless, Osborn had no trouble in declaring his full agreement to some significant modifications of terminology and usage in the field of organic selectionism, arrived at by Baldwin and Lloyd Morgan soon after the concept's joint discovery (and seemingly without his Osborn's consultation). Thus Osborn wrote:

> Professor Baldwin, of Princeton, and Professor Lloyd Morgan, of University College, Bristol, had at the same time independently reached the same hypothesis, and Professor Baldwin has aptly termed it "Organic Selection." Both writers have presented valuable critical papers on it, including in *Science* and *Nature* a complete terminology for the various processes involved. I concur entirely in their proposal to restrict the term *variation* to congenital variation, to substitute the term "*modification*" for ontogenic variation, and to adopt the term "*Organic Selection*" for the process by which individual adaptation leads and guides evolution, and the term "*orthoplasy*" for the definite and determinate results." (Osborn 1897, p. 946).

Evidently, Osborn's Lamarckist sympathies, Baldwin's and Lloyd Morgan's "orthoplasy," and the whole question of subsidiary versus dominant historical restriction upon selection (and its relation to true orthogenesis), were all areas of theory that Simpson understandably wished to avoid.[31] However, the reactionary Darwinism of one particular Oxford marine biologist who shared Osborn's Lamarckist sympathies, namely Alister Hardy, kept such questions uncomfortably close to the surface from the early 1940s and throughout the modern synthesis period.

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[30] That Osborn differed from Baldwin (and Lloyd Morgan) on this issue, is witnessed by Baldwin's adding of a footnote to this passage, pointing out to the reader his distance from Osborn's views in genteel fashion: "Professor Osborn is here possibly using the phrase 'determinate variation' somewhat loosely for 'determinate evolution'--in my opinion a different thing. It is necessary to say this to make entirely valid his kind citations from me" (Baldwin 1902, p. 337).

[31] Baldwin also spoke of "orthoplastic influences," defining them as "all agencies of accommodation (*e.g.* organic plasticity, imitation, intelligence, &c.), considered as directing evolution through organic selection" (Baldwin 1897, p. 558; see note 43 below).

2.4. Organic Selection versus External Natural Selection: The Reactionary Darwinism of Alister Hardy.

Deeply supportive, beyond any of his neo-Darwinian contemporary's, of the concept of organic selection (and especially with the behavioural aspect of Lloyd Morgan's and Baldwin's views) was the Oxford marine zoologist and tutee of Huxley's, Alister Hardy. Although a staunch selectionist in the tradition of Lankester, Goodrich, and de Beer, Hardy later made the confession that in the spring of 1942: "I first openly expressed my doubts about the validity of modern evolutionary theory and pointed in the direction from whence I believed a change of view would come" (Hardy 1965, p. 153). In his 1963 Gifford lectures, Hardy discussed the position he held during the 1940s and expressed deep sympathy for the "neo-Lamarckian intuition that changes in behaviour have played a much greater part in evolution than their colleagues will admit" (1965, p. 159). Hardy admonished many neo-Darwinians, in particular his "friend and colleague" C. D. Darlington, for being "biased and blind" whilst "with an almost religious passion, fighting to stamp out the last vestiges of the [Lamarckian] 'superstition'" (ibid.).

It was Huxley's 1942 classic book that had provided Hardy's initial contact with the concepts of Baldwin, Lloyd Morgan and Osborn, and that led rapidly to his conversion. Yet, attempting to distinguish himself from others similarly influenced, he remarked: "The few biologists who have seriously considered Baldwin and Lloyd Morgan's Organic Selection [sic] as a factor in evolution have mostly done so in relation to habitat selection. I am concerned to show that it is a principle which may profoundly influence the evolution of the structure of animals" (p. 162). In 1949, Hardy, as the then president of the Zoology Section of the British Association for the Advancement of Science, gave an extended speech on the significance of organic selection within an address entitled "Zoology outside the laboratory." Within it he began by echoing Julian Huxley, saying of organic selection that "it is in effect similar to that postulated by Lamarck but brought about on Darwinian lines." Importantly for our discussion of his views, Hardy maintained that "*external Natural Selection* must of course be important, but if organic selection can be shown to be a really significant factor, it may well alter our way of looking at evolution as a whole" (p. 169; emphasis added). Here, then, classical or external selection and organic selection are portrayed as separate forms of natural selection, by a prominent member of the neo-Darwinian establishment. Furthermore, in his later Gifford lectures, Hardy was adamant that his position has not changed at all since 1949. Quoting at length the passages from Huxley's book discussing the "unduly neglected" principle, Hardy then went much further than his Oxford tutor, and confessed: "I am saying nothing original. But what I am doing that *is* new is to say, jointly with R. F. Ewer, that this is not just a subsidiary effect but is indeed one of the major factors in the evolutionary process" (p. 163; author's emphasis).[32]

2.4.1. Hardy and Simpson Juxtaposed: Conflicting Darwinian Attitudes to Organic Selection.

Thus Hardy and Simpson, in the 1940s and 1950s, epitomised the extremes of viewpoint among Darwinian selectionists regarding organic selection, understood in Baldwin's original sense of all the processes leading up to, and including, the coincident selection of hereditary variations.[33] Their polar positions illustrate the depth of disagreement that existed, at the time of consolidation and hardening of the synthetic theory, over the evolutionary significance to be accorded adaptive modifications (Simpson's "adaptive somations"), and their apparent hereditary fixation. For example, Simpson clearly felt that more recently published investigations into the broader area of adaptive modification and evolution, provided

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[32] Hardy refers to Ewer's "illuminating paper" in *Acta Biotheoretica*, within which she stated that "it must be born in mind that an evolutionary change does not have to 'wait for the right mutations to turn up': the first advance will always be made on the basis of changes in frequency and recombination of genes already present in the population with new mutations bringing up the rear by continually replenishing the pool of variability" (Ewer 1960; in Hardy 1965, p. 187). To this point, Hardy added the footnote "Waddington's (1956) demonstration of the 'genetic assimilation' of the bithorax phenotype shows how very great a departure from the norm is capable of being produced in this manner" (ibid.).

[33] Baldwin's original, general sense of organic selection was used by him in early papers, before a change was agreed with Lloyd Morgan. Subsequently, from 1897 onwards (although Baldwin still applied the old usage in his letter to *Nature* of April 15 1897), they used organic selection solely to describe the process via which modifications, in Osborn's words, "lead and guide evolution," and the term orthoplasy solely to describe the "definite and determinate" evolutionary results of this guidance, as a result of coincident selection. However, few used organic selection in the strictly narrow sense of Morgan and Baldwin in the 1940s and 1950s. For example Lutz, writing about evolution in frogs, stated ambiguously that: "The modifications of reproductive behaviour and the habitat preferences of the adults obviously fall within the scope of organic selection, i.e. selection of the environment by the organism" (Lutz 1948, p. 30).

a more powerful conceptual framework in which to view the writings of Baldwin and Lloyd Morgan. Most significant of all for him were the writings of two evolutionists: Soviet morphologist I. I. Schmalhausen, who's 1946 *Factors of Evolution* had been translated into English by Dordick in 1949; and Waddington, the Cambridge experimental embryologist and Edinburgh geneticist who's 1952 *Nature* paper provided, in Simpson's view, the most up-to-date research then completed in the field.[34] Of the former, Simpson remarked: "Schmalhausen and some others (mostly Russian) speak of 'stabilizing selection.' The term is sometimes equated with Baldwin's 'organic selection' but the equation is misleading. Stabilizing selection applies to any mechanism tending to fix an adaptive type. . . . The Baldwin effect is one such mechanism, but not the only one and not (even in Schmalhausen's opinion) the most important" (Simpson 1953, p. 112). Of Waddington's recently published paper regarding the process of genetic assimilation, Simpson felt that "The phenomenon involves, again, a broader principle of which the Baldwin effect may be considered a special case" (1953, p. 116).

Whilst Hardy appeared publicly to value Simpson's review, his views contrasted starkly with Simpson's regarding the status of the original nineteenth century studies of Baldwin, Lloyd Morgan and Osborn. Hardy appeared only to mention Simpson's review in passing, describing it as "a valuable discussion, with references, on the views of more recent authors concerning its validity." But, he added, the recent researches "really add nothing to the original concept and hardly discuss the habit and behaviour aspect" (1965, p. 165). Hardy also made several very important references within the same lecture to Waddington's notion of genetic assimilation. Discussing Huxley's 1963 edition of *Evolution The Modern Synthesis*, he noted Huxley's neglect to discuss organic selection. Yet, said Hardy, Huxley "does refer to Waddington's principle of genetic assimilation" stating that Waddington had made a "notable contribution to evolutionary theory by his discovery that Lamarckian inheritance may

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[34] The depth and breadth of Waddington's adaptationist views in the 1940s and 1950s was quite remarkable. At the end of that synthesis period he wrote: "It is by now absolutely conventional and a matter of first principles to consider the whole physiological and sensory apparatus of any living thing as a result of a process which tailors it into conformity with the situations with which the organism will have to deal. The same principle undoubtedly applies to behavioural characteristics, and there is no obvious reason to deny it out of hand in relation to intellectual and even moral characteristics in those organisms which exhibit them" (Waddington 1960; reprinted verbatim in Deely and Nogar 1973, p. 300).

be simulated by a purely neo-Darwinian mechanism." (Huxley 1963; in Hardy 1965, p. 163). Hardy's response was to concede: "Whilst I recognise that Waddington's principle has great merit in that he has now demonstrated it experimentally several times, we should recognise that Lloyd Morgan and Baldwin with their Organic Selection first showed how such a Darwinian simulation of a Lamarckian effect could be possible" (Hardy 1965, p. 163). Most significantly, in the following breath of his lecture, Hardy fully identified organic selection with Waddington's genetic assimilation:

> Waddington, and most other biologists with whom I have discussed the matter, think that his theory is different from that of Organic Selection, or the Baldwin effect as so many prefer to call it. In his *The Strategy of the Genes* (1957) he gives what he believes is a diagrammatic demonstration of the difference; to me, however, what *he* calls Organic Selection seems to be only a shadow of all that was implied in the concept as originally put forward and particularly as enunciated by Lloyd Morgan. I have to admit that I really cannot see any difference between Waddington's theory and the earlier one, that is if the earlier theory is given in reasonable completeness. (1965, p. 164; author's emphasis).

Hardy was clearly quite adamant that no advances had been made, during the first half of the twentieth century, over late nineteenth century ideas regarding the evolutionary significance of adaptive modifications. He suggested that an over-simplification, bordering on dishonesty, had been employed when relating Lloyd Morgan's and Baldwin's principle, and concluded on a reactionary note: "Let us go back to Lloyd Morgan, Mark Baldwin, and Fairfield Osborn; their pioneer contributions should be remembered" (ibid.).

For Hardy, not only had modern theorists failed to improve upon the original concept of organic selection, but it was to be considered distinct from, and measurable against, classical or external natural selection.[35] The extent to which organic selection acted independently of external selection was the extent to which it was both an answer to, and a final explanation of, neo-Lamarckian criticisms against

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[35] The Russian Schmalhausen made just such a distinction between his own stabilising selection, and classical (or in his terms "dynamic") selection. In his 1946 *Factors of Evolution*, Schmalhausen stated that he had great respect for Baldwin and Lloyd Morgan's early analysis of the problem of adaptive modification. Nonetheless, he included all forms of coincident selection, including all neo-Mendelian interpretations of Baldwin's and Lloyd Morgan's principal, such as Simpson's "Baldwin effect" (which I collectively classify as "neo-organic selection"), within the category of dynamic selection. Also, like Hardy, Schmalhausen felt that the question of which form of selection was dominant in adaptive evolution was an empirical question, requiring more extensive research (See section 4.3.3.).

natural selection. In Hardy's view, "the relative importance of the two forms of selection must be the subject both of experiment and more research" (ibid.). Such a multiplying of forms of natural selection was, to Simpson's mind, a widespread and dangerous fallacy which he explicitly rejected. Drawing from his extensive study of the field, Simpson maintained: "From 1896 up to now, everyone who has discussed it at any length has taken the position that the Baldwin effect is something distinct from natural selection acting on genetical variation and that its real importance is in meeting or explaining away the criticisms levelled at natural selection by, especially, the neo-Lamarckians, the Michurinists, and the finalists. The Baldwin effect is both possible and probable, but assignment to it of that role in evolutionary theory seems to me fallacious" (1953, p. 115).

If, as Hardy thought, the complete sufficiency of organic selection to the explanation of evolutionary adaptation was still an empirical question, to extremists such as the Hovasse, the question had already been decided. According to Simpson, Hovasse had boldly proclaimed in 1950 that: "The application of this principle [that is, of organic selection] can lead to a general explanation of adaptation" (p.114).[36] Simpson felt he understood why extremist schools of thought such as Hovasse's should attempt to make the Baldwin effect all powerful in adaptation. The cause was straightforwardly, in Simpson's words, "acceptance at face value of all the criticisms of natural selection, advanced on one hand by the neo-Lamarckians and on the other by the finalists." As Simpson recognised, "each of those schools claims a general explanation of adaptation and Hovasse accepts the generality but substitutes the Baldwin effect as mechanism." Simpson inevitably felt that was "certainly going much too far." For him, there could be no third combatant in the battle over Dobzhansky's "real issue" (1953, p. 114).

Accepting a second form of natural selection, the action in nature of which was phenomenologically identical with neo-Lamarckism, as a universal explanation for adaptive evolution, would surely have been "going much too far" in the minds of all neo-Darwinian synthesis supporters. It would have raised the stakes over Dobzhansky's real issue much too high. Worse yet, to paraphrase Simpson, it would "still leave the final decision to be made" between neo-Darwinism and neo-

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[36] Simpson cites Hovasse's *Adaptation et Evolution* (1950).

Lamarckism. Much safer to allow a small space for organic selection; that is, as a subsidiary "effect" of some limited explanatory use within the broad range of phenomena explained by classical Darwinian selection. Should the phenomena referred to organic selection then fall prey to claims of explanation via a neo-Lamarckian mechanism, none of the great strides towards the new synthesis made during the 1930s and 1940s would stand to be lost. For, as Simpson maintained, "the synthetic theory rests on grounds that have essentially nothing to do with the Baldwin effect. . . . It is simply one way in which natural selection may effect populations, and clearly it is not a factor either contradictory or additional to natural selection" (p. 115).

2.5. The Attempted Assimilation of a Subsidiary Historical Factor: Waddington and Schmalhausen's "Broader Principles."

Here, then, Simpson vividly defined one of the major problems for the selectionist adaptationism of the new synthesis: as an attempt to settle Dobzhansky's "real issue"--namely, the question of which was the true "mechanism of the origin of the adaptations of organisms to their environment"--the acceptance of any more than a subsidiary role for organic selection, could serve to undermine the synthetic theory altogether. Yet the willingness of several notable modern synthesis supporters to re-embrace this late nineteenth century neo-Darwinian explanation of neo-Lamarckian phenomenology, was recognised as a danger by very few others. Simpson (and also Dobzhansky, as I shall discuss in Chapters 3 and 4) moved the agenda forward by embracing new conceptions which, in their opinion, encompassed organic selection. Thus for Simpson, the hereditary fixation of adaptive modifications to the phenotype could now be deduced from newly understood genetical principles, and incorporated properly into the modern synthesis. Simpson's 1953 paper expressed his belief that this had been fully achieved by 1952, in the form of Schmalhausen's theoretical writings, and Waddington's laboratory researches. Both these men's ideas were thought by Simpson to embody "a broader principle of which the 'Baldwin effect' can be considered a special case" (1953, p. 116).

Simpson's strategy, then, was to subsume both explanations of the universally accepted phenomena under a third and unifying principle. This third principle would explain, in Simpson's terms, "any mechanism tending to fix an adaptive type and bring it under more rigid genetic control" (p. 115). The theoretical foundation for Waddington's broader principle was, for Simpson, well expressed by the notion that "the ability to acquire a character has itself a genetical basis" (p. 116). On the face of it, this phrase appears closely related to Goodrich's dictum, "no single character is completely acquired or due to inheritance alone" (Goodrich 1924, p. 61). Indeed, it was in large part this observation of Goodrich's--and many other authors according to Waddington--that led directly to the concept of genetic assimilation. Waddington made explicit the generative link between his and Goodrich's ideas, when Waddington observed in 1961 that "the notions of 'acquired' and 'inherited' characters, as they are employed in evolutionary theory, are not entirely straightforward." Elaborating on these complexities, Waddington continued: "As many authors, e.g. Goodrich, have remarked all characters of all organisms are to some extent 'inherited', in the sense they can only be developed, if the organism contains the hereditary potentialities for developing them, and are also to some extent 'acquired', since all development involves some participation of the environment" (Waddington 1961, p. 258).

However, it can be argued that Simpson's own particular phrase, that "the ability to acquire a character has itself a genetical basis," merely stated an article of doctrine within synthetic neo-Darwinism: namely, that *adaptability* is the result of previously selected hereditary changes occurring in phylogeny, and not due to any innate power of the protoplasm. Waddington's phrasing was less ambiguous. Certainly, his strong rhetoric against organic selection, stimulated by Simpson's Baldwin effect paper, always emphasised the necessary genetic component to *all* developmental processes, including those involved in adaptive change. But this was to counter what he felt to be the implicit suggestion, made more explicit by new synthesis writings on organic selection, that the development of *specific* adaptive modifications was due to some vague non-genetic plasticity--regardless of the phylogenetic origins of adaptability in general. In this strict sense, then, Waddington maintained that many neo-Darwinian synthesis supporters wrote as if adaptive modifications had no hereditary foundation. Waddington's prime example came from Mayr's 1950s writings. Thus organic selection was, according to Mayr, "the hypothesis that a non-genetic plasticity of the phenotype facilitates reconstruction of the genotype" (Mayr 1958, p. 254; in Waddington 1959, p. 390). Waddington's response to this characterisation of organic selection was to object that "a plasticity of the phenotype cannot be 'non-genetic'; it must have a genetic basis, since it must be an expression of genetically transmitted potentialities" (ibid.).

The above quotation from Mayr originally appeared as a footnote in a paper on animal behaviour and systematics, within which Mayr made the following important observations within Avian ethology:

> There are at least two different possibilities for the acquisition of a new behaviour pattern by a species. 1. The new behaviour may have a genetic basis right from the beginning. Since much behavioural variation is correlated with the genetic variability of the species, any factor effecting the gene content of the species may also affect behaviour . . . 2. A new behaviour is at first a non-genetic modification of an existing behaviour, as a result of learning, conditioning or habituation, and is replaced *(by an unknown process)* by genetically controlled behaviour. (Mayr 1958, p. 354; emphasis added).

Discussing, as an example of mechanism 2., the incorporation of previously unrelated behaviour into modified courtship repertoires across species of birds, Mayr concluded: "The genetics of this process are still completely obscure. This is one of the few evolutionary phenomena where the 'Baldwin effect' might have played a role, although the behaviour, after its incorporation in the courtship, is in a different neural 'environment' than it was previously" (ibid.). Mayr was clearly in support of Simpson's view that the Baldwin effect was rarely responsible for adaptive evolutionary change. In any case, defenders of Mayr may argue that Waddington's objection was unnecessarily literal in its interpretation of Mayr's phrase "genetic basis." Mayr, it might be suggested, was only arguing for a distinction between new hereditary behaviours that were directly occasioned by the appearance of a new major gene (or by a novel arrangement of existing genes due to recombination), and new characters which, though necessarily having a genetically controlled foundation to their expression, were not so occasioned.[37] However, other aspects of Mayr's statement support Waddington's perspective, especially Mayr's suggestion that behavioural variation is normally closely correlated with the genetic variability, to the

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[37] The question of a 'major-gene-plus-modifiers' model of genetic assimilation, as opposed to Waddington's preferred 'polygenicity-plus-canalisation' model, is discussed in my Chapter 3, within the context of the genetic assimilation research programme undertaken at Edinburgh throughout the 1950s.

extent that "any factor effecting the gene content of the species may also affect behaviour." Such strong gene-character determinism was characteristic of synthetic neo-Darwinist writings on organic selection, both in the West and, particularly, in the Soviet Union. In the Soviet Union, then, Chetverikov's distinction between non-hereditary phenovariation and hereditary genovariation, appears to have been implicitly held by all neo-organic selectionists--and very explicitly upheld by Gause and Alpatov.

In any case, Western supporters of the new synthesis, varying greatly in their enthusiasm for neo-organic selection, only ever argued, to use Huxley's terminology, for its "subsidiary historical" role. Nevertheless, it was Simpson who uniquely described organic selection as ancillary to more general mechanisms for the hereditary fixation of adaptive modifications; namely, those espoused by Waddington and Schmalhausen. For Simpson, two problems existed for the success of such a strategic defence of the synthetic theory. Firstly, as we have seen vividly illustrated by Hardy's Gifford Lectures, interpretations varied hugely as to the status of organic selection in the 1940s and 1950s. Simpson as we know accepted its validity, but severely doubted its importance. Any support for organic selection might adversely encourage its more zealous supporters, including most notably Hardy, Hovasse, and almost all the Soviet biologist's working in that field between 1935 and 1944. These zealots accepted its validity, its independent status, *and* campaigned vigorously upon its great importance as a mechanism of evolutionary adaptation. Secondly, members of this group of enthusiasts believed that no legitimate distinction could be drawn between Lloyd Morgan's coincident selection, and Waddington's genetic assimilation. Similarly, in the understanding of the Soviet biologist Kirpichnikov, no distinction could be drawn between organic selection and Schmalhausen's stabilising selection. General acceptance by evolutionary geneticists of either one of these identifications, would have undermined Simpson's strategy.

Another problem for Simpson's defence came from the attitudes of the author's of the supposedly subsuming theories themselves. Though self-confessedly unaware in the 1940s of Baldwin and Lloyd Morgan's hypothesis, nevertheless by the time of reading Simpson's review, Waddington's position was deeply antagonistic towards organic selection and, in particular, towards Simpson's neo-Mendelian representation of it. Waddington's response was, therefore, particularly unfavourable toward

Simpson's close association of genetic assimilation with the Baldwin effect. Most unfortunately of all, from Waddington's perspective, Simpson's understanding was that Waddington's theory, and the Baldwin effect, coincided precisely at the point of genetic assimilation--that is, at the very heart of Waddington's mechanism. For Simpson, in other words, genetic assimilation and the coincident selection of hereditary variations were identical processes--namely, stage two of the Baldwin effect.[38]

Such a conception of the genetic assimilation theory was anathema to Waddington. He quickly replied to Simpson in the December volume of *Evolution*, 5 months after the appearance of Simpson's review paper. Concerning the evolutionary importance of the Baldwin effect, Waddington asserted: "Simpson comes to the conclusion that the Baldwin effect, in the sense he describes it, has probably played a rather small role in evolution. The genetic assimilation mechanism, however, must be a factor in all natural selection, since the properties with which that process is concerned are always phenotypic; properties, that is, which are the products of genotypes interacting with environments" (Waddington 1953, p. 386). Having introduced this as the principal distinction; namely, that the "variations" which the genetic assimilation mechanism causes to become hereditarily fixed were always, and only, adaptive modifications to the phenotype, Waddington continued: "By speaking of mutations as 'random', which is true enough at the level of the gene as a protein-DNA complex, we obscure the fact that the effect of a mutation, as far as natural selection is concerned, is conditioned by the way it modifies the reaction with the environment of a genotype which has already been selected on the basis of its response to that environment. This is not neo-Lamarckism, but it is a point which has been unduly neglected by neo-Darwinism" (Ibid.). Put in other words, the background genotype of any wild organism, selected for over a long period within a specific environment, must have been selected to produce only certain kinds of adaptive modifications in response to both (biochemically speaking) random genetic

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[38] Simpson's identification of the Baldwin effect and genetic assimilation was uncritically adopted by almost all evolutionary biologists from 1953 onwards. Hardy's views have already been made clear, but most other workers had the same understanding. For example, the entomologist Emerson wrote in 1958: "Genetic assimilation . . . or the 'Baldwin effect' is an interesting evolutionary change in the mechanism of development" (Emerson 1958, p. 318).

variation, and external environmental alterations. Or, in more biochemical terms, developmental reactions in organisms subject to strong selection pressures are biochemically buffered (up to a certain level of disturbance), so as to produce only pre-specified phenotypes under altered environmental and genetic conditions. That is, development has become canalised, and the phenotypic effects of subsequent minor genetic mutations will thus not be random at all, but will be guided along pre-existing canalised pathways.[39]

Furthermore, and perhaps most unfortunately of all for Simpson's strategy, the Soviet morphologist Schmalhausen also explicitly denied any place for organic selection, within what Simpson had also assumed as the "broader principle" of Schmalhausen's stabilising selection. Simpson had, in 1949, reviewed the English translation of Schmalhausen's famous and last major evolutionary work, *Factors of Evolution*. He and Schmalhausen were at least in agreement within their separate publications over organic selection's not constituting a special form of natural selection. They were also in like agreement, over the infrequency of the selection of coincident variations--that is, stage two of the Baldwin effect. Nevertheless, although both were apparently in agreement that the principle of organic selection (as rediscovered in the Soviet Union by Lukin and Kirpichnikov) definitely existed, nevertheless, Schmalhausen made an absolute distinction between the organic selectionism of his Soviet compatriots and his own stabilising selection.[40] As I will show in section 4.4.1., Schmalhausen, quite unlike Waddington, did not ever suggest the illegitimacy of organic selectionism. Schmalhausen's prime concern was for evolutionary biology's recognition of the separate identity of all forms of "common dynamic selection" (that is, classical Darwinian selection) from stabilising selection.

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[39] By 1961, Waddington's rhetoric had gone a step further as he suggested that, as authors who had recently referred to the subject understood it, the theory of organic selection "seems to be an impossible one" (1961, p. 287). This "impossibility" was, once again, due to Waddington's dim view of the concept of a non-genetic plasticity of the phenotype.

[40] In the English translation of *Factors of Evolution*, Schmalhausen asserts: "Stabilising selection is based upon a selective advantage possessed by the adaptive norm . . . over all deviations from it. It operates by the accumulation of all mutations which do not bring the phenotype beyond the limits of the established norm." By contrast, "common dynamic selection [which Schmalhausen identified with coincident selection, or organic selection] operates simultaneously in the same direction in which the modification of the organism is proceeding; that is, on the basis of *further deviation* over the established norm" (Schmalhausen 1949, p. 204; see section 4.4.1.).

Schmalhausen had at best a marginal relationship, during the 1930s and 1940s, with other Soviet researchers concerned with the subject of evolution and adaptive modifications. In Schmalhausen's view, then, far from organic selection being a "special case" of stabilising selection, organic selection and stabilising selection acted in completely different directions, and with a totally different relationship to the existing adaptive norm of reaction. Hence for Schmalhausen, the processes were complete opposites, both in terms of their direction in relation to the established 'adaptive norm,' and the genetic raw materials they used.[41] For Schmalhausen, then, the organic selection of Lukin and Kirpichnikov was simply classical Darwinian natural selection, and not a special form of selection at all. Thus it is only on this narrower point, of the Baldwin effect's failure to warrant independent status from classical selection, that Schmalhausen's and Simpson's viewpoints converged at all.

Thus we need to investigate more closely these apparent stumbling blocks to Simpson's defence of the synthetic theory, as Simpson's concerns over organic selection are important to any realistic evaluation of that defence's legitimacy. They are also important for evaluating the extent to which embryological and developmental genetic approaches to adaptive evolution were marginalised, as part of that same defence of the new evolutionary orthodoxy.

2.5.1. Stumbling Blocks to Simpson's Defence of The Synthesis: Lloyd Morgan's Original Concept of Organic Selection.

As mentioned in the previous section, Hardy defended his views by asserting the ignorance of other people's, at least over the character of Lloyd Morgan's and Baldwin's classical concept. It was Hardy's belief that in the 1940s and 1950s, the understanding that other commentators, most notably Waddington, had of the

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[41] Schmalhausen's use of Woltereck's (or, according to Dobzhansky, Raunkier's) highly influential notion of the "norm of reaction," defined the complete set of phenotypes, expressed by a particular genotype, within the range of environmental conditions (including biotic conditions) encountered by a population. Its derivative, the specific "adaptive norm," described a local adaptive phenotype within the overall norm of reaction (perhaps produced as an adaptation to a changed environment) which had only recently been subjected to stabilising selection. The continuing action of stabilising selection upon such local adaptive norms, eventually transformed these into new general norms with renewed potential for broader phenotypic expression. These secondary general norms subsequently develop their own subset of narrower adaptive norms, thereby continuing the cycle of widening and narrowing expression in response to ecological changes.

original concept of organic selection was superficial and prejudiced. In discussing the aftermath of his 1949 British Association address, Hardy remarked wistfully: "I had thought I might have started a discussion on the relative potencies of these two forms of natural selection [namely external natural selection and organic selection] but was disappointed." He suspected the influence of causes other than disinterested scientific rationality in the rejection of Lloyd Morgan's principle: "It has taken me some time to realise that there appears to be a curious, I might almost say psychological, block preventing the majority of biologists with whom I have discussed the matter from really appreciating the point I have been trying to make or even being interested in what they quickly dismiss as the 'Baldwin effect; a principle of only minor importance.'" Hardy blamed himself to some extent for this state of affairs, saying: "In part no doubt it has been my lack of explanatory skill but I think there have been two other reasons for their failure to grasp the possible significance of [organic selection]. One I have already dealt with: the imagined bogy of Lamarckism; the other is that so many people still think of evolution in terms of individuals rather than populations" (Hardy 1965, p. 169).

As we have seen, Hardy thought Waddington's understanding of organic selection "only a shadow of the original concept particularly as enunciated by Lloyd Morgan" (p. 164). For a clearer and truer understanding of the full theory, two sources were recommended by Hardy. The first constituted a statement drawn up by Baldwin, according to Hardy, "in consultation with Principal Morgan and Professor Osborn."[42] However, Hardy immediately stated his preference for Lloyd Morgan's

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[42] The more obscure joint statement was first published in an appendix to Baldwin's edition of Karl Groos's *The Play of Animals, A Study of Animal Life and Instinct* (1898). Hardy added, "it is actually a slightly revised version of a similar summary which appeared in *Nature*." (Hardy 1965, p. 165). The 1897 *Nature* summary provided its own nine point clarification of terminology which, though historically interesting, might indeed have been confusing. Its most interesting aspects were a strictly functionalist approach to the causes of modification; a yet more precise definition of organic selection (which, *sensu stricto*, now referred only to the further modification of prior *coincident* variations, and thereby supported Baldwin's directed evolutionary concept of orthoplasy); and Baldwin's para-Lamarckian concept of "Social Heredity." Thus Baldwin wrote: "It appears desirable that some definite scheme of terminology should be suggested to facilitate the discussion of these problems of organic and mental evolution ; and I therefore venture to submit the following :-- (1) Variation : to be restricted to "blastogenic" or congenital variation. (2) Accommodation : functional adaptation of the individual organism to its environment. This term is widely used in this sense by psychologists, and in an analogous sense by physiologists. (3) Modification (Lloyd Morgan) : change of structure or function due to accommodation. To embrace "ontogenic variations" (Osborn), *i.e.* changes arising from all causes during ontogeny. (4) Coincident variations

"much clearer statement" in *Science* for November 1896. This article, reprinted in *Habit and Instinct* from the same year, provided a twenty point summary of which Hardy felt only the following eleven were required:

> 8. Let us suppose, however, that a group of organisms belonging to a plastic species is placed under new conditions of environment.
> 9. Those whose innate somatic plasticity is equal to the occasion survive. They are modified. Those whose innate plasticity is not equal to the occasion are eliminated.
> 10. Such modification takes place generation after generation, but, as such, is not inherited. There is no transmission of the effects of modification to the germinal substance.
> 11. But *variations in the same direction as the somatic modification* are now no longer repressed and are allowed full scope.
> 12. Any congenital variations antagonistic in direction to these modifications will tend to thwart them and render the organism in which they occur liable to elimination.
> 13. Any congenital variations similar in direction to these modifications will tend to support them and to favour the individuals in which they occur.
> 14. *Thus will arise a congenital predisposition to the modifications in question.*
> 15. The longer this process continues, the more marked will be the predisposition and the greater the tendency of the congenital variations to conform in all respects to the persistent plastic modifications; while
> 16. The plasticity continuing the operation, the modifications become yet further adaptive.
> 17. Thus the plastic modification leads and the germinal variation follows: the one paves the way for the other.
> 18. Natural selection will tend to foster variability in given advantageous lines when once initiated, for (a) the constant elimination of variations leads to the survival of the relatively invariable; but (b) the perpetuation of variations in any given direction leads to the survival of the variable in that direction. (Morgan 1896; reprinted in Hardy 1965, p. 167; emphasis added).

2.5.2. Lloyd Morgan's Principle as Pre-Mendelian Genetic Assimilation: The Hardy-Waddington Controversy.

On completion of the above 11 point summary, Hardy immediately pleaded with the reader that "surely this *is* Waddington's genetic assimilation expressed in pre-

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(Lloyd Morgan) : variations which coincide, or are similar in direction to, modifications. (5) Organic selection (Baldwin) : the perpetuation and development *of congenital coincident variations* in consequence of accommodation. (6) Orthoplasy (Baldwin) : the directive or determining influence of organic selection in evolution. (7) Orthoplastic influences (Baldwin) : all agencies of accommodation (*e.g.* organic plasticity, imitation, intelligence, &c.), considered as directing the course of evolution through organic selection. (8) Tradition (Lloyd Morgan) : the handing on from generation to generation (independently of physical heredity) of acquired habits. (9) Social Heredity (Baldwin) : the process by which the individuals of each generation acquire the matter of tradition, and grow into the habits and uses of their kind" (Baldwin 1897, p. 558; emphasis added on point 5).

Mendelian terms" (ibid.; author's emphasis). Yet now, Hardy seems less than fully confident of his own understanding, saying "If, however, some subtle distinction escapes me and they are in fact different, then both may be working to bring about the kind of evolutionary change I'm discussing" (p. 168).

Waddington replied comprehensively and courteously to these assertions, within a private letter to Hardy (Waddington 1975, pp. 279-281).[43] Waddington's reply referred directly to Lloyd Morgan's version of organic selection, as reprinted by Hardy. Waddington was firstly eager to inform Hardy: "I don't believe I had ever heard of Baldwin and Lloyd Morgan when I first thought of the idea of genetic assimilation around 1942." To Waddington, "the real difference between our ideas arises because we approach the same basic notions from different directions." Between himself and Hardy, Waddington felt that there was much for them to agree upon, both with regard to the evolutionary importance of the phenomena, and to their relation to classical Darwinism. Thus Waddington argued: "You say on page 171 [of *The Living Stream*] that between Darwinism and what you are talking about there is a 'real if somewhat subtle difference: a difference which it is essential that we should understand.' I entirely agree with you and also I agree with your earlier remark (p. 163) that 'this is not just a slight subsidiary effect but is indeed one of the major factors in the evolutionary process.'" However, Waddington's protest against the classical organic selection theory of Lloyd Morgan, remained essentially the same as that employed against Simpson's Baldwin effect in 1953. Lloyd Morgan had, according to Waddington, failed to realise that "the entities which undergo evolution are not simply populations of genotypes, but are populations of developing systems," this being a development "in which the environment plays a role as well as the genotype." Next, bringing the discussion into the heart of the new synthesis debate, Waddington argued that a closely related anti-developmentalist approach also made "the conventional Neo-Darwinist theories of Haldane and Fisher (and to a lesser extent Sewall Wright) . . . inadequate." In the case of theoretical population geneticists, though, their inadequacy arose "*both* because they leave out the importance of behaviour in influencing the nature of selective forces, *and* because

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[43] This letter was published as a post script to Waddington's reprinted article "The Human Animal," from *The Humanist Frame*, ed. Julian Huxley (London, 1961).

they attach coefficients of selective value directly to genes, whereas really they belong primarily to phenotypes and only secondarily to genes." To this statement Waddington added the strangely anachronistic comment, "I still doubt whether Lloyd Morgan and Baldwin had got the second point" (Waddington 1975, p. 280; author's emphasis).

Most informative for our purposes was Waddington's application of these points directly to Lloyd Morgan's statement of the original principle of organic selection. Waddington produced the following detailed dissection of the principle, unlike anything found in his formally published material:

> Lloyd Morgan supposes that a population of a "plastic" species can survive under new conditions of environment ([Hardy 1965] p. 167 point 8). He even sees that there will be some genetic variation in plasticity (point 9) but he explicitly separates the environmental modification from anything to do with the genotype (point 10 [also 19 and 20]). In points 11 12 and 13 he seems to me to be postulating the occurrence of new gene mutations in genes quite unconnected with those involved in the variation of plasticity. These mutations being of a kind which tend to cause the organism to develop the appropriate modifications independently of the action of the environment. (Ibid.).

Waddington's belief that Morgan causally separated the environmental modification from the genotype, could not have been conclusively determined from the context of the eleven points provided by Hardy. However, such a separation was much more strongly suggested in the complete 20 point summary. In points 19 and 20, then, Morgan indeed seemed to suggest that the original modification has no ontogenetic hereditary foundation. Thus in point 19, he stated that coincident selection only fixed characters "*similar* to those produced by the modification," and added in point 20 that "the modification *as such* is not inherited, but is the condition under which congenital variations are favoured" (Lloyd Morgan 1896, p. 321; second emphasis author's).[44] Waddington seemed to ignore in his letter to Hardy the crucial

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[44] All the other nine points are of great interest, not least for the apparently Lamarckist suggestion of an innate organismic plasticity--probably of joint origin with Mayr's (and other 1930s converts from neo-Lamarckism) notion of a "non-genetic phenotypic plasticity" (Mayr 1958): "1. In addition to what is congenitally definite in structure or mode of response, an organism inherits a certain amount of innate plasticity. 2. Natural selection secures (*a*) Such congenital definiteness as is advantageous. (*b*) Such innate plasticity as is advantageous. 3. Both *a* and *b* are commonly present ; but uniform conditions tend to emphasize the former ; variable conditions, the latter. 4. The organism is subject to (a) Variation, of germinal origin. (b) Modification, of environmental origin, affecting the soma or body tissues. 5. Transmissionists contend that acquired somatic modification in a given direction in one generation is transmitted to the reproductive cells to constitute a source of germinal variation in the same

problem of anachronism within his criticism of Lloyd Morgan; a problem he nonetheless appeared publicly to be aware of. Lloyd Morgan could have had no concept of "genotype" from which to separate any observed "phenotypic" change since, as Hardy reminded his readers , the authors of the concept of organic selection "were writing some fifteen years before Johannsen established the distinction experimentally in 1909, as also, of course, they were writing before the dawn of Mendelism" (1965, p. 166). However, the organic selectionists patently did possess the strict neo-Darwinian distinction between germinal variations and somatic modifications, which Baldwin and Lloyd Morgan expressly advocated (see Baldwin's point 1, in footnote 44 above). Thus, if such an objection could validly be launched by Waddington against the neo-Darwinian convert Mayr, it was surely also legitimate to bring it against Lloyd Morgan.

Waddington's objections to points 11, 12 and 13 in Morgan's summary were conceded by himself to be weaker. Rather than suggesting any explicit separation, Waddington thought Morgan only "seems to be postulating" the hereditary unconnectedness of subsequent variations to the original modification. Ignoring the anachronistic use of the language of Mendelian genetics in Waddington's argument, his suggestion that Morgan postulated the "occurrence of new gene mutations quite unconnected with those involved in the variation of plasticity" was again ambiguous within the wording of points 11-13. Morgan's point 11 phrase "variations *in the same direction as* the somatic modification are now no longer repressed," did not necessarily imply any such unconnectedness. Again, point 13, that "any congenital

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direction in the next generation. 6. It is here suggested that persistent modification through many generations, though not transmitted to the germ, nevertheless affords the opportunity for germinal variation of like nature. 7. Under constant conditions of life, though variations in many directions are occurring in the organisms which have reached harmonious adjustment to the environment, yet natural selection eliminates all those which are disadvantageous and thus represses all variations within narrow limits" (Lloyd Morgan 1896, p. 319). Hardy omitted the following final sentence from point 18 supporting Baldwin's orthoplasy (a form of orthoselection dependent upon organic selection *sensu stricto*), along with the very important points 19 and 20, which put more forcefully the suggestion in point 10 focused on by Waddington: "18. . . . Lamarckian paleontologists are apt to overlook this fact that natural selection produces determinate variation. 19. The transmissionist fixing his attention first on the modification, and secondly on the fact that organic effects similar to those produced by the modification gradually become congenitally stereotyped, assumes that the modification *as such* is inherited. 20. It is here suggested that the modification *as such* is not inherited, but is the condition under which congenital variations are favoured and given time to get a hold on the organism, and are thus enabled by degrees to reach the fully adaptive level" (p. 321; emphasis author's).

variations similar in direction to these modifications will tend to support them," was similarly non-committal regarding the origin and character of these variations. However, point 14 was perhaps more telling in casting real doubt over Waddington's criticisms of classical organic selection. Thus Lloyd Morgan's statement that by these processes a "congenital predisposition to the modifications in question" will arise, would seem to imply, contrary to points 19 and 20, that he fully accepted the role coincidently selected factors play in supporting the ontogenetic development of subsequent modifications--that is, in facilitating Baldwin's organic selection *sensu stricto*, and hence also long-range orthoplastic trends.

However, in defence against the implications of point 14, Waddington took the significant step of siding with Huxley's and Simpson's neo-Mendelian interpretation of organic selection over Hardy's. Thus Waddington continued: "At least I have always thought that the point made under 14 on [Hardy's] page 167 meant that there was a congenital predisposition to develop the modified phenotype without any contribution from the environmental circumstances. This is also the way that Huxley (cf. your page 163) and Simpson have interpreted Lloyd Morgan." Waddington, perhaps assuming this point 14 to be the crucial one in Hardy's "mistaken" identification of Waddington's alternative synthetic theory with organic selection, nonetheless conceded, "I suppose, however that it would be possible to interpret it in a sense much closer to my genetic assimilation."

Thus, after a strenuous effort to discredit Lloyd Morgan's original concept, Waddington at least conceded organic selection's ambiguity in relation to his own genetic assimilation. Yet regardless of these apparently understanding and concessionary words towards Hardy, Waddington was, underneath it all, still adamant. No matter how close organic selection could be interpreted to have been to genetic assimilation, the two principles remained, in his view, completely distinct. Indeed, the principle of organic selection was ostensibly welcomed by him as a preliminary move away from the crude neo-Darwinian dualism. "But," said Waddington to Hardy, "I think the point I want to make adds on yours, in just as important a way as yours adds on to Darwinism." Genetic assimilation was, for Waddington, as important a departure from organic selection as that theory may or may not have been from Darwin's classical selection theory.

It was perhaps mystifying why Waddington should attempt such a discrediting, even within private correspondence, having publicly stated two years previously that "Baldwin and Lloyd Morgan's discussions were of course couched in pre-Mendelian language, and it is not entirely easy to see exactly what there meaning would be when translated into terms of our modern concepts" (Waddington 1961, p. 287). Nevertheless, it is clear that Waddington's agenda was to promote the identification of Lloyd Morgan's concept with an over simplistic, neo-Mendelian version of organic selection propounded by several supporters of the synthetic theory. If this could be achieved, then Hardy's attempts to synthesise organic selection and genetic assimilation would be all the more refutable. For Waddington, organic selectionism was always "merely an out-of-date speculation which should be allowed to lapse back into the oblivion from which Huxley and Simpson rescued it" (ibid.). What was more, Waddington's priority claim to the true mechanism explaining the hereditary fixation of adaptive modifications would be left unchallenged: Huxley, Simpson, and Mayr falsely understood, in Waddington's view, "the initial adaptation to the new environment to be a nongenetic phenomenon on which selection has no effect" (ibid.).

It is also clear that Waddington fully appreciated the neo-Darwinian's dilemma over defining the role of organic selection within the synthetic theory. In 1953, discussing Simpson's just published three stage Baldwin effect, Waddington asked rhetorically: "Is there supposed to be any connection between the developmental adaptations and the genes with similar effect, and if so, what ? Simpson says that either there is no particular connection, in which case the theory signifies very little, or the connection must be by way of a neo-Lamarckian causal connection" (Waddington 1953; reprinted 1957, p. 164).[45] Hence in his 1957 *The Strategy of the Genes*, Waddington made the point that an interpretation of the phenomenon of organic selection such as Simpson's, would inevitably exacerbate the problem of having to decide between neo-Darwinism and neo-Lamarckism. Waddington suggested that "Huxley (1942) seems to put the point originally made by Baldwin and Lloyd Morgan more clearly when he writes that the adaptive modifications operate

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[45] Waddington first published this section of *The Strategy of the Genes* in *Evolution: The Seventh Symposium of the Society for Experimental Biology* (Cambridge, 1953).

'by holding the strain in an environment where mutations tending in the same direction will be selected'" (ibid.). Waddington clearly felt that such a description, reminiscent of Baldwin's (and later J. A. Thomson's) "screen" metaphor, made explicit the fallacy inherent to all interpretations, whether modern or classical, of the original concept of organic selection.

It was Julian Huxley, then, who in Waddington's view most clearly and openly presented the crude neo-Darwinian credentials of organic selectionism. Simpson's writings on the "Baldwin effect," on the other hand, merely kept an outdated neo-Darwinism versus neo-Lamarckism debate alive. Far from accepting organic selection as a subsidiary form of his own theory as Simpson suggested, Waddington very quickly attempted to sever any relationship whatever between the two, denying the legitimacy of organic selection from that theory's very inception.

2.6. Neo-Organic Selection in The Soviet Union.

As Simpson related in 1953, many Soviet biologists rediscovered organic selection in the mid 1930s and 1940s. Therefore in 1957 Waddington published a highly critical appraisal of this Soviet research tradition. Waddington's detailed criticisms took on a particularly negative tone within his analysis of the work of the Moscow professor of biology, G. F. Gause. In the light of Waddington's own empirical investigations, begun and ended in Edinburgh in the 1950s, into the hereditary fixation of acquired modifications, Waddington's discussion of what he called the "Russian" research takes on a particular significance.

Kirpichnikov's very detailed paper of 1947 provided an indispensable English review of the whole field of Soviet research into organic selection from 1935 (Kirpichnikov 1947, 164-175). After a standard review of the late nineteenth century British and American organic selectionists' writings, Kirpichnikov discussed his own research relating to race formation in fishes, and its suggestion of organic selection as a phyletic mechanism at work in speciation. Thus he explained to the reader: "The existing parallelism of hereditary (systematic) and non-hereditary variability in nature points to the significance of the latter in speciation. There are many cases when closely related species and sub-species of plants and animals differ inherently from one another by characters that are easily altered by external conditions" (1947, p.

166). Immediately, then, Kirpichnikov expressed support for both a strong adaptationist interpretation of specific and sub-specific differences between organisms, and a much more than subsidiary status for organic selection in speciation and phylogenesis.

At this point it becomes necessary to deal with the bewildering array of synonyms for organic selection that emanated from the Soviet research during the 1930s and 1940s. To begin with, the term *substituting selection* seems straightforwardly attributable to E. J. Lukin. Gause believed it was "clear that Lukin re-discovered the principle of organic selection, which was not known to him and was entirely forgotten at the time of his writing" (Gause 1947, p. 22). Hence in 1936, Lukin published the paper: "On the causes of substitution of modifications by mutations from the viewpoint of the theory of natural selection." Gause appears to have appropriated the term substituting selection and, most importantly, along with Lukin believed it to be a perfect synonym for both organic selection and stabilising selection. Secondly, Kirpichnikov, in describing his own work in the 1930s on fish, asserted that "an attempt is made to give a general analysis of the origin and the significance of non-hereditary adaptive modifications in the formation of species and in evolution, (the hypothesis of '*indirect selection*')" (Kirpichnikov 1947, p. 166; emphasis added). Again, the term indirect selection appears to have been uniquely Kirpichnikov's. Yet by 1944 Kirpichnikov had, according to Gause, "proposed for the same [organic selection] process the term *coincident selection*, in as much as modifications are replaced by coincident mutations." Gause ended his account by bringing this new term into the growing fold, saying that "the terms organic, stabilising, and coincident selection are practically synonymous" (Gause 1947, p. 23; emphasis added). Kirpichnikov himself, however, appeared to have a less selfish (if inaccurate) view of the history of coincident selection, attributing its first use to J. T. Gulick's work *Evolution, Racial and Habitudinal* (1905).[46] In the opening page of

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[46] Gulick spoke of "habitudes (that is, traditional forms of accommodation), and aptitudes (that is, inherited forms of adaptive variation" (Gulick 1905, p. 60). Thus Gulick, in words that suggested his own coinage, stated: "When accommodation thus opens the way for successful selection, Professor Baldwin calls the process 'organic selection.' I am disposed to raise the question whether the term 'coincident variation,' suggested by Lloyd Morgan, does not meet the case more exactly ; and when the variations are accumulated, may it not be well to call the process 'coincident selection' ?" (ibid.).

his review, Kirpichnikov in fact implied that the term's coinage was attributable to Lloyd Morgan himself, but it is Gause who provided us with the relevant quotation from Lloyd Morgan's 1900 *Animal Behaviour* (1947, p. 21).[47]

In 1947, Kirpichnikov gave a full explanation for his change of terminology in appropriating coincident selection: "'Indirect' selection in the sense of Kirpichnikov is the selection of variations which are more or less similar phenotypically to adaptive modifications. The modified organ alters by selection very slowly. In other words we really deal in this case with coincident selection. The author therefore is of the opinion that it would be appropriate to substitute the term 'indirect selection' by the older term *coincident selection* the more so since Darwin (1859), Schmalhausen (1938), and many others use the word 'indirect selection' to signify correlated changes [in] development" (Gause 1947, p. 168; author's emphasis).

Lastly we come to Schmalhausen. As Gause understood it, "Schmalhausen (1939) in his book Ways and rules of the evolutionary process [sic] suggested for it [namely, in Gause's words, "the process of substitution of modifications by mutations"] the term 'stabilising selection' in as much as the unstable phenotypic response of an organism to the change of environment is here replaced by the stable genotypic one" (Gause 1947, p. 23). However, in Kirpichnikov's much more sophisticated account, "'Stabilising selection' according to Schmalhausen (1938 etc.) is the principal integrating factor of evolution perfecting development and establishing morphogenetic correlations. *Stabilising selection acts in all instances notwithstanding the presence or absence of adaptive modifications*" (p. 170;

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[47] Gause referred to the passage where Morgan stated: "Professor Baldwin, who has independently suggested such relation between modification and variation, has applied to the process the term 'Organic selection' [sic]; but it may also be described as the natural selection of coincident variations" Lloyd Morgan 1906, p. 115). An immediately prior passage again lends weight to Waddington's interpretation of classical organic selection. Thus Lloyd Morgan wrote, in the context of a discussion of bird behaviour selected to divert predators: "We must remember that acquired habits on the one hand, and congenital variations of instinctive behaviour on the other, are both working, in their different spheres, towards the same end, that of adjustment to the conditions of life. If, then, acquired accommodation and congenital adaptation reach this end by different methods, survival may be best secured by their co-operation. And the more thorough-going the co-operation the better the chance of survival. There would be a distinct advantage in the struggle for existence when inherited tendencies of independent origin coincided in direction with acquired modifications of behaviour; a distinct disadvantage when such inherited tendencies were of such a character as to thwart or divert the action of intelligence. Thus any hereditary variations which coincide in direction with modifications of behaviour due to acquired habit would be favoured and fostered; while such variations as occurred on other and divergent lines would tend to be weeded out" (ibid.).

emphasis added).[48] Schmalhausen himself explicitly rejected any similarity between the two conceptions. Stabilising selection, in the eyes of Schmalhausen and (with important reservations to be discussed in Chapter 4) Waddington, constituted a completely separate, much more sophisticated, and entirely independent theory from both the Soviet and Western forms of neo-organic selection. Yet Gause characterised stabilising selection as simply another synonym for organic selection. Kirpichnikov, locating himself alongside Lukin, clearly sympathised with Gause's view, but nevertheless understood and correctly stated Schmalhausen's objections to such an identification.

Perhaps fuelling Waddington's criticisms regarding the basic assumptions of the Soviet research, Section III of Kirpichnikov's review was provocatively entitled: "The replacement of non-hereditary changes by hereditary ones in evolution according to Lukin, Gause and Waddington." Kirpichnikov opened this section by saying: "Lukin (1935, 1936) supposes that adaptive modifications are rapidly substituted by phenotypically similar mutations. This substitution is due to the greater selective value of the latter" (p. 168). Kirpichnikov also described the work of Gause, who "in general agreement with Lukin, discusses the question of the replacement of adaptive modifications by mutations in the course of selection" (ibid.). As discussed below, Gause went to great lengths in his research to develop a method of separating, and separately measuring, the adaptive values of initial modifications and coincident variations. Importantly, Kirpichnikov interpreted Waddington's 1942 paper--ten years before Waddington's first protestations to the contrary--in very similar terms to Gause's work. Kirpichnikov's identification of Lukin's and Gause's ideas with Waddington's was perhaps surprising, in light of Kirpichnikov's following precise explication of Waddington's concept of canalisation:

> Waddington (1942) introduced the new idea of canalization of individual development. The ability to react develops under the controlling influence of natural selection. In later stages, as a result of further selection, this ability becomes canalized. This signifies that development may progress only in one or a few directions due to the regulation against accidental deviations and the perfection of threshold reactions. External stimuli act as 'arrows'; the differentiation of the intermediate type becomes impossible. The

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[48] Compare this distinction of Schmalhausen's stabilising selection with canalising selection. Waddington's canalising selection, as is discussed in later sections, continued to act regardless of whether the selectable character is a non-hereditary modification, or had become genetically assimilated.

> selective value of the complete independence of the end product from the environmental fluctuations during the development of an organ finally leads to the substitution of such arrow reagents by genetical ones. (Kirpichnikov 1947, p.169).

Thus the consequences of accepting the process of canalisation--in particular, the negative consequences for Gause's notion of substituting selection--had apparently not occurred to Kirpichnikov, or had not appeared significant to him.

2.6.1. Waddington's Disparagement of Soviet Neo-Organic Selectionism: The Experimental Research Work of G. F. Gause.

Waddington's universally dismissive response to what he characterised as the "Russian" research, and in fact to any formulation of the organic selection theory, was epitomised by his analysis of the work of Gause. A simple explanation for Waddington's focus on Gause extensive research of as a target for criticism, is that Gause's ideas provided an extreme example of what Waddington felt to be the original intention behind classical organic selection. That intention, Waddington believed, had been correctly reinterpreted in neo-Mendelian terms by Julian Huxley; namely, that there was complete causal independence of initial adaptive modifications from coincidently selected hereditary variations. In a chapter of *The Strategy of the Genes* entitled "the survival of the adaptable," and distantly separated from his limited discussion of Schmalhausen's theory in a separate chapter, Waddington discussed in detail the question of organic selection. After a standard introduction to late nineteenth century organic selectionism, its neo-Mendelian resurrection at the hands of Julian Huxley in 1942, and Simpson's three point summation of the Baldwin effect, Waddington expressed the belief that "similar reliance on random mutations, occurring independently of the environmental stimulus, is implicit in the work which was carried out by a group of Russian authors between 1936 and 1944" (Waddington 1957, p. 165).

A survey of Gause's research is an essential preface to Waddington's critique. Gause had collaborated in the early 1940s with fellow Soviets N. P. Smaragdova and W. W. Alpatov, producing several papers on organic selection. Almost all of this work was published in Russian, therefore it is not surprising that Waddington should focus attention specifically on a 51 page summary, entitled *Problems of Evolution*, discussing the research of Gause and his co-workers up to 1945, and published in an

American monograph series in June 1947. The monograph contains very readable accounts of detailed experiments on infusoria. Gause appeared throughout his writings to be making a morpho-physiological distinction between adaptive modification, or "phenovariant," and the subsequent replacing hereditary variations, or "genovariant."[49] For Gause, the absolutely distinct nature of these two separate causes of the adaptive phenotype--namely, phenovariation and genovariation--was determinable at the level of their respective adaptive values. Thus he stated: "It is clear that the theory of organic selection is based upon the consideration of adaptive values. It is believed that modifications are adaptive, but it is also implied that their adaptive values are in the long run overpowered by those of genovariations" (Gause 1947, p 23). To be so overpoweringly more adaptive, the genovariant had necessarily to be very different, with essentially an entirely different morphogenetic structure to the (only superficially) similar phenovariant.

We might here suggest how the concept of such separate adaptive values could be applied to, for example, the results of Thorpe's research on olfactory conditioning in *Drosophila* from my section 2.3.1. The likely implication, in the context of Thorpe's experiments, would be that the genetically fixed ability of coincidently selected descendant flies to recognise peppermint-smelling food as palatable, without having been reared as larvae upon such food, gives them an overwhelming adaptive advantage over any flies requiring for such conditioning. Hence the shift, from initial modification to coincidently selected genovariant, produces a substantial shift in the adaptive value of the adaptation. Further suggestion that such an absolute distinction between phenovariation and genovariation was being made by Gause, comes from his call for different methods of measurement of adaptive values for these two categories. With respect to genovariation, Gause asserted, "it will be sufficient to study the rate of growth of the population in mutants and normal individuals." Yet with phenovariation, he asserted, since in response to environmental changes "all

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[49] Gause's use of Chetverikov's obscure (and generally discarded) 1926 genovariation-phenovariation dualism was nonsensical within Waddington's genetic assimilation theory, where hereditary fixation of an adaptive phenovariant was due only to canalisation. During Waddington's canalisation, a developmental pathway leading to the singular morphophysiological endpoint of the phenovariant becomes more and more reliably and uniformly reproduced under natural selection. Crucially, if canalising selection continues, non-specific epigenetic changes at some point along this single pathway cause the *original phenovariant form* to become hereditarily fixed, or "assimilated."

animals of a given population produce modifications," it would be impossible to construct a control (that is, an absolutely invariant sub-population), against which to measure respective adaptive values. Hence, Gause concluded, "It is therefore impossible to say whether any particular modification possess adaptive value, and what is the magnitude of that value" (ibid.).[50]

Although a second but, in his words, "much more difficult" method of measuring the adaptive values of modifications is suggested by Gause at some length (footnote 52 above), such a methodological dualism brings into still clearer focus the overarching thesis. It was his understanding that genovariants were entirely distinct from phenovariants, in that they were heritable and phenotypically invariant characters, produced purely by germinal mutations. Thus the production of genovariant forms cannot easily be affected by environmental agents; if they were so affected, the same problems as precluded the straightforward measurement of the adaptive values of phenovariants, would apply in the measurement of genovariants. In this case, and as Waddington implied in his scathing critique, the only way such measurements could then be made unproblematic, would be by making them in populations isolated from the environments responsible for conferring adaptive value (on genovariant and phenovariant alike), which would of course be impossible. For Waddington, then, Gause's views would have most vividly illustrated the fatal problem with the modern synthesis understanding of heredity: namely, that it was based on the fusion of Weismann's rigid distinction between germinal (blastogenic)

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[50] Gause's answer to what he perceived to be the problem of measuring the adaptive values of phenovariants, or adaptive modifications, was to be content with relative measurements. Hence he made inter-racial measurements between forms with notably different innate modifiabilities, simulating as closely as possible the study of separate genovariant forms. Thus he stated: "It is well known that different races of the same species possess innate differences in adaptability: some of them yield strong modifications, the others weak ones, *under the same change of environment*. In this way, working with different races one gets access to *different dosages* of any specific modification, all other conditions being equal. It is then possible to enquire whether any relation exists between the magnitude of a modification and the rate of multiplication of the organism bearing it. Let us admit that the greater the modification, the better an animal multiplies itself under the new conditions. Such an observation is sufficient to conclude that the modification in question possesses a positive adaptive value. But if the magnitude of a modification is not correlated with the rapidity of multiplication of the organism bearing it, one can safely conclude that such a modification has no adaptive value." (Gause 1947, pp. 23-24; author's emphases) Gause's dual methodology clearly illustrated what Waddington described as an inability "to conceive of the genes as controlling the response of the organism to the external circumstances," and hence to realise the important developmental connection uniting both his modes of measuring adaptive values (Waddington 1957, p. 165).

and acquired (somatogenic) characters, and neo-Mendelian gene-character determinism (see my concluding chapter, section 5.1.). The strong neo-Weismannian influence in Gause's work meant that, for Gause, the appearance of genovariations in ontogeny was necessarily entirely independent of the modificational influence of the environment, which influence alone determined adaptive value.[51]

Such a rigid separation of genovariation from all other forms of adaptive change to the phenotype, was graphically reinforced by Gause's and Alpatov's extensive researches in the early 1940s. One of the results of this research was apparently the uncovering an inverse quantitative relation between inherent and acquired forms of an adaptive character, which the author's published in the briefest of articles in *The American Naturalist.* Using two graphs, Gause and Alpatov summarily illustrated an apparent inverse relation, holding between levels of "inherent" and "acquired" resistance to salinity in the infusorian *Paramecium caudatum.* In the words of the authors, acquired resistance was "distinctly inversely proportionate to inherent resistance." (Gause and Alpatov 1940, p. 478). Gause identified this phenomenon as being an instance of "the principle of compensation in biology . . . enunciated by Geoffroy St. Hilaire more than a hundred years ago." In 1940, Gause and Alpatov again wrote: "Geoffroy St. Hilaire realised that with the increase of some organs, others decrease . . . the compensation is due to a redistribution of the limited amount of matter in a biological system" (ibid.).

Thus for Gause and Alpatov, biological matter itself, a finite amount of which was allocated by the ontogenetic economy to meet each specific adaptive need, was diverted into one or the other of these two physically distinct, but phenotypically indistinguishable, adaptive forms. In the process of organic selection, the initial "receptacle" for matter allocated to some adaptive response to the environment was a determinate phenovariation; an adaptation produced on the basis of a purely phenotypic plasticity. This was followed by a second receptacle; namely, a randomly produced and (almost) identical genovariation, based solely upon genetic mutation. These two forms were even likened by Gause to physically distinct organ structures. In applying Geoffroy's resurrected principle, Gause stated that he had high hopes for

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[51] Compare this position with T. H. Morgan's very similar views, regarding the absolute phyletic insignificance of environmentally produced adaptive modifications (footnote 29 above).

forging a synthesis with evolutionary palaeontology. He laid down three generalisations regarding the principle "deduced easily from experimental observations."[52] Thus for Gause and Alpatov, the inverse relation between these supposedly distinct forms provided observational evidence for a physiological distinction between them. This in turn provided the necessary *a priori* grounds for the rejection of any genuine inheritance of acquired characters, since, it was now clear to the authors, the initial non-heritable plastic modification bore no material relation whatsoever to its subsequent heritable imitation. Direct inheritance of the modification was therefore obviated, and neo-Lamarckian inheritance was a biophysical impossibilty. According to Gause and Alpatov, Rensch had "mentioned several examples" of Geoffroy's antiquated principle in 1939. The authors themselves provided several examples from human physiology, such as the relationship between acquired and inherited resistance to low barometric pressure at high altitudes.

What might be the implications of Gause and Alpatov's principle, within one of our earlier examples of organic selection? Returning to Thorpe's *Drosophila* experiments, the suggestion is that there must, at some level, be an absolute neurophysiological difference between the mechanisms underlying feeding behaviour acquired by ancestral larvae, and that mechanism which finally becomes hereditary in descendant adult flies as a result of coincident selection. Such an extreme interpretation of the phenomena of organic selection seems highly implausible, and

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[52] The following is a paraphrased version of Gause's three generalisations "deduced easily from experimental observation:

First Generalization. When a heterogeneous group of individuals, whose members differ in the initial magnitude of some of their properties, is subjected to some external influence, *the acquired alteration is the greater the less is the initial value of a given property in a given individual.*

Second Generalization. The decrease of acquirement per unit of increase in the initial property represents a fixed value, and does not depend upon the absolute magnitude of the initial property. This directly follows from the rectilinear relation between acquired and initial properties. . . . The decrease of acquirement per unit of increase in the initial property can be termed the *specific resistance* of an organism. . . . With the aid of this term our second generalization can be written thus: *the specific resistance of a biological system maintains a fixed value during any constant action of an external force.*

Third generalization. The specific resistance increases with the increase in the intensity of the external action. When the same group of individuals is studied after some slight external influence at the time t_1, and later after a stronger action at t_2, the specific resistance being in each case a constant value, will be in t_2 greater than in t_1. (Gause 1947, p. 57, author's emphasis throughout).

begs the question: Why is there such similarity between the phenovariant and genovariant forms of adaptive morphological and behavioural characters? This problem of apparent morphological equivalence was, in fact, directly addressed by Gause in section II. 4 of *The Problems of Evolution* subtitled: "The resemblance of genetic adaptation to adaptive modification." Gause opened with the doctrinal assertion:

> It is unlikely on *a priori* grounds that the resemblance of genoadaptations to phenoadaptations which they substitute will be a far-reaching one. As far as substituting or organic selection is based upon a greater adaptive value of possible genovariations as compared to modifications, and not upon the inheritance of the latter, it is probable the likeness between these two types of acquirement will be limited to a superficial resemblance only. It is hardly reasonable to expect that genoadaptation will imitate all particulars of a physiological response. (Gause 1947, p. 37).

Again, Gause's improbable suggestion that the genetic response of the organism was entirely distinct from its adaptive physiology, added considerable weight to Waddington's deep misgivings over substituting selection. Furthermore, the empirical research to back up Gause's less than emphatic statement of doctrine was quite inconclusive, leaving Gause to suggest that "there is certainly an urgent need for further studies in this important field" (ibid.).

Waddington, whose genetic assimilation was not mentioned at all by Gause in his 1947 monograph, therefore found in Gause's research the perfect foil for all his objections to organic selection in general. He began by remarking that Gause "does not seem to conceive of the genes as controlling the response of the organism to external circumstances; he phrases his description always as though the action of the gene was quite independent of the environment" (Waddington 1957, p. 165). Waddington once again attacked the organic selectionist suggestion of a non-genetic plasticity of the phenotype, and focused his criticisms on work published by Gause in 1940 and 1941, investigating the acclimatisation of the ciliate *Euplotes vannus* to different salinities. In this work on *Euplotes*, Gause had discovered that the organism could easily withstand a sudden transfer from water at 2.5% salinity, to water of 5% salinity. Gause supposed this tolerance was "probably due to the fact that the salinity of the lake from which it comes sometimes attains about 5 per cent in the dry period" (Gause 1947, p. 28). *E. vannus* reproduced clonally in the laboratory, therefore by looking at the surface area changes of different clonal lines over several generations, Gause found that "When infusoria [*Euplotes*] are cultivated for some time at 5%

salinity in pure clones in the laboratory, the body size of all clones diminishes as compared to that observed in the 2.5% medium." Changes varied between a 2.2% decrease in surface area in some clones, up to a 20.1% decrease in one clone. For Gause, these changes were "obviously adaptive, bringing *E. vannus* closer to a smaller species inhabiting more saline waters." However, the organism also reproduced conjugatively, prompting Gause to ask: "How will the acclimatization of *E. vannus* to 5 per cent salinity be affected by the natural selection of chance inherent variations arising at the time of conjugation of the opposite mating types in the mixed cultures?" To investigate this problem, Gause explained, mass conjugation of infusoria was induced. Firstly, separate clones showing 2.2% and 9.9% surface area reduction in 2.5% salinity were mixed for conjugation. Secondly, two more clones showing 20.1% and 12.5% reduction in 2.5 per cent salinity were also mixed (ibid.). The results, Gause believed, showed that "*in the mixed culture* [sic] of exconjugant clones, the average body surface in mixed population . . . was considerably less than the average of the ancestor lines . . . living under the same conditions of increased salinity. In other words, natural selection in a mixed population works in the direction of strengthening the adaptive modification." From this result, Gause concluded: "It appears that we are dealing here with a case of organic selection, which improves the adaptive modification by selection of casual inherent variations in the same direction" (p. 29). However, he continued, with a further increase in salinity to 7%, "adaptive modifications in *E. vannus* are no longer formed and various strains entirely die out." Nevertheless, among exconjugants there was direct natural selection of viable individuals, which became the ancestors of the culture that survives. Crucially in this instance, as far as Gause was concerned, there was "clearly no organic selection," only classical Darwinian selection (or in Gause's terminology "direct natural selection") of spontaneously occurring mutations (p. 32).

Waddington clearly felt that Gause's explanation of the breakdown in adaptive response, when environmental change outstrips a population's adaptability, provided a decisive refutation of Gause's concept of substituting selection. Waddington therefore complained about his analysis:

> Gause showed that in several cases natural selection in a particular environment operates to produce changes, in characters such as body size, which are similar to the direct adaptations to that environment exhibited by vegetatively propagated clones. This he considers to be 'organic selection' in the sense of Baldwin, since it involves the selection of genes which act in

> the same direction as the environment. But he does not seem to conceive of the genes as controlling the response of the organism to the external circumstances; he phrases his description always as though the action of the gene was quite independent of the environment In fact, when the abnormal environment is so extreme that the initial vegetative clone cannot survive in it, although some segregating ex-conjugants succeed in doing so, he denies that this is also organic selection writing: . . . 'Among ex-conjugants direct natural selection of viable individuals occurs . . . in this case there is no organic selection'. Thus he does not consider that the segregated genotypes which are favoured by natural selection operate by making possible an adaptation of some kind to the environment; he seems to think of their phenotypic effect as merely selected by the environment but not otherwise modified by it (Waddington 1957, pp. 165-166).

Thus Waddington deplored that for Gause, genovariation consisted in the direct production of heritable characters unalterable by environmental changes. In Gause's view, the adaptive ex-conjugants described above must first have replaced a similar phenovariant from the initial vegetative clone, for organic selection to have actually occurred. In the example above, this was not the case, and therefore the selection process was by definition a classical neo-Darwinian one. Yet in Gause's understanding, since there can be no causal connection between the initial phenovariant and subsequently selected genovariant; the theoretical requirement for a preceding phenovariant form seems completely arbitrary. Waddington once more concluded that, in this complete separation of phenotypic plasticity from genotypic variation, Gause was "probably giving to the phrase organic selection, though in modern Mendelian terms, precisely the significance which Baldwin and Morgan intended it to bear" (ibid.). Thus, again, Waddington felt able to re-stake his claim to priority over the true mechanism for the inheritance of adaptive modifications; namely, genetic assimilation.

2.6.2. Gause and Schmalhausen: The Appropriation of Stabilising Selection by Soviet Neo-Organic Selectionists.

Regardless of the relationship of substituting selection to Baldwin and Lloyd Morgan's original concept, and of the legitimacy of the use of Geoffroy's obscure principle, Gause's use of stabilising selection was undoubtedly far from Schmalhausen's intentions. It is evident, from the Soviet literature on adaptive modification and evolution from the 1940s, that Schmalhausen stood apart from the rest of the Soviet research in this area. The group of authors that Waddington broadly identified as Russian in *The Strategy of the Genes*, all held to a conception of stabilising selection which reduced Schmalhausen's term to yet another synonym for organic selection. In spite also of Simpson's attempt to make organic selection subsidiary to the "broader principle" of stabilising selection, Schmalhausen in 1946 viewed his own concept as completely distinct from organic selection. To Schmalhausen, organic selection was merely the classical Darwinian, or, in his terminology, "dynamic selection" of coincident variations.[53] This fact did not, however, deter the Soviet organic selectionists from trying their best to keep Schmalhausen within the fold. Kirpichnikov, as we have noted, clearly understood the issues, but believed Schmalhausen's concept attempted to draw a distinction from his own "coincident" selection which could not be supported. Hence he wrote of Schmalhausen's views:

> The substance of the theory of stabilising natural selection in contrast to 'direct' natural selection is that the former takes place on the basis of selective advantage of the normal phenotype in comparison with the deviations. According to Schmalhausen, the selection of favourable deviations from the normal type does not occur in this case. Since, however, Schmalhausen (1941) agrees that the development of the organism is perfected and the role of regulation in its development is increased as a result of which a better adapted phenotype is achieved in the above mentioned case, the author of these lines does not see the necessity of drawing a strict line between these two conceptions. (Kirpichnikov 1947, p. 170).

The point Kirpichnikov makes here is a particularly important one which requires further clarification, since it is at the heart of the Soviet debate over the supposed independent status of stabilising selection--independent, that is, from all forms of neo-organic selection--in the 1940s. The crux of the argument was whether one may classify genetic changes that perfect an organism's development--along with others that increase the role of regulation in development--as "favourable deviations" from the pre-existing norm of reaction. In other words, was Schmalhausen's 1941 developmentalist differentiation between "stabilising" genetic changes and "deviating" ones (which latter, in his view, characterised all kinds of dynamic

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[53] Gause's and Kirpichnikov's "direct selection," Hardy's "external selection," and Schmalhausen's "dynamic selection," may all be understood as synonymous with classical Darwinian natural selection. Schmalhausen, however, also saw Lukin's and Gause's substituting selection as merely classical (dynamic) selection. Waddington went further and altogether denied the independent existence of classical Darwinian selection; independent, that was, of his own canalising selection--which latter was characterised by Waddington, after reading Schmalhausen's 1949 English translation of *Factors of Evolution*, as "stabilising selection *sensu stricto*" (Waddington 1957, p. 72).

selection including organic selection), a distinction without any discernible difference? Kirpichnikov's argument was simply that "perfection" of a phenotypic norm presupposed an alteration of that norm, and was therefore just as much a movement away from the previous norm as any other alteration. After all, Schmalhausen in *Factors of Evolution* had actually defined genetic mutation as a change to the norm of reaction.[54]

In any event, the developmentalism within Schmalhausen's theory is well illustrated within Kirpichnikov's contention, although Schmalhausen's emphasis upon the *epigenetic* stabilisation of the mechanisms of developmental regulation seems to be just as ignored by Kirpichnikov as by Gause. Schmalhausen's functionalist morphology, developmentalism, and ecological approach to the evolutionary significance of adaptive modifications, were all major elements contributing to the uniqueness of his synthetic theory. Collectively, these approaches presented evolutionary biology with a truly integrative synthesis; a definite breakpoint from the single visioned gene-character determinism of the synthetic theory. Yet Kirpichnikov, even whilst accepting Schmalhausen's antagonistic definition of the process of stabilising selection, still believed him to be talking about coincident selection. According to Kirpichnikov, Lukin felt precisely the same way as himself. Thus Kirpichnikov wrote: "Lukin makes no difference between the two phenomena observed in nature, namely; (1) the fixation of diversities or the elimination of the possibility of returning to the original state without compulsory automitization of development (coincident selection) and (2) the fixation of the character, the diminishing of its dependence upon the environment, its stabilisation and the growth of the role played by the autoregulatory processes in development (stabilising selection)" (1947, p. 168). Hence we may conclude that, at least for Gause,

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[54] A possible counter argument to Kirpichnikov's might revolve around the concept of regulation itself. Schmalhausen's increasing stabilisation of development, like Waddington's "canalizing selection" (1953a, p. 387), consisted in the ever better regulated unfolding of *existing* developmental pathways for each character, not the continual production of modified pathways. The stabilisation/canalisation mechanism, it may be argued, does not constitute a deviation from the original phenotypic norm, but a reinforcement of it (see my section 1.3.2. for discussion of the embryological origins of canalisation within the notion of reacting tissue specificity, and section 4.1.1. on the nature and action of Schmalhausen's stabilising selection).

Kirpichnikov and Lukin, Schmalhausen's intricate distinction between organic selection and stabilising selection had no basis in any real evolutionary mechanism.

In conclusion, then, Waddington and Schmalhausen did indeed stand very much alone in their understanding of the evolutionary significance of adaptive modifications to the phenotype--more so than many concerned theorists during the 1950s and 1960s may have wished to believe. Waddington suggested from the structure of his published writings, and clearly intimated in his private correspondence, that they both stood far apart from Western neo-organic selectionists of all kinds and all strengths. Thus they stood apart from Huxley, as well as the more extreme positions of Hardy and Ewer (and the absolute extremism of Hovasse). They were united in their refusal to allow the concepts of canalising and stabilising selection to be misrepresented, either by attempts at identification of those concepts with classical Darwinian selectionism or, uniquely to Waddington, with either classical organic selectionism or neo-organic selectionism.[55] Again, Waddington and Schmalhausen stood far apart from the Soviet neo-organic selectionists, whose relentless proliferation of apparently empty synonyms for Baldwin's original concept, both men recognised to be nothing more than classical natural selection in thin disguise. Most importantly, they both withstood attempts, made by the Western supporters of the modern evolutionary synthesis, to identify a resurrected and 'Mendelised' organic selectionism with their synthetic theories. As I shall discuss in the next chapter, Simpson's ostensible subordination of organic selection to Waddington's canalising selection *sensu stricto*, failed to conceal the attempted replacement of Waddington's and Schmalhausen's respective core mechanisms with stage two of Simpson's "Baldwin effect"; that is, with coincident selection itself.

In fact, neither Waddington's nor Schmalhausen's ideas were at all conformable to the continuation, to use Waddington's disparaging phrase, of the neo-Mendelian "heap of pebbles and gravel-sorter" of the modern synthetic theory (Waddington

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[55] By contrast, Schmalhausen appeared to hold the concepts of Baldwin and Lloyd Morgan in much higher regard than did Waddington. Hence Schmalhausen thought the works of Lloyd Morgan, Baldwin, and "a number of other Darwinian animal psychologists" to constitute an "excellent and hitherto unexcelled analysis of the evolutionary importance of adaptive modifications from the Darwinian point of view." In keeping with a lower regard for his compatriot neo-organic selectionists, he continued immediately: "Unfortunately, the more recent advances of genetics have prompted the spread of neo-Darwinian concepts" (Schmalhausen 1949, p. 198; see my Chapter 4, section 4.3.1.).

1960, p. 400). It was this reductionistic and atomistic mechanism that appeared so important, at least for many supporters of the modern synthesis, to the easy acceptance and complete institution of the hardening strong selectionist orthodoxy.

Chapter 3.

Waddington's Alternative Synthesis: Genetic Assimilation and the Canalisation Hypothesis.

> Is it, or is it not , the case that the effects of use and disuse are inherited ? It should be possible to decide by experiment.[1]
>
> C. H. Waddington.

3.1. The Edinburgh Genetics Institute and the Experimental Verification of Genetic Assimilation.

Waddington's work on the evolutionary fixation of adaptive modifications to the phenotype was primarily influenced in the post Second World War period by experimental genetics. In his biographical memoir to Waddington, Alan Robertson said of the career of Waddington the evolutionist: "I feel that he will be remembered as an experimentalist in this field mostly for his work on genetic assimilation, carried out mostly in the 1950s but in fact adumbrated in a paper of 1942 on 'Canalization of development and the inheritance of acquired characters'" (Robertson 1977, p. 599). In an autobiographical note published in 1969, Waddington complained about the prospects that had existed for geneticists in 1930s Britain. Describing how he came to work in experimental embryology, specifically Needham's chemical embryology, Waddington stated that had it been possible he would have focused on genetics much sooner in his career: "In fact, when I decided I wanted to do something more experimental than is possible in palaeontology, I first tried to become a geneticist. My first two published papers were, one in plant genetics, and another a collaboration with J. B. S. Haldane along classical neo-Darwinist lines. . . . But my attempt to become a geneticist was a failure, because at that time in Britain there

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[1] Waddington 1962, p. 8.

simply was no way in which one could earn a living at the subject" (Waddington 1969, p. 79).[2]

However, very soon after the war Waddington's fortunes as a geneticist were to change dramatically. As Robertson tells us, "early in May 1945, there came out of the blue an offer of the chair of genetics at Edinburgh, whose previous occupant, F. A. E. Crew, was returning from the war with changed interests to a new chair of social medicine. There were then only three chairs of genetics in the country and this was obviously a most attractive offer."[3] Having already accepted the post of chief geneticist and deputy director of the National Animal Breeding and Genetics Research Organisation, recently set up under the Agricultural Research Council, Waddington hesitantly refused the Edinburgh post. However, Robertson continues: "The matter was given a different twist after a chance visit by White to Edinburgh. There it was put to [Waddington] that NABGRO might find a permanent headquarters in Edinburgh (plans at the time were for Oxford) with Waddington combining the position of chief geneticist at NABGRO with the [Buchanan] Chair of Animal Genetics in the University. After much discussion this was in the end

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[2] See Gayon 1992, p. 354, for a description, including diagram, of Haldane's and Waddington's 1931 collaborative work on the eighth of ten monographs: "A Mathematical Theory of Artificial and Natural Selection. Part VIII. Metastable Populations." Gayon reproduces Waddington's diagram, which apparently represents the first mathematical model of evolution, in terms of changes in allelic frequencies, in a population subject to selection at two gene loci in epistatic interaction. This collaboration with Haldane may have had greater influence upon Waddington's evolutionary thinking than he gave credit to in his autobiographical sketch. Hence, within the general context of the concept of progress in evolution, and with particular interest in the source of inspiration for Wright's "adaptive landscape" metaphor, Ruse remarks of Gayon's analysis: "In [Bergson's] *Creative Evolution* there is something much like the landscape metaphor for evolution; but Gayon perceptively suggests that the direct influence may have been Haldane and his more artistically gifted assistant, C. H. Waddington, who were toying with landscape-like metaphors in Haldane [1931, Part VIII]" (Ruse 1996, p. 545; see also Kai Hahlweg 1981, for the concept of progress in Waddington's writings). Yet, Ruse adds, "given the date of Wright's letter to Fisher (February 3, 1931) with a proto-version of the landscape , the timing might be a bit tight to give Haldane and Waddington full credit" (ibid.). However, Waddington's own "epigenetic landscape" was first alluded to in his 1939 *Introduction to Modern Genetics*.

[3] Falconer adds detail to this account: "The outbreak of the second world war brought the Congress [the Seventh International Congress of Genetics, held in Edinburgh in August 1939] and most of the Institute's activities to an abrupt end. During the war Crew, who had a medical degree, worked in the War Office on medical statistics. He resigned his chair in 1944 because, so he said, he felt himself to be too much out of date in genetics, but he returned to Edinburgh to take up the Chair of Public Health and Social Medicine" (Falconer 1993, p. 138).

agreed."[4] In Robertson's estimation, this occurrence heralded "one of the most fruitful periods, not so much of [Waddington's] own output but of his influence both on his department and also on the development in Edinburgh of biology as a whole" (Robertson 1977, p. 581).

As Falconer recalls in his recent anecdotal history, the Genetics Section of NABGRO was moved from its temporary quarters in London up to Edinburgh in 1947. Falconer tells us: "It was housed together with the University Department in a building named the Institute of Animal Genetics. The main part of ABGRO [sic] was accommodated in a large rented villa not far away until a new building on the University campus close to the Institute was opened in 1964" (Falconer 1993, p.137). In Falconer's opinion, the location of NABGRO in Edinburgh "continued a distinguished tradition of animal breeding and genetics there." There were, he recalls in concurrence with Robertson's account, "only three university departments of genetics in the United Kingdom: London's University College (where J. B. S. Haldane was Professor), Cambridge (with R. A. Fisher), and Edinburgh (with F. A. E. Crew). Edinburgh's department was the first, established in 1919 as the Animal Breeding Research Department, with Crew as its Director but no other staff and no building." Crew was, says Falconer, a "forceful and persuasive speaker" who had apparently "cajoled several wealthy industrialists into providing funds for a new building and to endow a chair," founded in 1928, with Crew as occupant. The title of the chair changed to simply Genetics when Waddington took over from Crew (ibid.).[5] Falconer paints a bustling and cosmopolitan picture of Edinburgh genetics under Waddington's leadership. Describing Waddington as "an inveterate traveller widely known throughout the world," he recounts:

> Waddington's breadth of interests, and the reputation of the Institute, attracted many visiting research workers and Ph.D. students, so that there were usually more visitors than indigenous staff. New people seemed to be arriving almost every day and it was hard to keep track of who was who and doing what. An idea of the numbers can be got from a list of people present

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[4] According to Robertson, R. G. White was then Professor of Agriculture at Bangor, and director of NABGRO.

[5] Falconer tells us some of the names that graced the Edinburgh department prior to Waddington's arrival: "Crew's enthusiasm attracted many visitors who came for short visits or for long periods of research, among whom were some notable figures--Lancelot Hogben, Julian Huxley, J. B. S. Haldane, and H. J. Muller (who was there from 1938 to 1940)." Muller was awarded his D.Sc. there in 1940 (Falconer 1993, p. 137).

> in June, 1962. There were 22 permanent staff and 36 temporary research workers. The visitors came from 13 countries in addition to the United Kingdom. Their fields of work are recorded as development (12), quantitative genetics and animal breeding (10), mutation (7), Paramecium (4) Neurospora (2), and gametes (1). With so many people of such diverse interests the Institute was a lively and stimulating place. It was great privilege to work there during that time. (1993, p. 141).

Here, then, at the Institute of Animal Genetics--after some problems during the late 1940s with post-war re-establishment and recruitment--Waddington's team worked extensively upon the experimental verification of the genetic assimilation theory. It was this work which became the hallmark of his experimental contribution to evolutionary biology, though apparently very little of the experimental work was done by Waddington himself (J. H. Sang, personal correspondence 1998). There were clear connections with earlier experimental methods, adopted during the Strangeways embryological research into the chemical nature of the evocator. The particular connection was with Waddington's research into inorganic substances that mimicked true neural tissue evocation.[6] Thus, as Robertson has observed:

> He and his co-workers used environmental agents which produce 'phenocopies,' i.e. they mimic the morphological effect of known mutants. It is interesting that his basic knowledge of such agents came from his earlier use of them to interfere with normal development. Working with *Drosophila*, they then bred from those animals which had responded to the stimulus, repeating this over many generations. In the end, the selected lines would in a high proportion of cases give the developmental response without the external stimulus. Waddington referred to this process as 'genetic assimilation.' (Robertson 1977, p. 600).[7]

The emphasis upon these experimental techniques as a model for the hereditary fixation of adaptive modifications to the phenotype, and the use of the term genetic assimilation for the mechanism of such fixation, provided the foci for much criticism of Waddington's views. Furthermore, although many geneticists accepted genetic assimilation as a mechanism for the supersession of an external stimulus by an internal genetic one, many (including Alan Robertson) also denied that canalisation

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[6] See my section 1.3.1. for detailed discussion of the evocator substance research programme.

[7] Robertson refers to Waddington's 1930s work, in collaboration with the Needham's, at the Cambridge Strangeways laboratories to discover the chemical nature of the evocator. Interestingly, Waddington continued with an embryological investigation of these systems at Edinburgh in the 1950s, but employing a biophysical rather than a primarily biochemical approach. See Waddington and Yao (1950), Waddington (1952b), and Waddington and Deuchar (1952c).

was a necessary component of the process.[8] Canalisation, which for Waddington was a prerequisite for genetic assimilation to occur, was essentially an embryological notion. It had been developed out of the concepts of reacting tissue specificity, and natural selection for greater competence efficiency, in tissues responsible for important developmental reactions (See section 1.3.2.). Along a similar line of criticism, Gilbert tells us that Mayr and Dobzhansky "claimed that there was no genetic assimilation" in the Waddingtonian sense, and that "what Waddington saw in his experiments was merely the selection of pre-existing variants in the population" (Gilbert 1991).[9] As we shall see, in the view of almost all other contributors to the modern synthetic theory (whether they supported some version the concept of canalisation or not), the only acceptable explanation for the phenomenon of genetic assimilation was the selection of coincident mutations in the population.[10]

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[8] Robertson provides a definition of genetic assimilation, qualified by reservations over canalization: "The concept of genetic assimilation may be summarized briefly as follows. The capacity to respond to an external stimulus by some developmental reaction must itself be under genetic control. If such a reaction is adaptive, i.e. it increases the viability and fertility of the individual, then there would be natural selection for individuals capable of giving the optimum response. In the end, then, a population of individuals might be produced giving the optimum response without the external stimulus. To this, he added the concept of canalization" (Robertson 1977, pp. 599). Robertson (and many others) did not accept Waddington's opinions as to the necessary conditions for assimilation, hence Robertson added: "His concept of genetic assimilation provides an explanation of the 'inheritance of acquired characters' as a population phenomenon arising from natural selection of those individuals more capable genetically of the adaptive response. To Waddington, the concept of canalization was critical to this argument as providing a reason for the existence of much genetic variation hidden in the normal phenotype, concealed because of natural selection for those animals which under natural selection did not respond to a genetic stimulus, i.e. in situations where response would be non-adaptive. It is however not necessary to the main argument on genetic assimilation and, when applied to characters showing quantitative variation and not involving a threshold, has not in my view proved useful" (1977, p. 600).

[9] Gilbert has expressed the view that "Waddington's term 'genetic assimilation' was poorly chosen in that it did convey a notion that physiological responses could be readily fixed in the genome." Given such apparently neo-Lamarckist leanings in Waddington's terminology, Gilbert adds that "it is not hard to understand how Waddington's views could be thought of as subscribing to a goal-directed inheritance of acquired characters" (Gilbert 1991, p. 205).

[10] Genetic assimilation was, therefore, seen as essentially identical to Lloyd Morgan's and Baldwin's original concept of "organic selection." This was a process accepted in the early 1940s, by Mayr and particularly by Huxley, a neo-Mendelian interpretation of which was characterised by Simpson in 1952 as the "Baldwin effect" (see Chapter 2).

3.1.1 The Genetic Assimilation Research Programme in the 1950s: Waddington's Verification of the Canalisation Hypothesis.

In 1961, Waddington published a comprehensive 33 page review of an entire decade of experimental research entitled "Genetic assimilation" (Waddington 1961, 257-290). In the opening paragraph Waddington provided the reader with his own short definition of the process under investigation: "Genetic assimilation' is the name which has been proposed . . . for a process by which characters which were originally 'acquired characters,' in the conventional sense, may become converted, by a process of selection acting for several or many generations on the population concerned, into 'inherited characters'" (Waddington 1960, p. 257).[11]

Given the obvious possibility of a fully neo-Lamarckian interpretation being placed upon this definition, Waddington was quick to reassure the orthodox reader although, as is usual in Waddington's writings, far from unequivocally. Thus he stated: "The phenomena revealed by the experiments on genetic assimilation cast no doubt on the thesis, generally accepted by geneticists, that acquired characters are not inherited (except in very special circumstances), but lead to the conclusion that there is no justification for arguing from this that they have no effect on the course of evolution. On the contrary, it becomes apparent that the conventional and accepted facts and theories of genetics provide a mechanism by which 'acquired characters' must exert some influence--and probably a rather important one--on the direction in which evolutionary change proceeds" (1960, p. 258).

It is interesting to note that Waddington's rhetoric of the early 1940s, has been very significantly toned down for the modern synthesis geneticist of 1960. The Waddington of 1941 had felt at greater liberty to express the more challenging and contrary view that "adaptive characters are inherited and some explanation for this must be provided" (Waddington 1942, p. 563; see section 1.2.2. for full quotation). Yet twenty years of deepening selectionism within the modern synthesis, and

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[11] Waddington here makes reference to the paper where the genetic assimilation term was first used and defined by him: "Genetic assimilation of an acquired character," (Waddington 1953a, 118-126). Hall provides an interestingly embryological view of genetic assimilation, reminding us that it was from the embryological concepts that genetic assimilation developed: "Waddington proposes genetic assimilation as a mechanism to relate genetics, development, adaptation and environmental changes. Its essence is that embryos possess the genetic capability of responding to environmental perturbations" (Hall 1992, p. 117).

consolidation of a mathematical population genetic approach to evolution, had made a less strident voice expedient when addressing the evolutionary genetics community. Hence in 1960, Waddington carefully explained that "The notion of genetic assimilation involves both a phenomenon, and a mechanism by which this phenomenon is brought about." (p. 259). The phenomenology of genetic assimilation was, in fact, neo-Lamarckian, and "may be described as the conversion of an acquired character into an inherited one; or better, a shift (towards a greater importance of heredity) in the degree to which the character is acquired or inherited" (ibid.). Thus, in 1960, as in 1941 and throughout his career, Waddington did indeed support an actual, and not merely apparent, hereditary fixation of acquired modifications to the phenotype. The mechanism of this fixation is neo-Mendelian and selectionist, hence he added "the name 'genetic assimilation' is given to such processes of conversion when they are brought about by selection acting on the genotypes in [a] subpopulation" (ibid.). One of the problems for Waddington's research programme in the 1950s was that the founders of the modern synthesis, thanks primarily to Julian Huxley's 1942 *Evolution, The Modern Synthesis*, had already accepted this mechanism to be the neo-Mendelian version of Lloyd-Morgan and Baldwin's organic selection (see section 2.3.).

One way of expressing the central difference between neo-organic selectionism and Waddington's genetic assimilation, is that neo-organic selection failed to recognise any place for the notion of canalisation. Neo-organic selectionists could not accept (both for theoretical reasons, and for reasons involved with defending of the emerging modern synthesis) any actual inheritance of acquired modifications. Hence, whilst Waddington recognised that "other mechanisms of conversion have been suggested (e.g. the 'Baldwin effect')" yet, due principally to his insistence upon the necessity of canalisation, he consistently maintained that "there is considerable doubt whether they could possibly occur" (ibid.).[12]

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[12] Robertson, in support of genetic assimilation, remarks that: "Waddington found himself facing the argument that his ideas of genetic assimilation were merely a more sophisticated presentation of 'organic selection' put forward by Baldwin and Lloyd Morgan at the start of the century before the rediscovery of Mendelism. Though he confessed that he had not heard of organic selection before he did his work on genetic assimilation, he had little difficulty in showing that, when phrased in genetic terms, their theory was impossible" (Robertson 1977, p. 601). In fact, Waddington (apparently due to his own lack of familiarity with Lloyd Morgan's writings on coincident selection), only had "little difficulty" in refuting the neo-organic

Waddington began the programme for the verification of genetic assimilation in 1952, with an experiment that became a landmark in evolutionary genetics. This experiment, described by Maynard Smith in 1958 as "elegant and illuminating," focused upon the hereditary fixation under selection of an acquired morphogenetic defect of the *Drosophila* wing, namely the absence of the posterior crossvein (Waddington 1953a, 118-126). In the opening paragraph of the paper describing the procedures, Waddington was quick to introduce his prime theoretical concerns, and relate them to the current research:

> Under the influence of natural selection, development tends to become canalised so that more or less normal organs and tissue are produced even in the face of slight abnormalities of the genotype or of the expected external environment. . . . It has been suggested that if an animal is subjected to unusual circumstances to which it can react in an adaptive manner, the development of the adaptive character might itself become so far canalised that it continued to appear even when the conditions returned to the previous norm. . . . This mechanism would provide a means by which an "acquired character" in the conventional sense could be "assimilated" by the genotype, and eventually appear comparatively independent of any specific environmental influence. (1953a, p. 118).[13]

This was Waddington's hypothesis, developed from his embryological research into the chemical nature of the amphibian organiser, of the mechanism that facilitated genetic assimilation. He continued: "The purpose of the present communication is to describe an experiment in which the hypothesis was tested and shown to operate as expected" (ibid.). Concerning the method for producing the crossveinless phenotype, Waddington relates how "It was decided to select a strain of *Drosophila melanogaster* for its ability to form a phenocopy in response to some definite environmental stimulus. . . . After some exploratory tests, it was found that when pupae of a wild Edinburgh strain, S/W5, were given a temperature shock (4 hours at 40 C) at 17 to 23 hours after puparium formation, a fair number of crossveinless wings developed" (ibid.).[14] Deciding this would be an appropriate phenotypic

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selectionism of Huxley, Mayr, Simpson, and the Soviet school. As he himself stated of Baldwin and Lloyd Morgan's writings, "it is not entirely easy to see what their meaning would be when translating into terms of our modern concepts" (see my Chapter 2, section 2.5.).

[13] See Chapter 1, footnote 12, for Hall's definition of the concept of canalisation.

[14] In 1958 Landauer published a review of phenocopy research, and enquiry into the developmental significance of the phenomenon. Reminding us that the phenocopy concept emerged from experiments by Goldschmidt with Drosophila in which the developmental effects of heat shocks were studied, he concluded: "As mutant genes produce a dislocation in the integrated functions of the normal genotype, so do certain external agents, whether physical or chemical,

character to use, Waddington next pre-empted a criticism of his work which was to gain full force some time later, and which came from those questioning the adaptive evolutionary significance of his findings. Hence Waddington continued: "There is, of course, no reason to believe that the phenocopy would in nature have any adaptive value, but the point at issue is whether it would be eventually genetically assimilated if it were favoured by selection, as it can be under experimental conditions" (ibid.).[15]

The experimental protocol ran essentially as follows. Two phases of artificial selection were performed upon flies exposed to the temperature shock. In the first phase, two separate selection lines were set up. In the first line, "only those flies which showed the crossveinless effect after treatment were bred from ('upward' selection, which should increase the frequency of response), while, in the other line, the crossveinless flies were rejected, and only those still showing normal wings were used to carry on the line ('downward' selection)" (ibid.). In each generation of the upward selection line, a large number of flies from untreated pupae were examined,

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intervene in gene-determined developmental events by preventing them at one point or another from accomplishing their appointed ends, leading thereby to a mutant-like phenotype. The point of interference varies according to the existing genotype, the developmental stage at intervention, kind and quantity of the external agent, and still other factors. But I believe that in all instances the resulting phenocopies are the result of external pressure which has a suppressing , retarding or disorienting effect on one or more gene controlled components of the normal or mutant genotype in question" (Landauer 1958, pp. 210-211).

[15] The chief antagonists offering the above mentioned criticism were Maynard Smith (see text below), and, in the 1960s, G. C. Williams. Williams's objections focused not on the crossveinless experiments, but on experiments performed three years later by Waddington on the genetic assimilation of the bithorax phenotype in Drosophila. Like crossveinless, the assimilation of bithorax involved threshold phenomena. Accepting the phenomenon of genetic assimilation as real, and the experiments as important in their "demonstration of a previously unsuspected store of genetic variability," Williams nevertheless contested their value as a model of adaptive evolution: "One source of difficulty is in Waddington's tendency to think of the development of bithorax, after an ether treatment, as a response to a stimulus. The term 'response' usually connotes an adaptive adjustment of some sort, and would not be used for disruptive effects. . . . By favourably selecting the bithorax condition, Waddington produced an extreme but simple kind of degenerative evolution. He was selecting for simple kinds of inadequacies in the mechanisms of developmental canalization. . . . Waddington apparently sees no need to distinguish between response to environmental stimuli and susceptibility to environmental interference. It is my belief that these classes of phenomena are utter opposites and that no more fundamental distinction can be made" (Williams 1966, pp. 75-76). In making these criticisms, Williams appears unaware that this precise debate had been pre-empted by Waddington, both in the 'crossveinless' paper, and in response to Schmalhausen's notion of developmental morphoses (see my Chapter 4). Williams also overlooked Warburton's 1955 commentary on the crossveinless results, explaining that "Waddington's experiment is one of the rare cases of an advantageous exogenous modification [where] selective advantage . . . is a purely artificial condition of the experiment" (Warburton 1955, p. 136).

where a few crossveinless flies were found by the advent of generation 14, and 1 to 2 percent were found by generation 16. Crosses between these flies were set up (using non-virgin females) which indicated that the condition was heritable. From the F1 generation of these test matings, a series of new matings between crossveinless flies (this time taking care to use virgin females), were used to set up a further series of lines, ready for the second phase of selection. In the second phase of selection, flies from lines which were good producers of crossveinless were isolated from flies emerging from other lines which were poor producers of crossveinless. Thus separated, flies were then used to create further separate breeding lines. Consequently, said Waddington, four 'high' lines were produced "which threw fairly high percentages of crossveinless flies at 25 C. with no temperature shock." A similar number of 'low' lines were also isolated. These low lines, he added, "gave very low percentages of crossveinless individuals, although they were derived from the upward selected group and must have shared most of their genetic background with it" (p. 120).[16]

In the opening paragraph of the discussion, Waddington comes to his principal conclusion. After reiterating that the crossveinless condition only appeared in the foundation stock "as an 'acquired' character in the conventional sense," he says: "What is implied is that crossveinless flies only appeared when the original stock was subjected to some particular abnormal environment, in this case one involving a high temperature at a certain pupal age. In the 'high line' derived from the upward selected stock, however, the crossveinless character appeared in the normal environment which did not involve a temperature treatment. It has become a hereditary character as contrasted with an acquired one" (p. 123). Furthermore, it appeared that the genetic assimilation mechanism has been validated at the expense of

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[16] The similarity of genetic background between high and low lines was also, Waddington believed, evidenced by the results of outcrossing high line crossveinless females, firstly to low line wild type males, secondly to downwardly selected wild type males from the first phase of selection, and lastly the original Edinburgh wild type males: "It will be seen that the genetic background of the wild types has a considerable effect on the frequency of crossveinless. In the background of the low lines, which are more or less true breeding wild types derived from the upwardly selected strain, the condition behaves almost as dominant, whilst against the downwardly selected background it is nearly a complete recessive. Against the Wild Edinburgh stock from which the experiment started (W.E.), it shows a slight degree of dominance. This is not surprising if the genes concerned in producing the crossveinless phenotype behave in an additive manner, but, in the original Wild Edinburgh stock, are never present in sufficient concentration to overtop some crucial threshold" (1953a, p. 122).

both the rival 'Baldwin effect' mechanism, and any neo-Lamarckian instructional (that is, somatic induction) mechanism since, says Waddington: "This has certainly not happened solely through the selection of a chance mutation which happens to mimic the original acquired character. The genetic basis which is eventually built up for crossveinlessness differs from the genotype of the foundation stock in many genes" (pp. 123-124).[17]

Waddington clearly saw the results of these experiment as positive verification, not only of the process of genetic assimilation, but also of his canalisation hypothesis as the underlying cause of the eventual hereditary fixation of crossveinlessness. Canalisation was in evidence because, according to Waddington, the genetic basis for posterior crossveinless flies was polygenic. "There is evidence," Waddington added, "of polygenic segregation even in crosses between the high and low lines, both derived from the upward selected stock, and there are still more gene differences between the high lines and the downward selected stock" (p. 124). Hence the final point in Waddington's four point summary simply stated: "The genetic basis of the assimilated crossveinless character is polygenic. There is little evidence of any definite distinction between canalising and switch genes" (p. 126).

For Waddington, then, this first experimental demonstration of the genetic assimilation phenomenon agreed precisely with his 1940 embryological sketch of the theory: that is, with the notion that assimilation occurred as an event within the process of canalisation, where the internal morphogenetic stimulus to produce the character is superseded by a genetic one. However, as Waddington had suggested 12 years earlier in the context of the evolution of the amphibian primary induction mechanism, the heritable stimulus superseding the morphogenetic action of the evocator may actually be epigenetic and difficult to determine. Hence, in his explanation of Braus' phenomenon of double assurance, Waddington had stated that the evolution of a very efficient tissue competence would reduce the importance of the evocator, "which will probably tend to disappear;" leaving its function to be

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[17] This point clearly would not have impressed the (reluctant) neo-organic selectionist G. G. Simpson. In his 1953 *Evolution* paper "The Baldwin effect," published simultaneously with and adjacently to Waddington's crossveinless results, Simpson enthusiastically remarked of Waddington's genetic assimilation: "The phenomenon involves . . . .a broader principle of which the Baldwin effect may be considered a special case" (p. 116).

"taken over by minor variations in conditions which are very difficult to identify" (1940, p. 49; for full quotation see section 1.3.2.). By 1942, Waddington had become more specific about the nature of these obscure variations, in that they may be caused, "for example, by the internal mechanism of a genetic factor" (1942, p. 565).[18] For Waddington, not only might the final stimulus for assimilation be difficult or impossible to determine, it may in fact be unique to each separate *Drosophila* lineage. Hence, quite controversially, he concluded of the crossveinless experiments that "It seems quite possible that if a similar selection for crossveinless formation was repeated, perhaps using a different foundation stock, the same phenotypic effect might be produced with quite a different genetic basis" (1953, p. 124).

3.1.2. Crossveinless Revisited: The Work of K. G. Bateman on Four Venation Phenocopies and the Questionable Role of Canalisation.

In his 1961 review paper, Waddington gave an extensive account of the follow up research at Edinburgh of K. M. Bateman, on the genetic assimilation of four venation phenocopies, including posterior crossveinless. There appeared, to judge from Waddington's discussions of these experiments, to be nothing in Bateman's conclusions to contradict his own from four years earlier. Her research further elaborated the role played by each of the four *Drosophila* chromosomes, and pointed out, said Waddington, that "a considerable number of loci which produce breakages of crossveins are known on chromosome 3, while on chromosome 2 there are quite a large number of genes which tend to produce extra veins." Notwithstanding that it "remained very obscure," in Waddington's view, "why genes producing these two types of phenotypic effect should be, as it were, sorted out onto different chromosomes," nothing appeared untoward (Waddington 1961, p. 265).

Bateman produced her initial publications on genetic assimilation in 1956 as a Ph.D. student. In closing her first post-doctoral paper, which focused on the crossveinless class of phenotypes, she thanked Waddington for suggesting this problem, and acknowledged the "benefit of much useful discussion with many members of the Institute of Animal Genetics" (Bateman 1959a, p. 474). On the face

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[18] See my Chapter 1, section 1.3.1. for the story of the search for the chemical nature of the evocator in amphibian neural induction.

of it, Bateman's work appeared far more extensive and statistically rigorous than did Waddington's own. Four veination phenocopies, originating from the same S/W5 Edinburgh stock of flies used by Waddington, were investigated.[19] Essentially the same 2 phase selection procedure was adopted that Waddington had previously used. As Bateman tells us: "Selection of each character was carried out in two consecutive stages; with treatment, of the phenocopies; and without treatment, of assimilated individuals. The second stage was inaugurated when the frequency of assimilated individuals enabled a stock to be established" (1959a, p. 444). At the beginning of an extensive genetic analysis of the assimilated stocks, Bateman clearly stated what the principal aim "was to determine to what extent potential directions of assimilation are limited by the gene contents of a population: how specific is the genetic basis of assimilated characters ?" Thus, she elaborated, "At one end of the scale of specificity would be a situation in which the presence of a particular gene is obligatory for the process; at the other, one in which control is due to a large number of genes, the individual effect of which are small. Various tests were designed to determine which of these alternative is more nearly approached by the assimilated stocks" (p. 451).

Bateman also added that "the investigation of the three "pcvl" [posterior crossveinless] stocks was considerably more intensive than was that of the other assimilated stocks." This was, of course, the phenotype first chosen by Waddington in his own experiments. Clearly, then, Bateman's genetic analysis was designed to be an extensive test of the canalisation theory of genetic assimilation, where assimilation is by definition polygenically and non-specifically effected.[20] It would also be a test of the extreme hypothesis, predicted by the canalisation theory, that non-specificity may even be such that "the same phenotypic effect might be produced with quite a different genetic basis," as Waddington had surmised regarding the assimilation of posterior crossveinless. Chromosomal analysis brought Bateman to the same initial

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[19] These were extra crossvein in submarginal cell, extra crossvein in first posterior cell, anterior crossveinless, and Waddington's favoured posterior crossveinless.

[20] The origins of the canalisation theory of assimilation can hence be traced back to Waddington's concept of reacting tissue specificity, rather than internal stimulus or evocator specificity, in his 1930s Cambridge research. The notion of reacting tissue specificity was originally invoked as an explanation of the discovery by Spemann's team in 1932 of the evocatory activity of dead organiser tissue, and of several non-biological chemical species, in amphibian primary induction (see section 1.3.2.)

observational conclusions as Waddington, regarding the segregation of the assimilated crossveinless phenotypes. Statistically, appearance of the "pcvl" phenotype was most strongly correlated with the presence of chromosome 3 from assimilated "pcvl" flies. Although the X-chromosome was not discussed, Bateman asserted that "from the results of the chromosome substitution it is clear that, with one exception, both [chromosomes] II and III are involved in addition to I, since penetrance is reduced by the substitution of either autosome alone." Thus it appeared, in Bateman's words, that "in the majority of the assimilated stocks the three major chromosomes are concerned, although their individual effects are decidedly unequal."[21]

Waddington's review article, published fully two years after Bateman's paper, revealed a quiet but nonetheless clear disagreement over the significance of Bateman's cytogenetic and Mendelian genetic analyses. Firstly, from the canalisation viewpoint--where an unspecifiable collection of loci pervading all the chromosomes are presumed responsible for producing assimilation--the cytogenetic results seemed problematic. These results caused Waddington to comment quizzically: "As Bateman has pointed out, a considerable number of loci which produce breakages of crossveins are known on chromosome 3, while on chromosome 2 there are quite a large number of genes which tend to produce extra veins. It still remains very obscure why genes producing these two types of phenotypic effect should be, as it were, sorted out into different chromosomes." Secondly, the results of genetic analysis appeared to suggest an explanation of genetic assimilation in terms of straightforward allelism between known crossvein-breaking alleles, and the genes responsible for crossveinlessness in the assimilated stocks. Hence crosses were made between the assimilated crossveinless stocks, and various laboratory stocks of flies containing identified third chromosome factors, such as *cv-c*, *cv-d*, and *det.* After these crosses, Waddington noted, a "fairly high percentage of crossveinless flies appeared in the F_1." Yet, he added, "this could not be interpreted unambiguously to

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[21] Bateman explains that the X-chromosome cannot be discussed in relation to the autosomes for technical reasons: "No precise comparison of the relative importance of the X-chromosome and the autosomes is possible, for whereas replacements of II and III took place in the assimilated background, comparison of the effects of assimilated and non-assimilated X-chromosomes was made in the heterozygous F_1" (1959a, p. 460).

indicate that the assimilated stocks contained allelomorphs of the loci concerned, since similar results would be expected if the condition in the assimilated stocks had a multi-factorial basis" (Waddington 1961, p. 265).[22] For Waddington, regardless of there being several known recessive genes for the crossveinless phenotype on chromosome 3 (including the genes *cv-c*, *cv-d*, and *det*), the frequent appearance of the crossveinless phenotype, after outcrossing to the aforementioned laboratory stocks, could not be put down to the phenotypic expression of double recessives in the F_1. Production of the phenotype via straightforward allelism at a few pre-determined loci had to be rejected *a priori* within the canalisation hypothesis.

Bateman, on the other hand, had taken the same observational data and assumed a completely contrary explanation on the basis of its apparently greater simplicity. Discussing specifically the "pcvl" assimilated phenotype, in which she had the greatest interest, she stated: "The simplest interpretation of the pronounced effect of one chromosome is that it carries a major gene for the character. . . . The results of test (*f*) can also be accounted for on the hypothesis that a single major gene is being held, the drop in penetrance being due to the introduction of the gene into a foreign background. According to this hypothesis, therefore, construction of the assimilated stocks involved essentially the selection of penetrance modifiers" (Bateman 1959a, p. 460).[23] Thus although Bateman did leave, as a statistical possibility, the involvement of several important genes in the production of assimilated pcvl, the extremes of a Waddingtonian canalisation mechanism were never seriously entertained. Yet, she explained: "The evidence for single gene control is not, however, unequivocal: none of the results described above is incompatible with the hypothesis that several genes are of fundamental importance." Nevertheless, Bateman continued unequivocally

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[22] In fact none of Waddington's own evidence from genetic tests was unambiguously supportive of polygenicity, and thus of the canalisation hypothesis. For example, Waddington's findings that the degree of dominance exhibited by the assimilated "pcvl" stock "differed markedly in different crosses to various other stocks which had been derived during the process of selection," remained circumstantial without genetic analysis of these other stocks for *cv* alleles. (1961; reprinted verbatim 1975, p. 66).

[23] Test (*f*) was constituted of backcrosses between assimilated pcvl and wild type stocks. Selection was for wild type female flies (since crossing over of genes between homologous chromosomes can only occur in female *Drosophilae*). According to Bateman, "selection of crossveinless was impracticable on account of exceedingly low penetrance in later generations. In all cases, the frequency of wild type flies fell consistently with each generation of selection" (Bateman 1959, p. 456).

and in opposition to the canalisation hypothesis: "What appears certain is that the assimilated characters are not controlled merely by an indefinite number of genes of individually small effect, *i.e.* are not polygenic" (1959a, p. 461).[24]

In her final discussion, it is clear that Bateman was in agreement with her Edinburgh colleague Alan Robertson in believing that canalisation, as Robertson later insisted, was not necessary to the "main argument" on genetic assimilation (Robertson 1977, p. 600).[25] Here, Bateman attempted to reinforce the divide between Waddington's canalisation and genetic assimilation *simpliciter*, as she suggested an explanatory scenario for the assimilation of the crossveinless characters:

> Waddington has suggested that in a complete assimilation process there are two phases: a lowering of the threshold for the character, and an increase of the canalisation of the abnormal phenotype. If, however, selection is not applied for any optimum degree of expression of the character, there will be no direct pressure for constricting the canalisation, and selection will only operate on the first phase, namely the lowering of the threshold. This must be considered to be the case in the experiments described here since selection was only applied for the extreme of the abnormal phenotype; it is only ability to produce the character that has been assimilated, not any specific degree of development of the character. (Bateman 1959a, p. 470).

In other words canalisation was represented, within the context of these experiments, as something which may or may not ensue *after* the genetic assimilation event has occurred. In evolutionary terms, canalisation is an optional extra, reserved for populations which find themselves under more severe selection pressure than can be met by the hereditary fixation of the simple character. Such a severing of canalisation from the processes leading up to genetic assimilation could not be

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[24] Bateman suggested, as a concession to the possibility of a limited multigenicity: "It is, for example, possible to show theoretically that the backcross results described under (*f*) could follow from a situation involving a small number of genes if the probability of crossveinless manifestation were to increase gradually with the number of such genes present" (1959, p. 461).

[25] However, Robertson's misgivings were not based principally upon canalisation's application to threshold systems such as *pcvl*. Thus, he stated, "when applied to characters showing *quantitative* variation and not involving a threshold, [canalisation] has not in my view proved useful. Such quantitative characters, he added, "do not show the response to environmental stimuli which the concept demands (stability over intermediate ranges of environmental variables with greater sensitivity at extreme values) and the concept is not quantifiable in the sense that we do not know how to measure the canalization of any specific measurement" (Robertson 1977, p. 600-601; emphasis added). According to Sang, who worked with Robertson and Waddington at Edinburgh on the genetic assimilation programme, Robertson did not in fact oppose the canalisation hypothesis until after Waddington's death in 1975 (J. H. Sang, personal communication 1998).

acceptable to the Waddingtonian point of view. To begin with, Bateman's version of Waddington's complete assimilation process was in reverse. Canalisation from the beginning was, by definition, the process which facilitated the eventual hereditary fixation (that is, genetic assimilation) of acquired adaptive characters. Canalisation could, of course, continue on beyond the point of assimilation, because it was the fundamental mechanism at the heart of all forms of epigenetic developmental stabilisation. Canalisation was the process which brought about a genetic assimilation event; and from a Waddingtonian (that is, Whiteheadian) world view, only processes had real status. Bateman's scenario had put the Waddingtonian cart squarely before the horse.[26]

However, Bateman's overall conclusions regarding the genetic basis of crossveinless assimilation were unequivocal. She stated, in the general discussion: "It was concluded from the genetical analysis that the production of crossveinlessness depends fundamentally on only one or a few genes. Under the first situation, response to selection was attributed essentially to an increase in the frequency of penetrance modifiers, but it was suggested that such modifiers would almost certainly also be selected in a situation involving a few genes." Getting to the heart of the matter, she concluded: "The simplest interpretation of the fact of assimilation is that it has resulted from the exposing by treatment of genes of zero or near-zero penetrance, followed, during phenocopy selection, by the favouring of penetrance modifiers so that penetrance ultimately becomes appreciable even in the absence of treatment. Finally, selection without treatment has further enhanced penetrance" (1959a, p. 470).

Apart from the concluding hint at a subsequent canalisation of the character under further selection, as a necessary mechanism for the assimilation process it is not mentioned and, in fact, is more or less explicitly rejected throughout. One immediate corollary of these conclusions, is that the additional hypothesis of almost complete genetic non-specificity--the suggestion that completely different sets of genes may

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[26] See the biographical sketch of Waddington in section 1.2.2., for an elaboration of the development of Waddington's Whiteheadian tendencies. Thus Waddington himself expressed the view that his dialectical approach and process metaphysics had strongly influenced his scientific investigations, "both in the types of problems I set myself and the manner in which I tried to solve them" (Waddington 1969a, p. 72).

underpin a character's assimilation on different occasions and in different populations--is refuted. As Bateman said: "The foregoing suggests that assimilation of a modification cannot occur unless a specific gene, or a specific genetic mechanism, is available in the population." Nevertheless, even without such complete genetic plasticity as was suggested by Waddington, the range of potentially assimilable phenotypes is indeterminably high since, as Bateman reminded the reader, wild populations have been shown to have an immensely large store of recessive genes, including many of low penetrance.[27] Furthermore, Bateman added, because of the difficulty of detecting incompletely penetrating genes, "their frequency is probably considerably higher than the facts suggest, and this will be increasingly true the lower is the penetrance: there are probably a great many genes whose visible effects under normal environmental conditions are as rare as is crossveinless, and others whose manifestation even more improbable" (1959a, p. 471).[28]

Beyond Edinburgh, commentary on the crossveinless experiments was very varied in attitude, both to the experimental procedures themselves, and to the canalisation theory. For example, in 1958 Maynard Smith related the results of the original crossveinless experiment to Waddington's 1940s writings on the nature of genetic assimilation, and commented:

> This is an elegant and illuminating experiment, but there are two respects in which it does not reproduce the processes which Waddington had suggested might have occurred in the evolution of skin calluses [in the ostrich]. First, there is no evidence that canalization was involved, since in the final population the appearance of the crossveinless flies was highly variable, the crossvein sometimes being wholly absent, but more often showing gaps of greater or less extent; in this respect the flies resembled uncanalized mutant forms rather than wild type flies. (Maynard Smith 1958, p. 286-7).

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[27] In support of this assertion of widespread genic balance, Bateman referred to Dubinin (1936, 1937).

[28] In 1957, macro-evolutionist Goldschmidt made the very interesting comment in response to Landauer's phenocopy studies: "In classic genetics 100 percent penetrant and expressive mutants were marked as 'most useful' presupposing that genetics is identical with the study of crossing over. Simultaneously rare abnormalities, which could not be extracted as simple mutants or, at least, selected for successfully, were only noted as freaks, of no interest to genetics. Only a few geneticists realized that the low penetrant mutants and the apparently non-hereditary freaks may be excellent material for the study of physiological genetics. Therefore I am glad that Dr. Landauer has drawn attention to such facts as promise an efficient approach to the study of genic action via a comparison of phenocopic and mutant action" (Goldschmidt 1957, p. 91).

Maynard Smith went on to make the second criticism, fully elaborated eight years later by Williams, that "the response to the environmental stimulus was not adaptive to the stimulus which evoked it; there is no evidence that a fly which lacks a crossvein is therefore better able to withstand heat shocks, whereas an ostrich is better able to withstand pressure" (ibid.). Such a fly is, however, better able to survive in laboratories filled with potentially lethal geneticists screening for crossveinlessness: as we have already noted, both Waddington (in his original 1953 paper and in the 1961 review) and, much later, Eliot Sober, have offered quite convincing replies to this argument.[29] Questions of adaptive significance aside, Maynard Smith clearly followed Bateman's interpretation of the crossveinless experiments, seeing the results in terms of threshold responses to the quantity of a major gene product. Maynard Smith reproduced, in his words, a "possible interpretation of Waddington's experiment," which included a version of Bateman's diagram of "assimilation by a shift of mean" relative to the quantity of gene product (Bateman 1959a, p. 468).[30]

Meanwhile Warburton, working from the Prince Edward Island Biological Station in Canada, was seemingly the only commentator to have recognised one genuine significance of Waddington's choice not to select for so called "feedback adaptations"--that is, not to select for directly adaptive responses to the initial stimulus. Warburton was a keen supporter of the genetic assimilation experiments. He offered implicit support for canalisation, through his being both outspokenly anti

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[29] See footnote 15 above, and Sober 1984, pp. 199-211.

[30] This diagram consisted of three bell-shaped normal distribution curves, representing sequentially the effects of artificial selection for crossveinlessness, upon a *Drosophila* population. The curves were placed in slightly overlapping series along the x-axis, (with that axis labelled 'increasing amount of gene product'). 2 thresholds, represented by twin y-axes, intersected the x-axis at different quantities of gene product. The y-axis located at the lower level of gene product (proximal to the origin) was labelled 'treatment' threshold; that located at the higher level of product was labelled 'normal' threshold. Under curve 1, the mean of the population remained sub-'treatment' threshold with respect to production of the crossveinless phenotype. Curve 2 depicted how selection for crossveinless had succeeded in shifting the mean of the population well beyond the treatment threshold (such that the great majority of flies produced the crossveinless phenotype, in response to heat shock), and, additionally, the extreme distal region of the curve beyond the 'normal' threshold. Curve 3 depicted a further selective shift beyond the 'normal" threshold, such that *all* flies in the population expressed crossveinlessness *without* a heatshock (representing the fully assimilated state). Hence, in curves 1 and 2, some flies in the population always remained sub-treatment threshold, and never expressed crossveinlessness.

Kirpichnikov's neo-organic selectionist interpretation of stabilising selection, and uncritically supportive of Waddington's criticisms of Schmalhausen (Warburton 1956, p. 337). However, he did criticise Waddington (and many other experimentalists) for the "application of conclusions from experiments on arthropods, such as Drosophila [sic], in which adaptability is known to be greatly restricted by the nature of development, to other organisms in which no such restriction exists" (1956, p. 338). As Warburton explained, exoskeletal inflexibility is a functional necessity in arthropods, "Unlike the viscera, skin and bones of vertebrates, and the leaves, roots and stems of plants" (ibid.). Thus for Warburton, the adaptive importance of maintaining flexibility in plant and vertabrate systems precluded Waddington's assumption that assimilative fixation of the adaptive character *always* occurred, whatever system was under selection. Waddington himself mused upon this assumption of universal assimilation, stating: "It is not entirely clear why this should be so; possibly because it is difficult to build up a genotype which develops with the right degree of adaptive modification to the whole range of environments it has to meet, and that it 'pays better' to sacrifice something of the flexibility of the developmental system and to assimilate genetically the adaptation to the most usual environment" (Waddington 1956a: in Warburton 1956, p. 337).

Warburton's quick riposte was that "It is easy to array a mass of facts against this unsupported generalization." After two paragraphs of counter-examples from a range of organisms from amoebae to mammals, he added: "These are all cases in which, apparently, it has not 'paid better' to sacrifice developmental flexibility" (ibid.). Thus, whilst supportive of canalisation, and accepting of the adaptive evolutionary significance of the *Drosophila* experiments, Warburton ended on a strong note of caution: "Since genotypes are inherited but phenotypes are selected, the evolutionist must concern himself with the interaction of heredity and environment in the development of the individual. However, he must not have his hypotheses restricted by the developmental limitations of a single phylum, but must recognise and study the different modes of interaction available to different groups of organisms. Perhaps not all of these modes are exemplified by Drosophila [sic]" (1956, p. 338).[31]

Back in Edinburgh, controversy over the causes and mechanism of genetic assimilation in *Drosophila* arose again, in experiments using other threshold phenotypes. Bateman's paper, "The genetic assimilation of the dumpy phenocopy," described work done on another *Drosophila* wing defect, and was published simultaneously with the four crossvein phenotypes paper in the December volume of the *Journal of Genetics* (Bateman 1959b, pp. 341-351). Yet in 1961, Waddington accepted that "the situation was rather different in the stock in which Bateman had assimilated the dumpy phenotype" (Waddington 1961, pp. 265-266). What actually differed in this instance was the impossibility of arguing against a single major gene explanation for assimilation. As Waddington explained, the genetic analysis of this stock showed that it contained an allele of the dumpy locus extremely similar to, and in Waddington's words "perhaps identical with, the allele known as dp^{tp}." When this allele was removed from the assimilated stock, said Waddington, "the remainder of the genotype was not able to produce any dumpy phenotypes in the normal environment." Thus although the assimilated stock contained other factors influencing the dumpy phenotype, Waddington conceded that "the assimilation depended on the presence of the particular relatively powerful dp^{tp} allele, and did not occur in its absence" (1961, p. 68). In the short paragraph Waddington devoted to

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[31] These criticisms of Warburton's are of particular significance to my Chapter 4, where the extent to which Waddington was influenced by the American *Drosophila* genetics research tradition, in contrast to the morphologist Schmalhausen, becomes more apparent. Thus, in spite of his process philosophical focus upon canalisation, Waddington as evolutionary geneticist had far more professional investment in what his Edinburgh co-worker Sang has disparagingly described as the "bandwagon" of the genetic assimilation mechanism, as a suggested *universal* explanation of adaptive evolution (Sang, personal communication 1998). This provides an explanation as to why Waddington's arguments with neo-organic selectionists raged in the 1950s, whilst Schmalhausen practically embraced them. Schmalhausen was professionally far better able to accept the legitimacy of classical, or dynamic selection (and hence also the classical and neo-Mendelian forms of organic selection). Schmalhausen was also better able to remain flexible over the extent to which his stabilising selection predominated over dynamic selection, believing this to be an unanswered empirical question. There was, within Schmalhausen's monograph, less rhetorical insistence upon the inevitability of "autonomization" (Schmalhausen's term for assimilation), less focus upon autonomization as *the* key mechanism in adaptive evolution (and hence greater inclusion of natural historical examples similar to Warburton's), and greater insistence upon the insufficiency of the genetic level of description to the morphogenetic level of evolutionary development (see section 4.4.2.).

these results, the apparently negative consequences for a universal canalisation mechanism for genetic assimilation were not entered into.[32]

Subsequently, however, the consequences for canalisation of the results of the dumpy experiments were deftly side-stepped by Waddington, within a discussion of the ultimate nature and significance of the phenocopy phenomenon. The controversy was raised in relation to Goldschmidt and Piternick's attempts to discover, in Waddington's words, "whether the phenocopying effect of a certain environmental stress could, in all cases, be regarded as the unmasking of a sub-threshold gene which was already present" (1961, p. 276).[33] For Waddington this was a pseudo-question, because of the necessarily combined action of genotype and environment in producing any phenotype, including any phenocopy. Thus in truth, said Waddington: "The only question with which Goldschmidt was really concerned was whether, in the cases he investigated, there was any one gene which was of sufficiently great importance to be identifiable as *the* sub-threshold gene. The situation is strictly comparable to that in the assimilation experiments described above, in which, as we saw, it was sometimes possible to identify a single relatively important locus, and sometimes not" (ibid.; author's emphasis).

To Waddington's mind, the question of a major sub-threshold gene explanation for assimilation, was quite adequately dealt with--if not in canalisation terms--by Landauer, in his work on characterising sporadically occurring developmental abnormalities (and artificially produced phenocopies); or, to use Landauer's phrase,

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[32] The last 5 points of Bateman's 7 point summary of the "dumpy" experiments elaborate upon Waddington's brief discussion, and consolidate her own position on the causes of assimilation of threshold characters in *Drosophila*: "3. The genetical analysis of this stock showed that assimilated dumpy is produced only in the presence of the recessive lethal gene dp^{tp2}. 4. There is evidence that a second recessive lethal gene, which forms with dp^{tp2} a balanced lethal system, enhances, and probably is obligatory for, the production of the dumpy phenotype by dp^{tp2}. 5. The frequency of dp^{tp2}, and possibly also of the second gene, was increased by phenocopy selection; the frequency of both genes was increased by phenocopy selection without treatment. 6. Successful selection for expression in the assimilated dumpy stock indicated that modifying genes are also involved. The assimilation of dumpy, like that of crossveinless, appears therefore to have depended on major-genes and modifiers." Finally, and contradicting Waddington's beliefs that only his 1955 bithorax experiments showed evidence of the following phenomenon: "7. It is suggested that dp^{tp2} arose during the course of phenocopy selection as a consequence of the heat-shock treatment, and that this is the major difference between the dumpy and crossveinless experiments" (Bateman 1959b, 348-349).

[33] Here Waddington specifically refers to the paper by R. B. Goldschmidt, and L. K. Piternick: "A genetic background of chemically induced phenocopies in *Drosophila*" (1957).

his work on "pheno-deviants." For Landauer, these phenomena always had a complex genetic basis, and were produced as "the results of events through which ordinarily hidden weaknesses of developmental equilibria become manifest" (Landauer 1957, 79-90).[34] Since for Waddington all talk of "developmental equilibria" was merely "a shorthand form of referring to the notion of canalisation," it is clear that, in Waddington's theory, a universal canalisation mechanism for all genuine instances of genetic assimilation itself remained as deeply canalised as ever (ibid.).

3.1.3. The Assimilation of a Character of Macro-Evolutionary Magnitude: Waddington's Acceptance of Gausian Stabilising Selection.

In 1956, prior to Bateman's first publications in the genetic assimilation research programme, Waddington published experimental results which were uniquely significant for three reasons. Firstly, in the final paragraph of the discussion of his 1956 *Evolution* paper "Genetic assimilation of the bithorax phenotype," Waddington stated of his methods of phenocopy selection: "The fact that they have succeeded in producing a change of macro-evolutionary magnitude in the short space of 30 generations of selection suggests that such instabilities may on occasion be of considerable importance" (1956a, p. 12). Referring back to his pioneering crossveinless experiment, and by way of further explaining the rationale behind the attempted assimilation of the bithorax phenotype, Waddington contended: "It seems possible that considerable general importance should be attached to processes of this kind, which appear to be able to provide a satisfactory explanation of the evolution of certain types of adaptation which have in the past been difficult to explain

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[34] The context of Landauer's remarks, including his discussion of "crypto-genes," appeared to vindicate the genetic indeterminism of Waddingtonian genetic assimilation: "The occurrence of several independent mutations with similar phenotypic effects [in fowl] is presumably evidence for the conclusion that the corresponding normal sequence of developmental events is in precarious equilibrium, and this may well be true for more than one link in the chain of the particular developmental events. In the same sense our evidence leads us to conclude that sporadic defects as well as experimental phenocopies are the results of events through which ordinarily hidden weaknesses have a definite, if complex, genetic basis. If the phenocopy concept in its narrow meaning of a purely environmental interference with developmental processes must be abandoned, it is clear that the existence of crypto-genes and their spontaneous or experimental liberation confront us with many new problems" (Landauer 1957, p. 88).

convincingly. It was therefore thought desirable to investigate the genetic assimilation of other characters, so as to broaden the observational basis on which the theory rests" (p. 1). In other words, something radically different from the somewhat unimpressive phenotypic change to crossveinlessness was needed to gain the evolutionists' undivided attention. Waddington described Bateman's "rather mild developmental modifications, produced by temperature shocks applied to the pupa," contrasting them with his own "experiments on a phenotype of a rather different character," namely his "bithorax-like modification which can be produced by ether treatment."[35] This phenotype was described by him as "a profound modification," where the metathoracic imaginal disc, normally giving rise to the balancer organs or halteres in the adult, becomes so altered as to produce structures resembling those of the normal mesothorax, including the wings. In Waddington's estimation, this made the assimilation of the bithorax-like character highly significant: "If such a change occurred during phylogenesis it would certainly be accounted a macro-evolutionary phenomenon. It was felt that, if such a fundamental modification as this can genetically assimilated, then one would have some grounds for confidence that the process was powerful enough to be invoked to explain quite far-reaching evolutionary changes" (ibid.).[36]

The results of these experiments are of particular importance to the history of the attempted legitimisation of canalisation, in opposition to the major-gene hypothesis of Waddington's own Edinburgh colleagues. Three successfully assimilated stocks were designated after completion of two phenocopy selection experiments: first, the *He* stock which arose in generation 8 of experiment II, giving a bithoraxoid-like adult (*Bxl*-like). Second, a very similar stock (*He* 17) which arose in generation 29 of experiment I; and third, the very different *He** stock which appeared at the same time in experiment I, giving a more extreme bithorax-like (*bx*-like)

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[35] Waddington refers to a paper by Gloor (1947), as the first authority on production of this phenocopy.

[36] As early as 1941, Waddington had suggested that genetic assimilation could account for macro-variations, and therefore Goldschmidt's so-called "unbridgeable gaps" in phylogeny (see my Chapter 1, section 1.2.2.).

phenotype apparently inherited in a different manner.[37] It seems that Waddington had initially accepted a major-gene selection mechanism for the appearance of the assimilated of He (later re-named He7) and He17 characters. However, he did not accept a major-gene mechanism for assimilation of the extreme *He** bithorax-like phenocopy. This was because the phenocopies produced, as a result of exposure of eggs to ether, were of an extreme bithorax-like character, not the mild "haltere-effect" (*He*) of the bithoraxoid gene.

According to Waddington, the genetics of the production of the assimilated *He** stock was, as one would expect, as different as its phenotype. Thus he tells us: "Its genetic basis certainly does not depend on the chance occurrence of only a single mutation producing this effect: the variation in the proportion of abnormal phenotypes in the various crosses [to wild-type flies] clearly demonstrates that the character is affected by a polygenic system" (p. 10). The inevitable conclusion of a polygenic canalisation mechanism responsible for this, the only fully and genuinely assimilated character of these experiments, follows closely behind. Whilst allowing for a genetically mysterious maternally transmitted factor that strongly facilitated the assimilation, Waddington nevertheless asserted: "Whatever the origin of the maternal effect gene or genes turns out to be, there can be no doubt that the selection has brought together and concentrated a considerable number of minor alleles tending in the bithorax direction. Many if not all of these were presumably present in the original population" (ibid.). Finally, in a return contradiction of Bateman's views of the assimilation of both the crossveinless and dumpy wing defects, Waddington felt able, 6 years later, to say of the entire genetic assimilation programme: "Summarizing these results we may say that in all cases in which complete or near complete assimilation has been achieved, the process has involved changes at many loci

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[37] The range of phenotypes denoted here requires clarification. *He* stands for haltere-effect, where the halteres--the specialised balancer organs of the metathorax--become slightly enlarged, as in the known dominant mutation Bithoraxoid (*Bxl*), and indicating the initially stages of transformation to a mesothoracic wing-like structure. *He*17 is described as "indistinguishable" from the originally discovered *He* phenotype (the latter subsequently being designated *He*7). *He** was the last assimilated bithorax character to be identified. Unlike the mildly transformed *He*7/17 bithoraxoid-like characters, *He** produced a more extreme phenotype similar to the known recessive lethal mutation bithorax (*bx).* In describing the bithorax-like *He**, Waddington observed that "the genetic changes are more far reaching in their effects." Hence, "The abnormal individuals produced by this stock are much nearer to the phenocopy, showing all grades of bithorax-like appearance up to an extreme type with a large second pair of wings and a considerable extra mesothorax." (Waddington 1955, p. 10).

throughout the whole genotype. The only instances in which the genetic change was restricted, as far as is known, to a single locus are the two occurrences of a *Bxl*-like mutant in the bithorax experiments" (Waddington 1961, p. 267).

Thus, by 1956, the picture of a universal polygenic inheritance explanation of genetic assimilation is completed, by the experimental demonstration of its agency in a macro-evolutionary process. The anomaly of Bateman's experiments on the "dumpy" wing phenotype, was dealt with by Waddington's concession that "there is a considerable range between cases in which all the involved loci seem to be of relatively similar importance, to others in which one or a few loci are particularly strongly effective" (ibid.). This, however, fell far short of Bateman's suggestion that in no case is polygeny either necessary, or in evidence: and it certainly did not accommodate her suggestions that canalisation was not necessary for genetic assimilation at all.

With regard to the third major significance of these experiments in macro-mutational genetic assimilation, we may ask the question: Since the two genetic changes known to have been brought about by single genes could not be instances of true genetic assimilation, how were they to be characterised? In an intriguing passage, Waddington openly invoked a neo-organic selection mechanism very similar to the "substituting selection" of Gause, which Waddington had severely derided in his soon to be published *The Strategy of the Genes*:

> It is instructive to compare the process of genetic assimilation as it has occurred in the He stocks with the 'organic selection' of Baldwin and Lloyd Morgan [38]. They argued that if an animal subjected to any environmental stimulus is able to respond to it in an adaptive manner, the animal and the population of which it is a member will be able to continue existing in the region where the environmental stimulus operates, until such time as chance mutation produces a phenotypic effect which mimics the adaptive response. Now this is what seems to have happened in the first two sets of assimilated He stocks, in which a dominant allele of Bxl has appeared and produces a phenotype which has at least the lowest grade of the phenocopy appearance. The development of the full assimilation of the character in the He* stock can not, however, be accounted for in these terms. (Waddington 1956, pp. 10-11).

Thus, in Waddington's view, the answer to the untidy anomalies of He7 and He17 was to invoke the hitherto "impossible" mechanism of neo-organic selection.

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[38] Here Waddington refers to Baldwin's 1902 *Development and Evolution*, and Lloyd Morgan's 1900 *Animal Behaviour*.

This may appear an incongruous strategy, organic selection having ostensibly been Waddingtonian genetic assimilation's main rival as an explanation of the evolutionary fixation of adaptive modifications. Yet the only reasons Waddington had for opposing neo-organic selectionism of any stripe were twofold: the claims of its adherents that it provided a universal explanation for the hereditary fixation of highly determinate adaptive modifications (as made by Hardy and Hovasse), and appropriation of the canalisation mechanism. Such an appropriation had never been attempted by organic selectionists, notwithstanding Alister Hardy's efforts, from 1949 onwards, to argue that canalisation was always implicit in Lloyd-Morgan's classical theory.[39] In fact, in Waddington's view, it had always been the organic selectionists' denial of the necessary Mendelian hereditary basis to all adaptive modifications--and hence implicit denial of the possibility of selection for their more efficient canalisation--that Waddington chided when promoting genetic assimilation as a distinct mechanism.

The historical questions to be asked are therefore clear. First, did Waddington's proposed universal canalising selection mechanism--for him the only mechanism for true genetic assimilation--have any basis in the mainstream genetics of the 1940s and 1950s? Second, did Waddington's strong claim that canalising selection leading to genetic assimilation was the sole causal agency in all forms of adaptive evolution, gain any independent support in opposition to the equivalent claims of the neo-organic selectionists? These questions will be addressed in the final two sections of this chapter.

3.2. Orthodox Genetic Support for the Canalisation Hypothesis: Lerner, Mather, and Quantitative Genetics in the 1940s and 1950s.

Who, then, were the proponents of a genetics capable of supporting Waddington's canalisation hypothesis in the 1940s and 1950s; and were they, as evolutionists, supporters of Waddingtonian canalisation as an addition to the modern

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[39] See section 2.5.2. for a description of Lloyd Morgan's coincident selection mechanism, and the debate between Hardy and Waddington over its status.

synthetic theory of evolution? Several important workers from around the world, in response to the Edinburgh research, had published experimental papers supporting the concept. For example, in 1959, the geneticist J. M. Rendel's experiments provided a detailed statistical analysis of canalisation in the "scute" phenotype in *Drosophila*. Rendel, working from Sydney Australia, stated very supportively in his introduction: "There is abundant evidence that the manifestation of genetic variation in the phenotype depends on the environment and the rest of the genotype. Waddington, in a series of papers summarised in his book (1958) [sic], has suggested that where it is of advantage to an animal for its development to follow a certain path, a genotype will evolve which will resist forces tending to change the path ; in his terminology the developmental path, or creode, is canalized" (Rendel 1959, p. 425). Waddington, in his 1961 review, said enthusiastically of Rendel's attempts to genetically disrupt the canalisation of the wild type scutellar bristle number, that it gave "an indication of the degree to which the canalized normal phenotype can absorb or conceal genetic variation" (Waddington 1961, p. 281). Yet the paper was short on genetic mechanisms, and as Rendel began his discussion, he noted that "The way the phenotype reflects the genotype for scutellar bristle number is somewhat complex and it is not easy to find a suitable score in which to express what seems to underlie the phenotypic changes" (Rendel 1959, p. 436).

Likewise, the Soviet Berg from Leningrad State University had made a suggestion, closely related to Warburton's 1956 criticisms of genetic assimilation, about the circumstances in which canalised systems would evolve most markedly (Berg 1959, pp. 103-105). Specifically, canalization would be deepest when the phenotype under selection did not represent one of Warburton's "feedback adaptations." In Waddington's words: "It will then be necessary for the developmental system to produce an organ which is precisely tailored to meet the requirements of natural selection, and to do so without being able to use the selective factors to guide the process of development while it is actually going on" (Waddington 1961, p. 284). As an example, continued Waddington, "Berg quotes the very low variance (i.e., high degree of canalization) of the dimensions of insect-pollinated flowers which have to deposit their pollen on to particular portions of an insect's anatomy." Yet again, actual genetic mechanisms for such canalisation processes were not elaborated.

By the time of writing his 1961 review, therefore, Waddington was never more keen to show that canalisation was well founded upon concepts known to orthodox genetics at least since 1930. In the subsection of his review entitled "the canalization of development," he reminded the reader of the central principle: "The property of a developmental process, of being to some extent modifiable, but to some extent resistant to modification, has been referred to as its 'canalization'" (1961, p. 269).[40] He then made his claim to canalisation's orthodox roots more explicit: "The fact that phenotypes are somewhat resistant to modification is a commonplace of genetics. Its simplest exemplification is perhaps in the phenomenon of dominance. . . . The way in which geneticists have thought about this phenomenon was, for some years, directed on to rather inadequate lines by the assumption that dominance or recessiveness is a property of particular alleles. The origin of a more adequate view can be found in the work of Muller, Fisher, Stern, Goldschmidt, and others in the years around 1930" (1961, p. 270).[41] Thus Fisher's focus on the background genotype's role in regulating degrees of dominance, Muller's and Stern's work on dosage compensation in the sex chromosomes, and the study of epistasis (which even dated back to 1905 and the work of Bateson's, Saunders' and Punnett's) were all seen as genetic grist to

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[40] Waddington referred here to his work in Pasedena on *Drosophila* wing development, as the genesis point for canalisation, whence he published a 64 page treatise on "thirty-eight genes affect[ing] sixteen different, but not necessarily independent, processes which occur during wing development" (Waddington 1940a, p. 134).

[41] It is notable, especially regarding Waddington's view that canalisation required relatively small inbred populations incorporating much concealed genetic variability, that Sewall Wright did not figure in his list of canalisation's legitimators. As Provine elaborates: "His thesis research at Harvard in 1912-15 upon interaction effects in color characters in guinea pigs taught Wright clearly that organisms were built up of complex interaction systems rather than being, as Wright frequently said, a mere mosaic of unit characters each determined by a single gene. The same color gene might be expressed very differently in different genetic combinations; it followed that each gene had many multiple if indirect effects. To the animal breeder this meant that selection would be most effective by operating upon whole interaction systems rather than upon single genes" (Provine 1986, p. 235). However, Waddington may have feared undermining the proposed universality of canalising selection: Wright's theory of drift, viewed in the 1930s as anti-adaptationist, was generally neglected by strong selectionists of Waddington's ilk in the 1950s. In Provine's words: "As this shift towards adaptationism occurred, systematists had no further need for their conception of Wright's random drift and minimized the importance of the concept in their interpretation of the evolutionary process" (Provine 1983, p. 65). Nevertheless, after significant hardening of the selectionism of the synthetic theory in the 1940s, Wright himself continued to view random drift in the above interactionist and selectionist terms (ibid.).

the canalisation mill.[42] In Waddington's opinion, all these conceptions were dealing with an essentially similar phenomenon, "namely, a course of development which exhibits some resistance to being modified by genetic changes" (ibid.). As always in Waddington's evolutionary writings, the reader is deftly moved either from embryology and development to Mendelian genetics, or, conversely, from Mendelian genetics to embryology:

> It is, of course, also a well known fact, but one with which in the past embryologists have had more to do than geneticists, that development also tends to resist being modified by environmental agencies. Embryos tend to regulate, that is to say, to produce their normal end-result in spite of external accidents which may occur to them as their development proceeds. Again, the existence of some resistance to modification is shown by the fact that different strains of the same species differ in the extent to which they are modified by a given external stress. (Ibid.).

Once again, links were being forged in Waddington's writings between genetics and regulative embryogenesis. The notion of canalisation was, in Waddington's words, expressly "intended to be a very general summing-up of a large number of well-known facts in genetics and embryology, all of which are summarized in the statement that the development of any particular phenotypic character is to some extent modifiable, and to some extent resistant to modification, by changes either in the genotype or in the environment" (pp. 270-271).

Considerable support for the notion of canalisation came from I. M. Lerner. For Lerner, the "developmental homeostasis" at work in the maintenance of canalised adaptive phenotypes, both between and within generations, implied a causally related "genetic homeostasis" that acted solely, using Lerner's phrase, in a "time-binding" way "between, rather than within populations" (Lerner 1954, p. 2). In his 1954 *Genetic Homeostasis*, Lerner defined the concept given by the title as "the property

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[42] In his highly informative 1966 *The gene: A critical History*, Carlson discusses Muller's and Stern's concept of dosage compensation, and includes a pertinent quotation from Muller, showing intergenic interactions were an explanatory commonplace by 1932: "Muller, like Stern, suggested that a mechanism of 'dosage compensation' had evolved to equalize the effects of the sex chromosomes in the two sexes. 'This must be, of course, due to the interaction of other genes in the X-chromosome, whose simultaneous change in dosage affects the reaction. In some cases, at least, it has been possible to show by studies of the effects of different chromosome pieces, a) that genes other than genes for sex are acting as the "modifiers" in question, b) that the modifiers responsible for the dosage compensation effect on different loci are to some extent different from one another, and c) that more than one modifier may be concerned for a specific locus'" (H. J. Muller 1932, pp. 213-255; in Carlson 1966, p. 112).

of the population to equilibrate its genetic composition and to resist sudden changes," and added that it is "very probably the same property as *genetic inertia* of Darlington and Mather (1949)" (1954, p. 2; author's emphasis).[43] Lerner openly adverted to the priority of several other workers, particularly H. J. Muller on "genetic adaptation," and Mather on "polygenes and natural selection."[44] [45] Hence Lerner fully accepted that his work "rests upon the ideas expressed by earlier students," even to the point of accepting that the model he forwarded was "not unlike the one suggested in a very schematic way by Penrose (1948)" (Lerner 1954, p. 3). However, important for the present discussion is Lerner's overt attempt, in his words, to "establish a connection between genetic and developmental homeostasis [and] to suggest that heterozygosity

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[43] In his opening pages, Lerner discusses W. B. Cannon's elaboration of the concept of physiological homeostasis in Cannon's *The Wisdom of the Body* (1932). For Lerner: "The step that Cannon took from the organismal to the social level," that is, in his analogy between homeostasis of the body physiological and the body politic, "by-passed some intermediate stages," two of them being psychological and ecological homeostasis, the last being genetic homeostasis.

[44] Muller's later comments on epigenetics and development were particularly conducive to the genetic assimilation of characters via canalisation. Thus, after first discussing pleitropy, Muller wrote: "Second, not only do the reactions initiated by one gene branch, but the reactions initiated by different genes are apt to run into one another, with the result that various different genes cooperate in the production of most observed characters of the organism. Taking both branchings and anastamoses into account at the same time, we see that the processes of development as well as those of physiology constitute a complicated network of biochemical paths, leading from the genes at one side of the net to the observed or phenotypic characters at the other [cf. Waddington's 1950s network representation of the epigenetic landscape (1957, p. 36)]. *Hence a change in a given character can usually be caused by a mutation in any one of a considerable number of genes, some of these having much and others little influence on the character*, and some being obviously qualitative in effect while more of them are detectible [sic] only as differences in the degree or quantity of expression of the character" (Muller 1949, p. 423; emphasis added).

[45] Lerner added substantially to this list in 1955: "Various aspects of such self-regulating properties in development . . . have been referred to as plasticity (Salisbury, 1940), canalized development (Waddington, 1940), existential adaptation (Goldschmidt, 1948) stability (Mather, 1953), phenotypic flexibility (Thoday, 1953) and otherwise" (Lerner 1955, p. 29). Of these, existential adaptation was defined by Goldschmidt as "a minimal genetic adaptation to the general features of the environment," allowing important physiological reactions to ride out, as "a minimum condition of existence," environmental extremes (Goldschmidt 1948, p. 467). Thoday described his phenotypic flexibility concept as "a component of variability which is independent of genetic flexibility" (Thoday 1953, p. 99). Hence "a unit of evolution which had complete phenotypic flexibility could be perfectly fit, for it could have complete genetic stability, and nevertheless its members could function in all possible environments and hence meet all possible environmental change" (ibid.). Nevertheless, Lerner decided: "Perhaps, the simplest way of describing individual capacity to maintain steady states, at least in the context of the present discussion [on improving egg production] is by the term buffering ability (Waddington, 1940), while genotypes endowing the organism with homeostatic properties may be referred to as buffered genotypes" (1955, p. 29).

provides a basis for both phenomena" (ibid.). Lerner's modelling of genetic homeostasis took a conventional individual-selectionist approach, such that the "integrative properties of Mendelian populations can emerge from evolutionary forces acting on individual genotypes" (p. 5). However, for reasons central to defence of the canalisation hypothesis, Waddington could not accept Lerner's heterozygosity theory. Waddington began, however, by questioning the methods used to measure canalisation in experiments performed by Lerner's supporters:

> Several authors have studied Lerner's suggestion that heterozygotes exhibit better developmental canalization. Most of these investigations have used, as an indication of canalization, not the response of the phenotype to some external stress, but the variation, within the body of a single individual, of some phenotypic character which is repeated in a number of different parts of the body which might be expected to be identical. . . . .Doubts have been expressed . . . whether the character investigated in these studies [namely, the degree of bilateral assymetry in abdominal bristle number in *Drosophila*], which is the extent of the phenotypic variation produced by intangible alterations of conditions during development, is really an indication of the degree to which the developmental systems are canalized as against more definite environmental changes or alterations in genotype, and whether they can be taken to throw much light on the genetic makeup of canalization systems in general. (Waddington 1961, pp. 282-283).[46]

On the face of it, these comments seem at odds with Waddington's own understanding of canalisation. After all, his own *prima facie* evidence for the canalisation of the wild type was that any two wild individuals would invariably be, in his words, "as like as peas in a pod" (Waddington 1941). However, in the context of the canalisation of individual adaptive characters--the context in which these criticisms were necessarily made--heterozygosity was not an important indicator. This is because, in Waddington's scheme, one of the most important genetic mechanisms facilitating the canalisation of a character was the accumulation of hidden recessive alleles, gradually promoting its more stable expression. Obviously, then, the suggestion of a positive correlation between the degree of homozygosity in a population, and the loss of canalisation of certain characters of the wild type, would

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[46] Waddington linked names to experiments, holding the results in suspicion: "Mather (1955), Jinks and Mather (1955), Tebb and Thoday (1956, 1958), and Reeve (1960) have studied the degree of asymmetry in numbers of sternopleural bristles on the two sides of a fly, while Reeves and Robertson (1954) have considered the correlation in numbers of abdominal bristles on the various sternites of *Drosophila*. The results make it clear that there is some genetic influence on the degree of asymmetry or repeatability of such characters, but the heritabilities found were in most cases very low" (Waddington 1961, p. 282).

not fit easily into such a scheme. Waddington therefore cast doubt over both the experimental methods and conclusions of Lerner's supporters, adding reference to a late experiment of his own, saying: "It is worthy of note that in Waddington's (1960) experiments on the Bar phenotype, the lines showing a high degree of canalization were considerably more inbred than the foundation population. It is therefore clear that a high degree of heterozygosity is certainly not necessary for strong canalization. . . . This suggests that the variation between parts which are repeated within the same individual is not a good indication of canalization in general" (1961, p. 283).[47]

An influential evolutionary geneticist apparently supportive of canalisation, and concerned more directly with developmental homeostasis than Lerner, was the Birmingham based Kenneth Mather. Co-author with Darlington of the textbook *The Elements of Genetics* (1949), Mather wrote several articles in the 1940s on the relationship between polygenic inheritance, natural selection, and canalisation in relation to evolution. Here, then, would appear to be an explicit endorsement of the Waddingtonian system, coming from a staunch advocate of modern synthesis genetics. Mather took an orthodox Mendelian-gene selectionist view of evolutionary change, and followed closely the form of Dobzhansky's famous 1937 definition of evolution, with his own statement that "evolution is the occurrence of persistent changes in the hereditary constitution of a population of organisms" (Mather 1943b, p. 32). To this he added that during the last ten years "more attention than ever has been devoted to the genetical study of populations, and the consequent contribution to evolutionary theory has been great." Citing Timofeef-Ressovsky (1940), Muller (1940), and Darlington (1940) in his support, Mather claimed that "so far, nothing has been discovered about evolutionary change that is in conflict with, or demands an extension of, the known genetical principles of variation and natural selection (Mather 1943b, p. 33). Waddington would perhaps not have disagreed with Mather's views with regard to variation and selection. Nevertheless, he expressed strong antagonism to Mather's 1943 characterisation of two types of genes, involved in quantitative and qualitative inheritance respectively; namely, "polygenes" and "oligogenes."

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[47] Waddington then made a tactical move common in such scientific arguments, and suggested that these observations of character variation made by Lerner's team should be referred to as "developmental noise" (ibid.).

The empirical background to the development of Mather's polygene-oligogene distinction is relevant to the strong antagonism which developed between him and Waddington. Mather's extensive investigations into meiosis and the phenomenon of crossing-over ended in the late 1930s, and in 1941 and 1942 he published two papers concerned with polygenic inheritance in *Drosophila*.[48] In the introduction to the 1941 paper, Mather immediately stated that genetics had long been concerned with the inheritance and behaviour of genes producing sharp phenotypic differences. These, he said, were the so-called "qualitative" genes, and added: "It has long been recognised that there exists another type of heritable variation, termed 'quantitative' or 'metrical'. Such variation does not allow of individuals being separated into distinct types; all gradations between certain limits are to be observed" (1941, pp. 159-60). Touching upon the historical debate between the biometricians and Mendelians over the mechanism of inheritance of such characters--which mechanism the biometricians believed to be blending inheritance--Mather concluded: "It is now generally accepted that these characters are (*a*) controlled in inheritance by an indefinitely large number of genes, many of which have approximately equal effects, and (*b*) markedly subject to environmental variation. Thus it is clear that characters of this kind will be difficult to study by the common techniques of genetics" (p. 160). For Mather in 1941, though the distinction between qualitative and quantitative characters was "far from ideal," it was nevertheless still useful, since qualitative variation was "usually monogenic or digenic in inheritance." The study of polygenic rather than monogenic inheritance was, said Mather, "the prime need" of applied genetics (ibid.).

Mather chose variation in abdominal hairs in *Drosophila* as a probable candidate for a polygenetically inherited character: specifically, "the combined number of chaetae on the ventral surfaces of the fourth and fifth abdominal segments," since the numbers were easily determined. The data suggested that in particular related strains, there existed within chromosomes genetically balanced collections of alleles which, though differing from each other, had "approximately the same effect as each other on hair number." However, recombination between these balanced groups significantly disturbed this quantitative uniformity, promoting "the

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[48] Mather published a comprehensive 40-page review of his work on crossing-over (Mather 1938).

release of considerable variation on which selection can act" (1941, p. 183). In 1942, Mather published a more specific investigation into this balancing of polygenic combinations in *Drosophila.* This time, taking up the perennial problem of speciation, he concluded that "balanced polygenic combinations provide ample storage for the variation necessary to give selective changes of the magnitude required by species formation" (1942, p. 336). Mutation provided the ultimate source of variation and constantly kept up the existing reservoir, whilst recombination events of the nature described above slowly exposed this genotypic reshuffling as phenotypic variation, thus made available for natural selection to act upon. Hence Mather believed, as did Waddington and Schmalhausen in the 1940s, that "stable, or nearly stable, phenotypic characteristics of a population hide an ever changing genotypic constitution" (ibid.).

The notion of the "polygene" as a distinct kind of gene from those traditionally studied in Mendelian transmission genetics, appeared only to be tentatively forwarded at this stage of Mather's investigations.[49] However, by 1943, the language of two classes of genes, separately responsible for qualitative and for quantitative variation, was very clear. Hence Mather stated: "The familiar genes of genetical experiment fall into the category of what we have called switch genes. They are not usually known by this name, being more often called major mutants or qualitative genes, to distinguish them from the minor genes controlling quantitative characters. These two classes have also been called oligogenes and polygenes respectively from the oligogenic and polygenic nature of the variation which they determine" (1943a, p. 68).[50] In his 1943 review, Mather suggested that a totally separate genetics was needed for studying the behaviour of the quantitative polygenes:

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[49] In 1941, Mather does not use the term polygene in description of a separate kind of gene. Rather, it is used in contexts which suggest its use as a collective noun, describing linked groups of ordinary genes having very similar quantitative effect upon a subject phenotype. Hence Mather states: "Where, on the other hand, many of the genes are linked into a number of groups, depending on the number of chromosomes of the organism, the rate of advance with selection must be influenced by the organization of the combinations of these polygenes within the chromosomes" (1941, p. 310).

[50] Interestingly, Mather's loosely designated "switch, major or oligogenes, call them what we will," were not be found in the wild, except as phenotypes resulting from recent mutations. This was, he asserted, simply because unless some selection pressure existed for maintaining oligogenic variance, "one allelomorph will have an unconditional selective advantage over the rest and

> Polygenic characters are controlled by many genes having effects small in comparison with non-heritable fluctuations. In consequence, polygenic inheritance is marked by certain peculiar features which distinguish it from oligogenic behaviour and which throw a fresh light on the interactions of variation and selection. *Polygenetics* represents a new level of integration by means of which a better understanding of natural selection and its action may be achieved. . . . Laboratory genetics has been almost solely concerned with oligogenic variation, and so has proved disappointing to the evolutionist. Both types of gene are, however, inherited in the same way and so the success of polygenic analysis depends on the utilization of the principles elucidated in laboratory studies. (1943b, p. 38; emphasis added).

How, we may ask, did this dualism of Mendelian transmission genetics and "polygenetics" dispose Mather to Waddingtonian canalisation? In his 1943 *Nature* paper, Mather introduced canalisation via a discussion of early Mendelism's fixation on a non-interactive, one-gene-one-character genetics; that is, in Mather's terms, its undue focus on "what we may perhaps call the characteristic expression of the gene." Mather continued: "Soon, however, several lines of approach led geneticists to doubt the validity of this simple interpretation and finally to abandon it altogether." Citing, as Waddington later did, the work of Fisher (1927) and Muller (1932), but also Bridges (1922) and Huxley (1942) with respect to the dependence of individual gene expression on the genetical background, Mather introduced Waddington's contribution by way of a definition of canalisation:

> Some further consequences of this view have now been discussed by Waddington. In particular, he points out that the dependence in expression of one gene on the action of others permits a more coordinated response of the organism to its environment. Using both embryological and genetical data he shows that development may be regarded as canalized, that is, that although an organism may follow any one of a number of developmental paths, it is difficult to make it develop along lines intermediate between these possibilities. In genetical language, the integrated genotype acts as a buffering system, in such a way as to limit the variation of the organisms response to environmental fluctuations. (1943a, p. 68).

For Mather, the oligogene-polygene theory fit nicely in with the phenomenon of canalisation, since "major or switch genes may determine which of the paths will be followed, but systems of other genes, the buffering action of which can be adapted by natural selection, will delimit the possible paths with greater or less precision" (ibid.). The polygenes, responsible for minor quantitative variations, also fitted in well with the requirement of the large numbers of genes of small effect to canalise the

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will, apart from the slight effect of mutation pressure already noted, oust its competitors" (ibid.).

developmental pathways. Mather's novel classification of genes, and the details of how canalisation is achieved, appeared to mesh still more satisfactorily. Hence Mather related his proposed genetic mechanism for canalisation to his own previous work, as discussed above, on the behaviour of genetically balanced groups of genes responsible for polygenic inheritance. Insisting that the "organization of the system of genes buffering the development of wild type individuals is of paramount importance to the organism," since it must produce a "uniform type" regardless of external conditions (that is, it must be canalised), he then claimed: "The way in which uniformity is combined with potential elasticity has been revealed by Mather's analysis of polygenic variability" (p. 69). Natural selection, he suggested, builds up linked combinations of polygenes "in which the constituent members of the combinations balance each other in action." Such uniformity of action could be altered "to produce new combinations of different action by means of recombination between existing combinations;" that is, by means of Mather's much-studied process of crossing-over (ibid.). Thus buffering depended on polygenic balance, which can and does change as a result of recombination. This then permitted the emergence of new combinations, which were capable of re-aligning the developmental path to provide fresh variation, thus facilitating adaptation to changed circumstances. Polygenic variability, therefore, was hidden or "potential in the genotype" and not free in the phenotype. In other words, Mather concluded deferentially, "we can see how, as Waddington puts it, the system has absorbed its own variability" (ibid.).

Despite the apparently supportive acknowledgement of Waddington's ideas, Mather's view of canalisation was not Waddingtonian according to the criteria discussed in section 3.1.2. In fact, it was far more akin to Bateman's and Robertson's views at the Edinburgh Institute than to Waddington's.[51] The reasons for the divergence between Mather and Waddington are evident in Mather's discussion of genetic assimilation: for Mather, the genetically determined event of switching into a new developmental pathway--that is, genetic assimilation--constituted a large-scale qualitative change to the phenotype. As such, it could only be carried out only by his "switch," "oligo," or "qualitative" genes. As Bateman was

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[51] Hence Mather's view of genetic assimilation appeared to be very similar to Bateman's classical selection of a major gene (Mather's oligogene) causing assimilation, *followed* by, according to the level of selection pressure, modifier gene (Mather's polgene) canalising selection.

to corroborate experimentally in the 1950s, there was no possibility of a Waddingtonian gradual canalisation leading up to some ephemeral, genetically non-specific assimilation event (p. 68).

Waddington's response to Mather in 1943 was immediate, appearing in the very next volume of *Nature*. It was also, given their previous history of conflict when Mather was based at the John Innes Horticultural Institute in London, and given the implications of Mather's views for Waddington's canalisation, predictably caustic.[52] Waddington portrayed Mather's notions as an attempt to appropriate Waddington's own process approach to embryology and genetics into a weak-minded conceptual scheme. Waddington first reminded the reader of his recent paper, discussing embryology in terms of two kinds of processes, namely, "switching" and "buffering," then continued: "Mather afterwards attempted to develop this idea by identifying the genes which act in a buffering manner with his so-called 'polygenes' and the genes acting by switch mechanisms with 'oligogenes'--a new word which he coined to include the genes with comparatively large effects normally studied in genetic laboratories. I wish to show that this identification cannot be sustained and has only been suggested by extremely confused thinking" (Waddington 1943, p. 394). For Waddington, quite simply, "genes with large effects may nevertheless act in a buffering manner." Furthermore, "genes with small individual effects may act together to constitute a switch." The latter, he added, by way of alluding to their

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[52] The two had also clashed three years earlier, in a odd argument over the acceptable extent of teleological thinking in evolutionary biology. Waddington accused Mather of false teleological reasoning. For Waddington, "a genetic system which achieves its 'purpose' provides in so doing the mechanism for its survival. . . . There is, however, a danger that the teleological method of argument will be carried over, by association into regions in which it cannot be sustained. This seems to have occurred, to some extent, in the valuable article by Mather [1940] in which he discusses the evolutionary significance of the formation of two different sexes in the diploid phase" (Waddington 1940b, p. 705). Waddington also chided Mather's supposed rejection of a developmentalist explanation of diploid sexual separation. Mather terse reply appeared immediately beneath Waddington's letter, and read: "In the first place, I am taken to task for the unwarrantable use of teleological expressions, particularly in the specific case of my paraphrase of his own discussion of sex separation. Inasmuch, however, as the dicsussion was originally Waddington's and not mine, I can scarcely be called to account for its nature, whether teleological or otherwise. In any event, the point is trivial, as I feel confident that Darlington and Waddington would agree with me in regarding adaptation as the outcome of selection and in denying that it was purposeful, whether the discussion concerned genetical or morphological questions. Secondly, I am criticized for wishing to 'dismiss' the 'developmental-genetical idea'. This I have no desire to do in general as, clearly, developmental studies can contribute much to our understanding of genetics" (Mather 1940, p. 705).

1940 row over Mather's work on diploid phase sex differentiation in plants (Mather 1940, pp. 484-486), "seems to be the case with the sex differential genes in many forms." Writing with the apparent preconception that whatever was true in Mather's views was not new, Waddington continued his short critique with the dismissive comment: "What remains true in Mather's thesis is the obvious fact that genes which produce very minor changes in a character must be acting as rather ineffectual buffering agents on the last phases of its development. Such genes have been a commonplace of genetic thought since they were first considered by Nilsson-Ehrle [sic] in 1908." What was more, Mather's term "polygenes" implied for Waddington the fallacy of "making a one-one correlation between the gene and one of its effects." This same fallacy, which Mather himself had described as the narrow focus of laboratory genetics upon "the characteristic expression of the gene" was, said Waddington, entailed in discussing of the "white eye" gene in Drosophila, which is actually responsible pleiotropically for a number of other characters. Waddington concluded his criticisms with a convincing argument:

> There is a true distinction between polygenic variation (determined by numerous genes) and oligogenic variation (determined by few genes); but this is certainly not a distinction between the kinds of genes involved, and need not correspond to a distinction between the modes of action of the genes during development. . . . With these considerations in mind, it might seem advisable, while retaining the useful adjective 'polygenic', to dispense with the substantive 'polygene', or at least always to use it with suitable qualifications; for example, in a phrase such as "the gene A acts as a polygene with respect to the character X." (Waddington 1943, p. 394).

Continuing their 1940s tradition of acrimonious exchanges via the *Nature* letters column, Mather immediately replied to these attacks. With regard to the suggestion of polygenic switch mechanisms, Mather only partially conceded, unable to resist the caveat: "But such jointly acting genes cannot constitute a switching system which is efficient, and hence able to survive the test of natural selection unless they are completely linked and segregate as a unit. They will thus jointly act, and will appear in genetic analysis, as one gene of large effect, that is, as a major gene, not as polygenes. This is in fact one of the ways in which I envisaged the evolution of switching genes from polygenes in the discussion which is being criticized" (Mather 1943c, p. 560). With respect to Waddington's assertion that genes may simultaneously determine oligogenic and polygenic variation, Mather again partially accepted the point, whilst adding the riposte: "But can the secondary effects of such genes be regarded as determining polygenic variation ? The polygene notion was developed . . . in relation to the action of selection, both in experiment and in nature. Natural selection must act on the total phenotypic effect of a gene, and hence genes of the kind Waddington considers will be selected almost entirely on their drastic main effects. Their secondary effects cannot thus give rise to polygenic variation of the kind which I have discussed" (ibid.). Thirdly, Mather completely rejected Waddington's statement that genes of small effect could only be late acting, and "rather ineffectual" buffering agents, retorting that "a number of them acting in aggregate can be far from ineffectual" (ibid.). Lastly, and quite creditably, Mather tempered his response to Waddington's more *ad hominem* historical observations, stating: "In conclusion, I must mention Waddington's equation of polygenes to Nilsson-Ehrle's polymeric genes. The latter are defined only by similarity of action to one another, whereas the former are defined also by the magnitude of their individual effects, which are small when compared to the total non-heritable fluctuation" (Ibid.).[53]

By the time of publishing *Biometrical Genetics* in 1949, Mather's structural and mechanistic defence of his two kinds of genes had become quite elaborate. There was further support for the idea expressed in his early 1940s writings of the polygenes being located in the presupposed "inert" heterochromatin. "The heterochromatin is of special interest," Mather proclaimed, "because wherever tests have been possible it has proved to be devoid, or virtually so, of major genes. In this sense it is inert, and is often so termed by geneticists" (1949, p. 19). However the heterochromatin was, Mather maintained, polygenically active; so the cytological and

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[53] This brought a temporary (if unsatisfactory) end to hostilities between London and Edinburgh. We may speculate that Waddington would have discerned several problems with Mather's defence. Firstly, the same problem (of meiotic segregation) would surely face the polygenic determination of *all* critical processes, not only developmental switch mechanisms. Yet if some do survive selection, as Mather did not deny, then Waddington's conditions for canalisation (namely, relatively small, inbred, and therefore extensively homozygous populations), would provide an explanation for their non-disruption. Secondly, natural selection surely does act upon different aspects of a gene's expression, in accordance with changing adaptive requirements in altered environmental and biotic circumstances (as Schmalhausen demonstrated using Kamshilov's experimental results). Thus the magnitudes of a gene's major effect may become irrelevant, should its minor effect gain greater adaptive significance. Thirdly, Mather's argument that "small gene changes can accumulate without mechanical limit," making their cumulative action "far from ineffectual" (Mather 1943, p. 560), seems to weigh against Mather's own argument against the evolution of efficient polygenic switch mechanisms.

genetical evidence agreed "in showing that polygenes must be capable of existing as a class distinct from major genes" (ibid.). Yet research had shown that the polygenes were not confined to the heterochromatin. It did not seem likely to Mather that polygenic activity in the oligogenically active euchromatin was "to be accounted for by the inclusion of small pieces of heterochromatin within it." Instead, it appeared to him that "polygenes, as well as existing separately from major genes, may exist side by side with them" (p. 21). Rather than accept the possibly negative implications of these facts for his gene dualism, Mather constructed in 1946 an elaborate, though *ad hoc*, structural explanation for this intimate proximity of oligogenes and polygenes:

> It would appear likely that at a locus recognised as that of a major gene by the existence of a major discontinuity of effect between two allelomorphs, there can also exist allelomorphs differing in action only in the way typical of polygenes. If this is so the major gene must be so constructed that it may vary to produce on different occasions a major and specific change of action, and a smaller non-specific change. . . . Furthermore, the assumption is difficult to avoid that the drastic and unique effect of the change, which leads us to class the gene as major, must imply a greater disarray of parts or a disarray of more parts than does the smaller effect, reproducible by other genes, by which we recognise the polygene. (1949, pp. 21-22).

Surely, then, as Waddington the orthodox Mendelian would undoubtedly argue, Mather's terms for the two classes of gene merely described different degrees of mutational disruption--whether those disruptions are supposed unique or repeated in other genes--to one and the same kind of gene. This apparent collapse of Mather's position back into orthodox Mendelian genetics, perhaps precipitated by Waddington's criticisms, appeared almost to be supported by Mather himself. Hence Mather wrote, in a passage that offered very little support for his dual categorisation, genes "owe much of their individuality to their organization, just as two proteins might contain similar amino-acids yet differ in properties because these amino-acids were carried in different proportions and in different arrangements" (ibid.).

By the time of writing the 1961 review of genetic assimilation, Waddington's critique of the oligogene-polygene distinction had altered somewhat. It now suggested a less strictly qualified acceptance of Mather's terminology than in 1943, whilst still totally rejecting the substantive dualism. Waddington now objected that "the same allele can appear as a polygene in one genotype, but as a well-recognizable oligogene in some other genotype." Nevertheless, he felt that the crossveinless experiments had already proved that "systems of genes each of small effect" were indeed capable of switching development between pathways; two facts Waddington claimed Mather did not--and by virtue of his genetic typology could not--account for (ibid.).

Finally, a clear indication of the depth of impasse between Edinburgh and Birmingham precipitated by this theoretical dispute, is entertainingly provided by Falconer within his anecdotal history of the Edinburgh Institute. Falconer's description of the unfortunate occasion merits full quotation:

> In 1950, near the end of Wright's visit, a symposium on quantitative inheritance was held in the institute; it was published in 1952. Wright gave a lengthy talk on the interactions between coat color genes in guinea pigs. But the manuscript was lost on his way home and a quite different paper appeared in the published symposium. It was a synopsis of the current state of quantitative genetics and was surely more generally useful than the guinea pig paper would have been. The symposium, however, had unforeseen and regrettable consequences of a political nature. Kenneth Mather, then Professor of genetics in Birmingham, was invited and talked about his chromosome-balance theory of quantitative inheritance. This asserted that + and -- genes (those increasing and decreasing the trait) are arranged in repulsion linkages. The net effect of a chromosome is minimal but it holds a large amount of hidden variation that can be released by recombination. His theory was not well received by the audience and he was criticized in a forthright but injudicious manner. Mather, as a guest speaker considerably senior to us, was understandably affronted. I believe that the cool relationship between the Birmingham and Edinburgh schools that persisted for many years may have had its origin in this unfortunate episode. (Falconer 1993, p. 140).

Thus, by 1950, the obviously charged relationship existing between Waddington had Mather through the 1940s had apparently collapsed into outright hostility. Yet, despite the witnesses accounts (for example Sang, who was present at the fateful 1950 symposium; personal communication 1998) of such insults emerging from the Edinburgh Institute in criticism of Mather's polygenetics, Waddington's ideas continued to figure very prominently in Mather's theoretical writings. For example, in Mather's extensive 1953 *Heredity* paper, "Genetical control of stability in development," Waddington completely dominated the introductory section on "canalisation and stabilisation." Yet Schmalhausen, the Soviet creator of the concept of stabilising selection who's *Factors of Evolution: The Theory of Stabilising Selection* had been translated into English in 1949, was nowhere mentioned. By contrast, Lerner's 1954 *Genetic Homeostasis* was dominated by Schmalhausen's concepts, with Waddington's theory not mentioned at all in that work's extensive review of stabilising selection. Lerner, a visitor from California to the Edinburgh

Institute in 1948, and a bringer of many new techniques from the United states, appeared to have had no reason for his omission of Waddington's canalisation, other than a simple preference for Schmalhausen's very similar theory.

Lastly, then, we come to the support for canalisation provided by Schmalhausen's writings. There can be no doubt of the received view in the historiography of modern synthesis embryology, development, and genetics. That view has been that Schmalhausen's morphological synthesis of embryology, genetics and evolution--backed so strongly by one of the key developers of modern synthesis genetics, Theodosius Dobzhansky--was Waddington's main rival in the claim to the "missing embryological chapter" of the modern synthesis (see Hamburger 1980, p. 108). Yoxen, in his reflections on the significance of Waddington's career, remarks of Waddington's landmark 1957 book *The Strategy of the Genes*, that it was "revised and updated . . . to take account of the work of classical geneticists like Dobzhansky, Schmalhausen, Thoday and Mather in the 1940s and 1950s" (Yoxen 1985, p. 325). Regarding Thoday (as an active supporter of Lerner's experimental approach to canalisation research) and Mather, we have already noted the damning criticisms issuing from Waddington during the 1940s and 1950s. Regarding Dobzhansky and Schmalhausen, we need to delve into Waddington's deeper and more personal scientific concerns.

3.3. Private Support and Public Rejection: Dobzhansky and the Denial of Waddington's Genetic Assimilation.

On 25 July 1959, Waddington sent a letter to Dobzhansky expressing his obvious frustration. In the ten years since Schmalhausen's *Factors of Evolution* had been translated into English, Waddington clearly felt he had suffered unnecessarily and could no longer remain silent. The causes of his resentment were very clear:

> I always feel a bit disappointed that whenever you want to refer to someone on developmental buffering and such subjects, you always quote Schmalhausen and not my work. Admittedly we were both developing very similar ideas at about the same time, i.e. 1940, though at that time his were only published in Russian or Ukrainian and little known over here. But I feel that mine were more solidly based on facts--on a detailed study of 40 genes affecting the *Drosophila* wing, in particular as discussed in my

> *Organisers and Genes* of that year--while in his case it was more a matter of theory to bring genes into the story (Waddington 1975).[54]

In section 2.6.2. I proposed that both Waddington and Schmalhausen stood apart from all other leading investigators, whether in the West or in the Soviet Union, regarding the evolutionary significance of adaptive modifications to the phenotype. Whilst Waddington, in his terms, appeared to find it easy to distance his concepts from the "impossible" theory of the Soviet organic selectionists and the "extremely confused thinking" of Mather, he could not as readily dismiss Schmalhausen's contemporary work. The most Waddington was able to suggest in his letter to Dobzhansky was that "Schmalhausen still seems to me, on re-reading him, to have got the theory muddled up" (ibid.). In his 1957 book, *The Strategy of the Genes*, Waddington's assessment of Schmalhausen's was significantly placed in a separate chapter from his discussion of the Soviet neo-organic selectionists. Discussion of Schmalhausen's work was placed in chapter 3, discussing alternative modes of action of natural selection. Yet the work of the Soviets Lukin and, most especially, Gause, was discussed in a section toward the end of chapter 5 on the genetic assimilation of adaptive characters. Here, all forms of organic selection were dismissed in detailed contrast to Waddington's own theory of evolutionary adaptation. In this part of Waddington's book Schmalhausen's stabilising selection theory, so strongly claimed by the Soviet organic selectionists, was not mentioned at all.

Schmalhausen's *Factors of Evolution*, was expressly concerned with the problem of the evolutionary significance of adaptive modifications. It had long appeared to Waddington that only he, Waddington, truly understood this problem at the time of the modern synthesis; and he alone had the vision to inform a misguided orthodoxy. However, by 1949, Schmalhausen's *Factors of Evolution* had been translated into English, and it had been resoundingly endorsed by Dobzhansky for

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[54] Waddington would have had plenty of available evidence to support this complaint. Dobzhansky's 1950 *Science* paper, "Heredity, Environment, and Evolution," seems to have begun the trend. The 1951 edition of *Genetics and The Origin of Species*, much influenced by Schmalhausen, gave no report of Waddington's ideas, whilst in Dobzhansky and Wallace's 1953 *Nat. Acad. Sci.* paper, "Genetics of homeostasis in *Drosophila*," the situation was the same. Dozhansky's 1956 *Am. Nat.* paper, "What is an adaptive trait," managed to cite Lerner's 1954 *Genetic Homeostasis*, as well as *Factors of Evolution*, without mentioning Waddington, whilst the 1955 *Evolution, Genetics, and Man* added insult to injury by only mentioning Waddington in relation to science and ethics. Apparently not until his 1962 *Mankind Evolving*, did Dobzhansky go any distance towards redressing the balance in a major work.

expressing a very similar collection of ideas to Waddington's own. Writer of the Foreword to the English translation, Dobzhansky lauded Schmalhausen as "perhaps the most distinguished among the living biologists in USSR" (Dobzhansky; in Schmalhausen 1949, p. x). Waddington's first writings on the canalisation of development were, according to the author Schmalhausen, unfortunately unavailable to him since "only after the re-evacuation to Moscow, at the end of 1943, when the manuscript was completely ready for publication did I have the opportunity to read the article of C. H. Waddington published in nature in 1942." Schmalhausen then deftly combined apparent remorse with a claim to priority: "It is regrettable that I was unable to make use of this interesting work, for Waddington suggests a solution to the problem of the role of individual adaptation in evolution . . . very close to ideas I had previously evolved in a series of books and articles beginning in 1938. The difference between Waddington and myself amounts to a somewhat different terminology" (Schmalhausen 1949, p. viii).[55]

Waddington's objections to Schmalhausen's writings, "on re-reading him" ten years after the *Factors* first appeared in English, revolved around several matters. Principally, Waddington argued over the correctness of Schmalhausen's usage of his own (Schmalhausen's) concept; namely, stabilising selection itself. Thus Waddington felt that Schmalhausen had failed by "not really distinguishing 'stabilising selection type 1', which holds the gene pool constant, and 'stabilising selection type 2' which builds up genotypes which determine developmental pathways which exhibit what you [Dobzhansky] call homeostasis and I call homeorhesis" (Waddington 1975, p. 96).[56] Dobzhansky's response to Waddington's chiding was initially repentant:

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[55] Schmalhausen elaborated: "I employ the terms 'autoregulation' and 'autoregulating mechanism' in approximately the same sense as Waddington uses the term 'canalization' of development" (ibid.).

[56] The "facts" Waddington placed such importance upon, were derived from his work on *Drosophila* wing development done in Pasedena, U S A in 1938-1939. In *Organisers and Genes,* which he began working on whilst at Pasedena, Waddington elaborated in three pages a 16 step process of wing development, involving 38 genes. Waddington stated: "One must think of the genetic control of a developmental path as a very detailed and continuous acting on every phase of the developmental process" (1940a, p. 85). Robertson discusses this work from the point of view of epigenetic homeostasis stating: "He [Waddington] and his student Lees considered the effects of environmental interference with development such as pricking the wing with a needle or subjecting the pupa to temperature shocks, to produce phenocopies'-- which eventually led to his experimental work on genetic assimilation some 15 years later" (Robertson 1977, p. 594).

"First, concerning quoting Schmalhausen and not you. Having thought about it, I plead guilty and apologize. To be frank I have also felt that the Edinburgh group is averse to quoting anybody's work but their own and their friends in Great Britain, but as a matter of fact this does not apply so much to you, and in any case I did not consciously try to redress the balance. And so, I promise to do better in future." Yet Dobzhansky's tone changed markedly when talking in more specific terms about Schmalhausen's work: "I would like to defend Schmalhausen a little. Of course, he did not express things exactly as you did, but it seems to me that he had quite clear ideas concerning homeostasis, homeorhesis, etc., and concerning their roles in the grand scheme of evolution, although it is written in a remarkably heavy language, both in the Russian original and especially in the English translation, which I have not 'edited' enough, for the good reason that editing might have meant in this case doing another translation job" (1975, p. 98).

One may justifiably speculate that Schmalhausen's failure to express things "exactly as Waddington had," was quite probably a determining factor in Dobzhansky's decision to favour Schmalhausen's writings. In 1942, Waddington had outspokenly invoked the discredited but still much feared inheritance of acquired characters within his first writings on canalisation (Waddington 1942, pp. 563-565). Dobzhansky next added to this defence of Schmalhausen with an open appeal to charity, entreating Waddington over his obviously failing comrade: "Let us also remember that he is one of the victims of Lysenko, and any support which we may give him, especially while he is still alive, is a good deed" (1975, p. 98).

Prior to the publication of *Factors of Evolution*, Dobzhansky had avoided all discussions surrounding the hereditary fixation of adaptive modifications. In the first and second editions of *Genetics and The Origin of species*, mention of organic selection had been conspicuously absent, both with respect to its enthusiastic rediscovery among the Soviets in the mid 1930s, and the similar revival of interest in the West going on in the early 1940s. His evident distaste for all matters remotely relating to the inheritance of acquired characters had been clearly expressed in the 1937 first edition. There he made the forced observation that "this question has been discussed almost *ad nauseum* in the old biological literature," quickly adding the disclaimer that "any text book of genetics may give the reader a review of the present status of this problem so that we may refrain from the discussion of it altogether"

(Dobzhansky 1937, p. 31).[57] However, in 1952, Waddington referred directly to this passage and noted that Dobzhansky, "in dismissing the matter so cavalierly, was explicitly referring to 'direct adaptation', that is, the hypothesis that when the environment produces an alteration in the development of an animal, it simultaneously causes a change in its hereditary qualities such that the development alteration tends to be inherited" (Waddington 1952a). Such direct adaptation or "parallel induction" was, as Mayr has more recently noted, at the heart of the evolutionary mechanism of Geoffroy, though also "adhered to by most neo-Lamarckians" (Mayr 1980, p. 5).[58] Perhaps, therefore, Dobzhansky's only concern was to refrain from rekindling any discussions over the possibility of direct adaptation. It is nevertheless also clear that he would have fully appreciated the adaptationists' dilemma regenerated over the question of neo-organic selection, and might equally have wished to avoid adverting to that. Hence a decision to take organic selection seriously could, as Simpson was to suggest persuasively in 1952, have been construed as an argument in favour of neo-Lamarckism, and not neo-Darwinism. Dobzhansky had already elected his particular champion over the issue of the fixation of adaptive modifications, and thus refrained from entering the organic selection debate entirely.[59]

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[57] By the time of printing the second edition in 1940, this short passage, along with the section on the "Production of Mutations by External Agents" which contained it, had disappeared from the text.

[58] The difference then between Geoffroy's direct induction and somatic induction, was that in somatic induction the adaptive somatic changes are causally interposed between the specific environmental stimulus, and the eventuating hereditary adaptive change. Arguments that direct and parallel induction could not count as evidence of neo-Lamarckian inheritance (and that somatic induction which could count did not in exist in nature), had long been the focus in all neo-Darwinian anti-Lamarckist writings. In de Beer's words, discredited somatic induction consisted in "a change in the internal factors *produced by a change in the structure of the body* which latter change was itself produced by external factors." It was, in de Beer's view, this chain of causes which "constitute the kernel of the Lamarckian point of view" (de Beer 1930, p. 19; emphasis added).

[59] In the 1951 edition, Dobzhanky's passage discussing the "real issue" of neo-Darwinism versus neo-Lamarckism in adaptive evolution had also disappeared, indicating that the issue had been solved to Dobzhansky's full satisfaction in favour of the former. However, a derisory single line reference to organic selection was added: "As pointed out by several authors, notably by Gause (1947) and Schmalhausen (1949), there is a trend in evolution towards fixation of long established and adaptively important traits. A perhaps unnecessary term, "organic selection," was coined to describe this very real and important trend. In a group of animals which has evolved in cold climates the genes for warm fur may become fixed, and the capacity to have a less warm pelage on exposure to heat may be lost. The opposite may occur in tropical forms."

Such assiduous caution, together with clear avoidance of support for Waddington in the 1940s and 1950s, implies that Dobzhansky may have taken a calculated risk in so strongly endorsing his compatriot Schmalhausen's views. The more so since Schmalhausen's contemporaries, the Soviet neo-organic selectionists, had without exception in the 1930s and 1940s claimed Schmalhausen's stabilising selection mechanism as simply another pseudonym for the coincident selection of hereditary variations--that is, neo-organic selection. It was a decision that in no way undermined the progress of the synthetic theory in the West, perhaps not least because of the linguistic and conceptual difficulties involved in reading the English translation of *Factors of Evolution.*

3.3.1. A Recent Historiographical Assessment of the Waddington versus SchmalhausenControversy.

Why might Dobzhansky have only discussed Schmalhausen's work in the 1950s? Why, in both the 1940 or the 1951 editions of *Genetics and the Origin of Species* was no mention made of either Huxley's views on organic selection, Waddington's 1940 monograph *Organisers and Genes*, or Waddington's theoretical writings of 1941 and 1942? These questions are underscored as Huxley tells us in the preface to *Evolution, The Modern Synthesis*: "Waddington's [1940] and Goldschmindt's [1940] valuable and distinctive books did not appear until after the present volume was in proof; but I have tried to take advantage of them where possible" (Huxley 1942, p.7). Schmalhausen himself had claimed that Waddington's writings from the 1940s were only omitted from his book because the manuscript of the *Factors* was already, according to Schmalhausen, "completely ready for publication." Gilbert has recently addressed the question of Dobzhansky's obvious preference for Schmalhausen's work. In his 1994 paper on the relationship between Dobzhansky, Schmalhausen and Waddington, he proposes five points of similarity between Schmalhausen's and Waddington's theories (Gilbert 1994). Firstly, Gilbert takes note of all the clear similarities between them, asserting "they both took

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(Dobzhansky 1951, p. 155). Perhaps the most significant aspect of this belated mention of organic selection is its strong indication that Dobzhansky did not support any identification of the principle with his champion's (Schmalhausen's) stabilising selection concept. Thus Simpson stood alone among leading supporters of the modern synthesis, in trying to identify his neo-organic selectionist "Baldwin effect" with Schmalhausen's concept.

embryology seriously and felt that the current version of the Modern Synthesis was incomplete without it" (1994, p. 147). Secondly, says Gilbert, they stressed the cell-cell interactions in organ formation as well as "the interactions between heredity and the environment in producing the phenotype" (p. 148). Gilbert's third point, that both used a form of systems analysis and became interested in cybernetics at the end of their careers, does not help us understand Dobzhansky's discrimination between them in the early 1940s. However, Gilbert's next two points focus upon the most central issue. Fourthly, then, "they hypothesized a model for the channelling of possible traits into a relatively narrow allowable range. Waddington called it *canalization*; Schmalhausen called it *stabilization*" (ibid., emphasis author's). Fifthly, "they maintained that physiological adaptations can be taken over by the genome." For Schmalhausen, Gilbert adds, "this was another example of stabilizing selection" (p. 149).[60] As discussed earlier, it was over these issues--namely, the correct understanding of developmental stabilisation--that Waddington complained to Dobzhansky about Schmalhausen's supposedly confused thinking.

There are several other important questions to be asked. For example, to what extent do Waddington's historical criticisms of Schmalhausen appear well founded, going by a present day reading of Dordick's translation of *Factors of Evolution*? Bearing in mind Dobzhansky's concerns regarding that translation, is it possible to make any decision over the matters with which Waddington took issue? Next, to what extent did Waddington's theory, *circa* 1940, express such distinctions as he began making in 1953, particularly as between "normalising" (stabilising type 1) and "canalising" (stabilising type 2) selection? More generally, were Waddington's objections to Dobzhansky's favouritism reasonable when comparing the relative sophistication of Waddington's and Schmalhausen's theories prior to 1949? We may also ask, as a consequence, whether Waddington's principal objections were only voiced in the light of changes to his own ideas, made soon after reading *Factors*.

Gilbert concludes that Dobzhansky's choice was based upon his obvious desire to support modern synthesis population genetics. Thus Waddington presented his

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[60] Whilst Gilbert appears to suggest an asymmetry between canalising and stabilising selection on this point, my section 3.2. provides evidence to the contrary. For Waddington, genetic assimilation was likewise an example of the action of canalising selection, and canalisation was a process of developmental stabilisation independent of genetic assimilation.

theory as an addition to population genetics, which in Waddington's view, says Gilbert's, was "not sufficient alone to explain evolution." By contrast, Schmalhausen insisted that genetic stabilization should be made part of the population genetical model of evolution. For Schmalhausen, Gilbert maintains, "embryological evidence did not fall outside the current definition of evolution; it fell nicely within it" (1994, p. 153). Gilbert also implies that Waddington and Schmalhausen differed in their positions over the gradualist versus saltationist debate, with Schmalhausen denying the frequent and rapid appearance of qualitative novelties in evolution. This would indeed have meant that Schmalhausen's views smoothly conformed to Dobzhansky's own gradualist selectionism. Hence, in Gilbert's words, where Waddington stressed that genetic assimilation could give new types of organisms, "Schmalhausen emphasised that 'in these instances of adaptation, nothing new actually arises.'" (Schmalhausen 1949, p. 200; in Gilbert 1994, p. 153). Gilbert's concludes that Waddington saw embryology as complementing the modern synthesis, whilst Schmalhausen saw embryology as completing it (ibid.). Since Gilbert's history represents the latest word on the Waddington versus Schmalhausen controversy, I shall address these views in the next chapter.

Chapter 4.

Stabilising Selection Versus Canalising Selection: The Competing Evolutionary Syntheses of C. H. Waddington and I. I. Schmalhausen.

> Samuel Butler said that a hen is an eggs way of producing another egg. Thus in the Darwinian epoch he foreshadowed a reorientation of evolutionary studies that did later occur. . . . Then came the shift of emphasis to the egg by the geneticists from about 1900 onward. In extreme form, their views practically eliminated behaviour as an essential element in evolution. What a hen is and does depends on the egg, that is, on the mechanism of heredity complete within the fertilized egg. Evolutionary changes in the hen, so some of the early geneticists submitted and a dwindling few still hold, arise without any prior relationship to the hen and its behaviour. . . . The most widely held modern theory of evolution may be presented as a reconciliation between the naturalists' hen-evolution and the geneticists' egg-evolution. It reinstates behaviour not merely as something to which evolution has happened but as something that is itself one of the essential determinants of evolution. . . . In the course of this theoretical synthesis natural selection has turned out to be something broader than and in some respects different from Darwin's concept.[1]
>
> George Gaylord Simpson.

4.1. Introduction: The Structure and Arguments of Schmalhausen's *Factors of Evolution: The Theory of Stabilising Selection*.

In 1988, historian of Russian biology Mark Adams commented: "Since the 1950s Ivan Ivanovich Schmalhausen (1884-1963) has been recognised in Western biological literature a one of the founders of the synthetic theory of evolution. This recognition rests almost entirely on one book, *Factors of Evolution*" (Adams 1988, p. 281). Adams describes *Factors* as "Schmalhausen's broadest theoretical statement," and a work that "shows the greatest divergence from his teacher." That teacher was one of the fathers of evolutionary morphology in the Haeckelian

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[1] Simpson 1958, p. 7.

tradition, A. N. Severtsov (Adams 1980, p. 220).[2] Schmalhausen completed his doctoral dissertation under Severtsov at Moscow in 1916, and worked on the classical morphological problem of the origin of the extremities in amphibia. Schmalhausen had been successful in publishing major works in morphology for 20 years, prior to the completing *Factors of Evolution.* His 1923 textbook of comparative anatomy had four editions and was widely used in Soviet Universities (Adams 1988, p. 281). The cause of divergence from Severtsov's programme, Adams suggests, was Schmalhausen's ever increasing focus in his major works upon the results of genetics; a trend that culminated in *Factors of Evolution.*[3]

However, it is interesting to note a suggestion from Schmalhausen himself, made right from the outset, that the new population genetics is not going to be his primary focus in this, his grandest statement of evolutionary theory. Schmalhausen discussed the section addressing theoretical population genetics in his Preface, and stated: "Following the examination of variation [Chapter 1] is an analysis of the causative forces of evolution on the lower level, especially the transformation of the genetic composition of population. From the point of view of population genetics this may appear as an incomplete survey of its contemporary achievements. However, I did not propose to write a review of this field, nor do I dwell on the problem of species formation" (Schmalhausen 1949a, p. vii). After deferring to the recent publications of Dobzhansky, Timofeeff-Resovsky, and Dubinin, Schmalhausen continued: "Instead I wish to analyse only the elementary processes of general importance. The causative forces of evolution are discussed more fully here but, as in my previous books, only in so far as they are necessary for the main task. We are interested primarily in justifying our emphasis upon the *stabilising* aspect of natural

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[2] Such divergence is notable since according to Adams, Schmalhausen's career showed "a remarkable parallel to that of his teacher." Like Severtsov, he became a professor first at Dorpat [1917-1920], then at Kiev [1920-1927] (Adams 1980, p. 197). When at Kiev Schmalhausen set up a laboratory of phylembryogenesis, and his interest grew in experimental embryology, and in the relationship between genetics and evolutionary theory. Thus in Adams' opinion, Schmalhausen's publications "rarely stray from the problematics established by Severtsov and from his approaches, and all give major play to him as a great founder of evolutionary morphology" (1980, p. 219).

[3] Adams relates that "over half its references are to works in genetics or population genetics, with an average of six citations apiece to Alpatov, R. L. Berg, Gershenson, Dubinin, Kamshilov, Rapoport, and Timofeeff-Ressovsky." Also notable, says Adams, is that "Dobzhansky is referred to for the first time" (Adams 1980, p. 220).

selection" (ibid.; emphasis added). Schmalhausen explained almost apologetically that "Since the basic evolutionary processes occur only in populations of interbreeding individuals it was necessary to consider the subject of population genetics" (ibid.). Again, after paying the subject close attention in Chapter 2, Schmalhausen's apparently deep reservations, held specifically towards mathematical population genetics, resurface with some force in Chapter 3:

> The mathematical analysis of evolutionary transformation . . . suffers from several deficiencies for the necessary simplifications involve extreme abstraction and a withdrawal from concrete reality. Actually, both mutability (mutation pressure) and elective [sic] importance (coefficient of selection) of traits do not remain constant, and these variations in mutability and in coefficients of selection are not only due to constant changes in the external environment but also to changes within the organism itself. Even an individual mutation does not have a constant effect. (1949a, p. 141).

Returning to the Preface, at the end of describing the content of the second chapter, Schmalhausen introduced what for him was its most important subsection, noting that "Special emphasis is placed upon the processes involved in the accumulation of hidden reserves of variability. This portion of the book concludes with a discussion of these processes, and the entire analysis contained in subsequent parts of the book is based upon this discussion" (1949, p. vii). Indeed, hardly a section of the book passes without mention of the importance of such hidden reserves.

It is therefore intriguing that the second chapter of *Factors*--notwithstanding the penultimate subsection on hidden variability reserves--can be passed over by the reader without any diminution in her appreciation of the central thesis. One interpretation of the author's prefatory comments is that he was, in fact, advising that the reader was at liberty to do so. Perhaps then, Schmalhausen did not diverge quite so far from his mentor Severtsov's views as Adams suggests. Severtsov certainly did not see genetics as having accomplished much at all in terms of evolutionary theory, and observed in his last, posthumously published work of 1939: "Despite the brilliant successes in hereditary theory, the results of genetic research have brought little to the solution of evolutionary questions" (Severtsov 1939, p. 80; in Adams 1980, p. 218). Schmalhausen himself appeared highly sensitive to suggestions, made by the Soviet biological establishment, that he had deserted Severtsov's programme. Hence, on the morning of August 6th 1948, at a sitting of the Lenin Agricultural Academy, Schmalhausen answered directly to allegations that he held with several bourgeois scientific theories. He asserted quite courageously : "The first and chief charge is that I believe in autogenesis. It was, moreover, stated that in this respect I am not a continuer of the line of my teacher, Academician Severtsov. Severtsov, presumably, was of a different opinion, since, of all his numerous disciples, he chose me as his successor. He evidently considered that I was the most consistent of his followers" (Schmalhausen 1949b, p. 489). It seems implausible that such a model student, so long devoted to completing his teacher's research programme, would leave such a task at the very end of his own career, and desert Severtsov's morphological approach to evolution. In the same address to the Lenin Institute, Schmalhausen reasserted his morphologist credentials before his accusers: "Attempts have been made here to class me with the geneticists, and, what is more, with the formal geneticists. For the sake of those who are not familiar with the facts, I must say that I am not a geneticist at all, but a morphologist, an embryologist, a phylogeneticist. At most, the only connection I may have with genetics is my work on the phenogenetics of racial characters in domestic fowl" (Ibid.).[4] Regardless of the seriously threatening adverse political circumstances which it should not be forgotten formed the backdrop to these comments, and despite Schmalhausen's obvious genetic competence, *Factors of Evolution* nevertheless fully testifies to their veracity.[5]

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[4] Adams testifies to Schmalhausen's forthright opposition to Lysenkoism, and provides an important historical backdrop linking the content of *Factors* with Schmalhausen's fateful August 6th interrogation by Lobanov: "The post-war years involved Schmalhausen in a major controversy with T. D. Lysenko over the central theme of the book--the nature and significance of selection in evolution. Lysenko claimed that intraspecific competition played no evolutionary role and, further, that one species could be completely transformed into another in a single generation. For Schmalhausen and many others, these claims struck at the very core of Darwinism. At Moscow University, Schmalhausen organized a major conference on intraspecific competition, mobilizing the 'reserves' of the entire biological community to demonstrate the reality and evolutionary significance of the phenomenon. As the proceedings were being published, Lysenko and his followers launched a polemical press attack on Schmalhausen and his concept of Darwinism. Shortly thereafter, at the infamous August 1948 session of the Lenin All-Union Academy of Agricultural Sciences, Lysenko mobilized his own hidden reserve--Stalin's official support--and his views became official Soviet policy in biology until 1965. Fired from his posts and in public disgrace, Schmalhausen found refuge in the Zoological Institute of the Soviet Academy of Sciences, where he worked until his death in 1963" (Adams 1988, p. 283).

[5] Graham also notes Schmalhausen's importance in bringing about the liberation of Soviet biology from Lysenkoism, and further testifies to his courage in speaking his mind. Thus Graham states: "Vavilov was gone from the scene of Soviet genetics by 1940, but Lysenko's control over biology in the Soviet Union was still not complete. In the research institutes of the

Indeed, *Factors* clearly shows the depth of Schmalhausen's understanding of genetics, as accumulated over a decade marked by the publication of three other remarkably scholarly synthetic works. As Urbanek remarks, "Schmalhausen demonstrated how morphological and embryological studies and Severtsov's 'speculative' concepts could be integrated with genetics and the theory of natural selection, and how they created the historical cornerstone for the emergence of the synthetic theory of evolution" (Urbanek 1988, p. 201).[6] Although the text of *Factors* is extremely turgid, and in places almost unreadably so, it is nevertheless a very scholarly monograph.[7] Rich in both natural historical examples and experimental data, it provided many morphological descriptions of developmental processes in plants and animals. Much of the material in its Chapters 1 and 3 overlaps in the style

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Academy of sciences and on some of the university faculties the teaching of genetics still quietly survived" (Graham 1993, p. 131). In fact, continues Graham, from 1946 to 1947 there was a brief but definite improvement in the situation: "In 1947 the Soviet biologist I. I. Schmalhausen published an article in the main Soviet philosophy journal that was clearly critical of Lysenko's position" (ibid.). Graham also relates how "a number of biologists, including A. A. Liubishchev, V. N. Sukhachev, I. I. Shmal'gauzen [sic], and I. I. Puzanov, vainly disputed Lysenko's claims and criticized his arrogance" (1993, p. 133).

[6] Adams well describes the synthetic significance and scholarly power of Schmalhausen's works, following his take-over (after Severtsov's death) as director of the Moscow based Severtsov Institute of Evolutionary Morphology in 1936, and his appointment to the new chair of Darwinism at Moscow University: "The move launched a remarkable decade of evolutionary theorizing that produced four highly original and important books. In 1938 [*The organism as a whole in individual and historical development*] presented the phylogenetical and embryological development of organic characteristics from an organismic point of view, making liberal use of information from experimental embryology and physiological genetics. The next year he produced [*Trends and laws of the evolutionary process*] (1939/40), a masterful statement of evolutionary theory showing the relationship between long-term morphological trends, the nature of variations, the different kinds of selection, and the different forms of the struggle for existence. During the war years he completed work on a remarkable 527-page textbook for the new field entitled [*Problems of Darwinism*], published in 1946. The work was a *tour de force*, integrating systematics, paleontology, morphology, embryology, population genetics, physiological genetics, biogeography, and selection theory into an evolutionary synthesis that was broader and deeper than that in any contemporary Western text. In 1943, working in Central Asia without recourse to any library (including his own), Schmalhausen completed a fourth major book . . . which was also published in 1946" (Adams 1988, p. 282). The fourth work was *Factors of Evolution*.

[7] This description of *Factors* occurs in an interesting passage toward the end of Schmalhausen's August 6th address to Lobanov, defending his omission of the Lysenkoist Michurin's ideas: "The last accusation--why I do not speak of Michurin or of the achievements of other of our plant breeders. Very simply, because *Factors of Evolution* does not deal with these questions at all. If I had thought of writing a book--and I may yet do so--on the question of governing variability and evolution, it would at all events be a bigger book than this. This is a special subject. Here I confine myself to an examination of the factors of evolution of animals and plants, and that only in order to substantiate the theory of 'stabilizing selection.' That is why in this special monograph I cite other works" (Schmalhausen 1949b, p. 495).

of "one long argument," as might be expected of an evolutionary morphologist who so openly held Darwin in adulation, and who also had such apparent disdain for anti-Darwinian and neo-Darwinian views alike. Hence Chapters 1 and 3 can virtually be read as a separate work; that is, as an evolutionary synthesis of developmental genetics, embryology, and morphology under the overarching theory of stabilising selection.

Looking more closely at its structure, *Factors of Evolution* is divided into four chapters. Chapter 2 we have discussed, and will return to briefly for its working definition of the stabilising form of natural selection, and discussion of the mechanisms for maintaining hidden genetic variability. Chapter 4, the shortest at only 39 pages, concerns the rate of evolution and the factors determining it. Schmalhausen devoted a paragraph of only a single line to describing this chapter, perhaps betraying negative feelings on its content, and indicating its overall insignificance to the general argument.[8]

As mentioned above, it is Chapters 1 and 3 that constitute the indispensable core of the argument for stabilising selection. Chapter 1 provides a full survey of the forms of individual variation and their causes. Here, Schmalhausen gradually moved from inside the organism to the external environment, as part of a tour of the factors involved in producing heritable structures, all under the influence of stabilising selection. He built up a picture of the physical and historical influences upon development from the nucleus out. Thus the reader travels outward through the cytoplasm, to the level of cellular and tissue interactions--morphogen gradients and induction processes--until finally emerging into the biotic environment. Then, looking back in from outside the organism, Schmalhausen leads once again through the evolutionary processes involved in the progressive stabilisation (or canalisation) of morphogenesis, but now from an ecological perspective. More precisely, Schmalhausen added the ecological perspective to an increasingly holistic approach,

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[8] Simpson's review of *Factors* is in agreement with this opinion, stating: "The last and briefest section of the book (chapter 4, 38 page) is devoted to the rates of evolution and to a summary of the history of life from the author's special point of view. Stimulating concepts and flashes of insight are not lacking, but to the reviewer this chapter is disappointing. Point by point criticism is not called for, but on these topics the author, here outside his immediate field, occasionally betrays inadequate grasp of the facts and becomes diffuse and confused" (Simpson 1949, p. 324).

since his descriptions always returned to discussion of the internal factors or determinants of development. Also within Chapter 1, divergence from the existing modern synthetic theory becomes increasingly evident. Hence the causal evolutionary role of the occurrence of numerous small mutations was, in his view, not simply provision of direct micromutational changes to the phenotype, some of which may be selectively advantageous. Its most important causal role was, by contrast with the neo-Darwinian synthetic theory, the provision of constantly shifting (and generally phenotypically invisible) hereditary support for the morphogenetic stabilisation, and eventual hereditary fixation, of adaptive modifications. In the final section, Schmalhausen's continuing theme throughout the chapter received a concise restatement: namely, that the ever changing hereditary constitution of the organism provides the genetic raw materials for stabilising selection to act upon, facilitating the progressive stabilisation of development. The existence of a number of mechanisms for concealing extensive genetic variation in the population gave added empirical support to this thesis, which, together with the overarching theory of stabilising selection, provided an explanation of the hereditary fixation of adaptive modifications to the phenotype.

Schmalhausen's Chapter 3 was in many ways very repetitive of Chapter 1. For example, there is too frequent repetition of the evolutionary development of regulating mechanisms of morphogenesis--though, admittedly, each time within a novel biological context. Hence this evolutionary development was first described in Chapter 1 as the transition from dependent to autoregulative development (for which Schmalhausen coined the general term "autonomisation"). Later, essentially the same process is described within the ecological context of the transition from his "eurybionty" to "stenobionty" (see my section 4.4.1.). Further on, in Chapter 3, Schmalhausen again redescribed the autonomisation process, this time in terms of the transition from "ergontic" to "morphogenetic" correlation in ontogenesis (my section 4.4.2.). However, these reiterations are often useful changes of perspective, from which the reader may acquire a fuller picture of the nature and purported biological effects of stabilising selection. It was also in this chapter that Schmalhausen made the crucial mechanistic distinction between stabilising and dynamic selection, described below in my section on the definition of stabilising selection.

In Chapter 3, Schmalhausen's accelerative progressivism also becomes more and more evident. As Urbanek's appropriately states, "to Schmalhausen morpho-physiological progress implies a greater isolation from the direct influence of environment and, generally, a more active way of life" (Urbanek 1988, p. 200). Yet, in the most general terms, progressive evolution for Schmalhausen was simply the outcome of processes of somatic differentiation, based upon the continual division of biological labour, and the hereditary fixation of the adaptive results under stabilising selection. The ever increasing evolutionary importance of what Schmalhausen called functional modifications, produced by the emergence of novel relationships between the environment and complex adaptive behaviour in higher vertebrates, was frequently reasserted. At this level of evolutionary development, progress continuously accelerates since, Schmalhausen tells us: "If the new relationships are stabilized rapidly--and stabilizing selection is faster than dynamic selection--they may provide a basis for further adaptive modifications which constitute the next stage in the adaptation of a species to new conditions of existence" (p. 201-202).[9] Differentiation as a direct result of an organism's activity is also an often repeated theme in Chapter 3 of the *Factors*: for example many skeletal transformations are said to occur as a result of associated muscle functions. The conclusion to Chapter 3, though not a general conclusion, is a powerful summary to the argument for stabilizing selection, where Schmalhausen restated his progressivism, asserting that "the increasing activity of organisms becomes of utmost importance in the course of progressive evolution, since the active struggle with harmful influences and active competition are associated with highly rigorous selective elimination" (p. 243). Chapter 3 thus ends with Schmalhausen discussing the resultant accelerating rate of progressive evolution. Moreover, the evolutionary plasticity of the higher organisms in particular attains a maximum due to their increasing adaptability, autonomous development, and highly developed regulating systems (p. 245).

Dobzhansky, in a preface to the book, wrote as though he understood that too close an editing of *Factors* would inevitably bring with it the distasteful necessity for

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[9] Such further adaptive modification corresponded closely to Baldwin's organic selection *sensu stricto*, which he redefined soon after the initial publication of the organic selection concept in 1896 (see section 2.5.1., footnote 43). Schmalhausen was very much better disposed towards classical organic selectionism than Waddington was.

a second translation. There were indeed too many long and tortuous passages, too many repetitious descriptions and poorly defined neologisms, and generally too many opportunities for confusion.[10] Adams, however, paints a different and intriguing picture of Dobzhansky's editing, stating that: "Actually, he edited the text rather more heavily than he indicated, cutting roughly half of the first part and more than a third of the second part, and reducing the original by almost a third of its total length" (Adams 1988, p. 283). As far as Adams is concerned, then, "Dobzhansky shaped Schmalhausen's text to fit the role he hoped it would play in the West" (ibid.). It is also apparent that the complexity of *Factors* has allowed a broad confusion to continue, regarding the nature of stabilising selection itself. The significance of this confusion to the adaptationists' dilemma within the early modern synthesis years and beyond, has been far from properly discussed. In an attempt to clarify some of these issues, I have reviewed at some length the concepts central to Chapters 1 and 3 of *Factors*. Before dealing with these ideas, I focus upon Schmalhausen's central concept of stabilising selection as explicated in his Chapter 2, and the importance he placed on hidden reserves of genetic variability.

4.2. The Nature and Action of Schmalhausen's "Stabilising Selection."

In Chapter 2 of *Factors*, Schmalhausen gave a combined definition of the dynamic and stabilising forms of natural selection:

> The *dynamic type of selection* is based upon the selective advantage under altered conditions of the external environment which certain variations of organization have over a norm established during previous conditions of existence. It involves a partial elimination of the previous norm and the establishment of a new one. The *stabilizing form of selection* is based upon the selective advantage under definite and, especially, fluctuating conditions

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[10] For example, within subsections D and E of Chapter 1, the reader needs to be aware that the term stabilisation is being translated in two contrasting senses. In addition to the central concept of stabilising selection, there is a discussion of "genetic stabilization," referring to the chemical (or thermodynamic) stability of the material gene itself. Thus Schmalhausen makes the potentially confusing statement that "the normal (wild type) organisation *would gradually be destroyed* as a result of the stabilization or mutation of the genes were there not a mechanism counteracting this process" (p. 25; emphasis added). We are reminded that Waddington's main claim to Dobzhansky, though in a different context, was that on a re-reading *Factors*, Schmalhausen seemed to have got the nature of stabilising selection "muddled up" (Waddington 1975, p. 96). The complexity of Schmalhausen's writings demanded much greater clarity and thoughtfulness in translation than were originally granted.

> possessed by the normal organization over variations from the norm. It is associated with the elimination of most variations and the establishment of more stable mechanisms of normal morphogenesis. (1949a, p. 73; emphasis author's).

A clear understanding of Schmalhausen's concepts of dynamic and stabilising selection is crucial, both to an understanding of the *Factors*, and to an appreciation of his position with respect to the modern synthesis. The stabilising form of natural selection was almost universally misinterpreted by supporters of the synthetic theory. The essence of Schmalhausen's distinction between dynamic selection--identified by him with classical Darwinian selection--and stabilising selection, consisted in their opposing relations to the existing adaptive norm of reaction.[11] Dynamic selection disrupted the norm, whereas stabilising selection reinforced it. It is immediately apparent from Schmalhausen's diagrams, that the necessary conditions for the stabilisation process are a subset of the conditions for dynamic selection. For Schmalhausen, stabilisation continued regardless of whether or not dynamic selection was in operation. Thus the paradigm conditions for dynamic selection to operate are described as a "homogeneous environment, which varies in a definite direction, and a variable organism with a stable (independent of changing external factors) morphogenesis" (ibid.).

To illustrate the two forms of selection, Schmalhausen provided a diagram consisting of two normal distribution curves, placed side by side. These were duplicate curves; that is, both represented the distribution of variation existing within a single population, and for a single adaptive phenotypic trait. The left hand distribution illustrated the effect on such a population of stabilising selection. In this case, selective elimination of unfit individuals within a stable but *invariant* environment, produced a slight symmetrical narrowing of the curve. The area under the apex of the curve represented the best adapted members of the population, which therefore remained stationary under selection. The shaded area between the broader curve (pre-selection distribution) and the narrowed curve (post-selection distribution), represented the eliminated, non-adaptive extreme phenotypes at either limit of the norm. Continued selection would continue symmetrically to increase this shaded area of elimination.

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[11] See section 4.3.2. for a discussion of Schmalhausen's important concept of the norm of reaction.

The right hand distribution curve of the diagram illustrated the effects of dynamic selection. Here, selective elimination had occurred within a stable but *varying* environment. By chance, the changing environment gave a selective advantage to those better adapted phenotypic variants to the right of the mid-point, and decreased selective advantage for those to its left. Consequently, a broader shaded band of eliminated phenotypes was depicted to the left of the distribution, and a narrower shaded band to the right. This result was represented as a shift in the phenotypic distribution to the right (in Schmalhausen's diagram, from M to M'). Hence, as a result of dynamic selection the curve of *surviving* phenotypes, in Schmalhausen's words, "becomes skewed and the average is shifted towards the favoured side" (p. 74). This, he added, had consequences for the stability, or degree of canalisation, of the newly adaptive variant forms since: "The accumulation of [newly adaptive] variations and, hence, of mutations which were previously eliminated upsets to some extent the regulative mechanism ('genic balance') and the entire system of morphogenic correlation as a whole. This disturbance, in turn, favours the appearance of suppressed mutations (hidden reserves) and an increase in mutability. Accordingly, the frequency curve expands and moves in the favoured direction *beyond the limits of the variants observed earlier*" (ibid.; emphasis added). However, such resultant distortion of the initial curve is not shown in Schmalhausen's diagram. This second process, of moving "beyond the limits of the variants observed earlier," is precisely the production of a new norm, and, said Schmalhausen, "proceeds more slowly than the first phase of evolution." Only the first phase, which has not yet produced a new norm, is shown in the diagram; that first phase being, in Schmalhausen's words, "the shift of the mean at the expense of already existing variants and the mobilisation of hidden reserves of intraspecific variability" (p.75).

Since the initial phases of both stabilising and dynamic selection leave the original normal phenotype distribution--that is, the norm of reaction--fully intact, what distinguished dynamic selection was specifically the slower second phase disruption, or in Schmalhausen's words, the "partial elimination" of the original norm. In other words, it appears (in this part of the discussion, though confusingly not later in the book) that it is only by the ongoing dynamic selection of hereditary variations (mutations) that the species can actually alter the norm; that is, can eventually produce novel phenotypes not found within the previous norm.[12] By the same token, when the species is particularly variable or "labile," the eliminated phenotypic variants would include many more non-heritable modifications as well as heritable mutations. Therefore, the wider range of modifications for natural selection to act on in a labile organism, limits the extent of genuine dynamic or "directional" selection. In other words, if many of the extreme deviant forms being selected are still only non-heritable adaptive modifications--and still within the existing, labile norm of reaction--then there will be little observable difference between the stabilising and dynamic forms of selection *in their initial phases.* In Schmalhausen's words, in this circumstance "the dynamic and stabilising forms of selection are combined" (ibid.). This, clearly, was an unfortunate and confusing consequence of having an operational definition of dynamic selection, which rendered the results of its initial phase indistinguishable from the results of stabilising selection.

In any case, for Schmalhausen stabilising selection was in the front line against the breakdown of developmental systems. The stability of the morphogenetic system was constantly being destroyed, due either to variation in environmental factors, or to genetic mutation. Yet in the course of evolution, stability was to be re-established by the continuous action of stabilising selection. This was effected, in Schmalhausen's terms, by natural selection's "creating a regulating apparatus," via developmental mechanisms described in depth in his Chapters 1 and 3.[13] Briefly, the regulating apparatus was constructed via selection for individuals with ever more stable morphogenesis. Stabilising selection uniquely brought this about by accumulating "all mutations which do not bring the phenotype beyond the limits of the established norm" (p. 204). Hence, both dynamic and stabilising selection act by the natural selection of hereditary variations, or mutations. Nevertheless, as Schmalhausen

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[12] However, this appeared to contradict Schmalhausen's belief, discussed in my later sections, that totally new forms can be produced by continuous stabilising selection alone.

[13] As I elaborate below, some commentators on Schmalhausen, most notably Simpson (1953) and Waddington (1953), argued that selective elimination of non-adaptive extreme variants from the norm, and positive selection for Schmalhausen's regulating mechanisms of development, constituted two forms of stabilisation, and therefore required (fallaciously in my view) two separate kinds of selection. Waddington designated the former "normalizing selection," and the latter, unsurprisingly, "canalizing selection." The dubious nature of this distinction, and equally suspect complaints that Schmalhausen did not recognise the phenomenon of "normalisation" in his monograph, are addressed fully in my section 4.5.

further explained in his Chapter 3, stabilising selection by definition was "based, not upon advantageous deviations, but upon neutral variations." More radically, he continued, "it is based not only upon indifferent but also upon partially harmful mutations whose injurious effects are neutralized, and, primarily, upon small mutations." These were much more frequent, and "freely accumulated and combined in populations within the limits imposed by the normal wild type" (ibid.). Hence Schmalhausen's central concept explicitly synthesised the population genetic, phenogenetic, and developmentalist approaches to evolution. Quite contrary, therefore, to the opinions of commentators on Schmalhausen writing at the time of the modern synthesis, stabilising selection had a singular meaning, and a single mechanism.[14]

As Schmalhausen constantly restated, the single most important factor facilitating the action of stabilising selection, was the existence of hidden reserves of genetic variability in natural populations. Schmalhausen spoke of four classes of mutations, together making up a selectively neutral "mobilized reserve," which could be appropriated to the task of morphogenetic stabilisation. The reserve included, firstly, all small mutations with only slight phenotypic effects, allowed to persist within a species because of morphogenetic regulation. Hence Schmalhausen's particular brand of neutralism stated: "All mutations that are not manifested perceptibly because of a perfect regulating mechanism which mitigates the disruptive effects, should be regarded as neutral" (p. 120). Most importantly, Schmalhausen stated somewhat long-windedly: "The diversity of expression of many mutations, which varies not only in different races, populations, and lines . . . but also in particular individuals, and the incompleteness of expression of many mutations, even

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[14] Kirpichnikov, and other Soviet neo-organic selectionists in the late 1930s and early 1940s, viewed Schmalhausen's exclusivist notion of stabilisation as completely mistaken. Kirpichnikov in particular denied--given that for Schmalhausen mutant gene selection and the progressive perfection of morphogenesis both characterised stabilisation--any genuine distinction between stabilising selection and the "direct" (Schmalhausen's "dynamic") natural selection of coincident variations; that is stage 3 of Simpson's "Baldwin effect." Thus, Kirpichnikov argued in reference to stabilising selection: "According to Schmalhausen, the selection of favourable deviations from the normal type does not occur in this case. Since, however, Schmalhausen (1941) agrees that the development of the organism is perfected and the role of regulation in its development is increased as a result of which a better adapted phenotype is achieved in the above mentioned case, the author of these lines does not see the necessity of drawing a strict line between these two conceptions" (Kirpichnikov 1947, p. 170; see my section 2.6.2. for the full quotation from Kirpichnikov).

in strictly controlled identical cultures, indicate the existence of numerous small, not easily analyzable genetic differences between populations, between different lines, and between individuals" (ibid.).

As Schmalhausen was to elaborate in Chapter 3, these crucial points had been demonstrated experimentally by Shifrin, and especially by Kamshilov, via what Schmalhausen described as "the successful results of artificial selection for either maximum or minimum expression of a definite trait" (p. 121). Without such a radical plasticity of gene expression, relative to the organism's internal genetic and external "biotic" environments, the stabilisation and hereditary fixation of adaptive modifications postulated by stabilising selection could not occur. Put differently, if gene expression were of a fixed 'one gene one character' nature, with narrow limits placed upon the alterability of a gene's phenotypic consequences, then only the coincident selection of the neo-organic selectionists would be left to account for morphogenetic stabilisation. Thus one line of support for Schmalhausen's conception of stabilising selection (as opposed to the Soviet neo-organic selectionists' conception of the term) was, he believed, the rapidity of stabilising selection. To use Medawar's apposite expressions, waiting for the dynamic selection of a "genocopy" to "imitate" an adaptive modification would, in all probability, be a maladaptively long process.[15]

Secondly, Schmalhausen continued, "the category of neutral mutations may also include *the more important mutations* if, in the heterozygous state, they do not disrupt the general viability of the organism. This, he added, was "primarily true of recessive and semi-dominant mutations" (ibid., author's emphasis). Hence, the simple matter of overdominance is not to be overlooked as a means for hiding genes. Nor either is the fact of inter-locus modifying effects since, as Schmalhausen added, the reserve "includes, of course, the larger mutations, whose harmful expression is partly suppressed in process of selection of modifiers" (ibid.).

Thirdly, and perhaps most radically for a Darwinian selectionist, Schmalhausen stated that the full reserve of variation "may also include that category of neutral mutations that constitutes the mobilized reserve and *partially harmful--partially beneficial--mutations* that are disadvantageous in some and beneficial in other

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[15] See my section 1.4. footnote 57 for Medawar's synthetic neo-Darwinian concept of genocopy.

circumstances." In Schmalhausen's view, such mutations were "actually neutral as far as the organism as a whole is concerned." Finally, the category of neutral mutations included what he called "*conditionally harmful--conditionally useful--mutations*," the conditional nature of which was dependent upon a population's living in a heterogeneous environment, with local conditions producing varying demands (ibid., author's emphasis throughout). Thus armed with abundant, hidden, and selectively neutral genetic resources, stabilising selection was ready to act within natural populations.

4.3. Individual Variability as a Source of Historical Changes in Organic Nature.

When discussing of the nature of individual variability, Schmalhausen openly appealed to Darwin's distinction between "determinate" and "indeterminate" changes in organisms. These terms, Schmalhausen believed, related directly to the contemporary usage of "mutation" and "modification" respectively. Thus Schmalhausen said: "It has, until now, been impossible to establish a causal connection between the environment and the specific hereditary reaction of the organism or its germ cells. Darwin thought that the specific nature of the reaction is determined principally by the individual characteristics of each organism and designated such changes as individual or 'indeterminate.' Today they are termed mutations." In the second case, causal connection between environment influences and variations was easily established. Hence, said Schmalhausen, "Darwin has called these changes 'determinate.' Today they are termed modifications" (1949a, p. 1).[16]

This statement is noteworthy, since Schmalhausen immediately appealed to Darwin's authority, rather than to modern synthesis views on the nature and

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[16] In his 1946 book *Problems of Darwinism*, Schmalhausen made clear his support of Darwin's continuing authority on the matter of forms of variation: "The Darwinian definition of the major forms of variation is the most happy of all existing definitions, since even the modern definition of modifications and mutations, as hereditary and non-hereditary changes, lacks sufficient clarity and has given rise to many misunderstandings" (Schmalhausen 1946, p. 210; in Schmalhausen 1949b, p. 492).

determination of variations.[17] Schmalhausen described evolution as "on the whole, a liberation of the developing organism from accidental environmental changes" (p. 2). The determinate nature of modifications was due, according to Dordick's translation, to the previous action of canalisation.[18] Thus for Schmalhausen, the process of canalisation meant that: "Reactions of the organism to basic environmental factors to which it has become adapted are always strictly specific. This specificity of reaction is determined by the historically developed nature of the organism, by its evolution in a certain environment, and by the constant interaction of the latter with the internal factors of the organism" (p. 3).

4.3.1. The Disputed Concept of Morphosis.

Schmalhausen concept of morphosis was hotly disputed by Waddington, in a letter to Dobzhansky of 1959. The concept also became central to the debate over Waddington's genetic assimilation, which began during the mid 1950s. In discussing modifying responses that have not yet become canalised, Schmalhausen added the

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[17] In his Preface, Schmalhausen upbraided both anti-Darwinians and neo-Darwinians for having far too narrow a view of the modes in which natural selection can act upon such variations. After discussing these modes, including, of course, his own stabilising selection, he stated: "Usually, authors stress only one of these aspects of natural selection, and ignore the others, particularly the most important feature, which is the role of selection as the basic creative factor in evolution. It is precisely this one-sidedness which distinguishes not only the anti-Darwinians but also the modern neo-Darwinians, and which brings them into conflict with the logically impeccable concept of the immortal creator of the theory of evolution" (1949a, p. vi). Simpson, who through no coincidence reviewed the English translation of *Factors* in 1949, believed that Schmalhausen's attacks against the "'neo-Darwinians' (who are mainly the capitalistic geneticists)", were "all too plainly lip service." For Simpson, it was "clear enough that [Schmalhausen's] whole outlook on evolution is neo-Darwinian, in the ideologically damned sense, and he flatly opposes Michurinism, without of course mentioning Michurin or Lysenko by name" (Simpson 1949, p. 323). I intend to show that Schmalhausen's supposed neo-Darwinism was nowhere near as evident as Simpson suggested.

[18] The translator employed Waddington's canalisation term within Schmalhausen's statement that the organism "benefited from favourable influences and changes resulting from these influences were canalized into the most profitable forms of reaction" (1949a, p. 3). Waddington first wrote on canalisation in 1942: "The main thesis is that developmental reactions, *as they occur in organisms submitted to natural selection*, are in general canalized. That is to say, they are adjusted to so as to bring about one definite end-result regardless of minor variations in conditions during the course of the reaction" (Waddington 1942, reprinted verbatim 1975, p. 17; author's emphasis). He continued: "It seems, then, that the canalization is a feature of the system which is built up by natural selection; and it is not difficult to see its advantages, since it ensures the production of the normal, that is, optimal, type in the face of the unavoidable hazards of existence" (1975, p. 19; see Hall 1992 for a current interpretation of Waddington's concept; see my section 3.1.4. for discussion of the genetic mechanisms Waddington maintained facilitated canalisation).

concept of morphosis to the class of indeterminate changes; a class otherwise solely occupied by heritable variations (that is, mutations). A morphosis was defined as the response of an organism that had not yet evolved either adequate means of physiological protection against some new environmental factor, or adaptive ways of utilising that factor. Thus a defenceless organism is unable to respond to such influences by adaptive change, and all completely new changes produced in the organism are therefore by definition morphoses (ibid.).

In his letter to Dobzhansky, Waddington argued strenuously against the concept of morphosis. He objected that Schmalhausen's distinction between adaptive modifications and morphoses seemed "a very artificial and almost metaphysical one. Waddington argued: "I don't see that there is any reason to suppose that there is any essential physiological difference; what we presumably have is a graded series of the effectiveness which natural selection has had during the past history in moulding the type of reaction to external stress" (Waddington 1975, pp. 96-97). To Waddington, the eventual outcome of selection for an organism's response to some environmental stimulus, was the only criterion by which to judge the adaptiveness of some variant form. He appealed to Dobzhansky that "it is the *effectiveness* of selection, not its existence which is important" (p. 97; authors emphasis). For Waddington, there were no *a priori* maladaptive variations; the "morphosis" term could only refer to changes to the phenotype which selection had not had the time, or the opportunity, to act upon.[19] This did not constitute grounds for creating a separate category for such changes. Furthermore, the arbitrariness of the type of selection involved--that is, whether natural or artificial--was stressed by Waddington in relation to his own then recently undertaken experiments, designed to prove the existence of a universal canalisation mechanism for genetic assimilation. Waddington made the point that in his experiments with crossveinless and bithorax in *Drosophila*, "the phenotypes were

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[19] This new concept became the focus of long-running debate within the philosophy of biology. In 1965, Williams' supported Schmalhausen's concept and used it to attack Waddington's experimental verifications of genetic assimilation, produced during the early 1950s, as valid models of adaptive evolution. Hence, in choosing the crossveinless phenotype for his experiments, said Williams, Waddington rendered his results irrelevant to the experimental investigation of adaptive evolution, because crossveinlessness was a morphosis (Williams 1966, pp. 71-83). As a defence of Waddington's views, Eliot Sober's response to Williams is sophisticated and effective, focusing upon the relativity of the concept to the kinds of selection pressures being exerted (Sober 1984, pp. 199-211).

originally just what Schmalhausen would call morphoses, but [artificial] selection could mould the genotypes' reaction to the stress exactly as natural selection moulds the adaptive response in the case of salt acclimatization."[20] In any event, Schmalhausen applied the term in relativity to adaptive normal development, that is, to the hereditary "norm of reaction."

4.3.2. The Concept of the Norm of Reactions.

Schmalhausen introduced this concept in the context of the dependency of modifications upon the environment.[21] This dependency relation was most clearly expressed in organisms that are the least evolved in terms of their mode of development. Such organisms express "dependent" development, where there are no physiological mechanisms to accommodate adverse environmental influences. The qualitative outcome of an effect upon the organism is determined by its hereditary organization; that is, by its capacity to undergo specific adaptive modification. Geneticists, said Schmalhausen, "therefore speak of a hereditary 'norm of reaction'" (p. 4). Modifications produced by the internal reactions that constitute the norm, although determined by the genotype, can only be realized in the presence of definite environmental factors.[22] Hence, he concluded, "every genotype is characterised by

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[20] Bateman, who repeated and elaborated upon Waddington's original crossveinless experiments at Edinburgh, maintained that no such canalisation or "moulding" of the genetically assimilated phenotypes actually occurred--at least not under the artificial selection conditions as chosen by them both. This, Bateman maintained, "must be considered to be the case in the experiments described here since selection was only applied for the extreme of the abnormal phenotype; it is only ability to produce the character that has been assimilated, not any specific degree of development of the character" (Bateman 1959a, p. 470; see my section 3.1.2. for discussion of the Edinburgh controversy over canalisation).

[21] The term "norm of reaction" was, according to Dobzhansky, "the somewhat awkward expression proposed by the Danish biologist Raunkaier" (Dobzhansky 1950, p. 161). However, according to Harwood, the German Woltereck "was best known for his formulation of the concept of 'norm of reaction'" (Harwood 1993, p. 108).

[22] The concept of the norm of reaction is well expressed by Dobzhansky, in the 1951 edition of *Genetics and the Origin*. Here the concept is linked strongly to Dobzhansky's favoured notion of evolution as population genetical change: "The most general definition of evolution is change in the genotype of a population. Modifications of the phenotype alone, brought about by alterations of the environment, do not constitute evolution, unless they are accompanied by some genotypic changes. Nevertheless, what counts in evolution are the phenotypes which are produced by interaction of the genotypes of the organisms with the environments that are encountered in different parts of the world. It is the phenotype which is adaptive in some environments and unfit in other environments. Infirmity or well being, survival or death of an individual or a population in a given environment are determined, in the last analysis, by the genes which they carry. But the genes act through the developmental patterns which the

its own specific 'norm of reaction,' which includes adaptive modifications of the organism to different environments" (p. 7). Furthermore, when expression of a particular adaptive modification is so complete that it transforms the entire organisation, the genotype is said to possess an *adaptive norm* which is a particular expressions of the general norm of reaction.

There is, as seen in the section 4.2. discussion of stabilisation, a continual process under selection of producing ever narrower adaptive norms. Viewed alternatively, there is a gradual focusing of development upon one mode of expression of the general norm in a specific environment. This is precisely the process of canalisation.[23] The formation of such localised norms is contrasted, in Schmalhausen terms, with the production of "non-adaptive modifications or 'morphoses' which are of an entirely different character" (p. 8). The distinction constantly made by Schmalhausen, was between reactions which have an historical basis--that have relatively long been selected for--and those which have not. Thus we see the close cyclical relationship that emerges in Schmalhausen's theory between morphoses, narrower adaptive norms, and general hereditary norms: Uncanalised expressions of the general norm (including morphoses), are canalised to produce local adaptive norms, and further canalisation then transforms these adaptive norms into new general norms.

The crux of Schmalhausen's synthesis, was his redescription of this cyclical process in terms of the gradual institution of more complex regulatory mechanisms of development.[24] Such mechanisms were absent from species possessing only the

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organism shows in each environment. What changes in evolution is the norm of reaction of the organism to the environment." Thus Dobzhansky added: "A complete description of the norm of reaction of a genotype would require experiments placing carriers of this genotype in all possible environments, and observing the resulting phenotypes. Since the number of possible environments is virtually infinite, our knowledge of the reaction norms is at best fragmentary" (Dobzhansky 1951, pp. 21-13).

[23] Waddington maintained in 1953, after reading Schmalhausen's writings and Simpson's criticisms of them, that Schmalhausen had confused two forms of stabilising selection, only one of which (type 2) was identifiable with his own canalising form of natural selection. (Waddington 1975, p. 96). Yet It is difficult to support Waddington's claim (see section 4.5.).

[24] Again it is clear that Simpson and Waddington would both have argued, from very different agendas, that Schmalhausen's stabilising selection explanation of the narrowing of the norm of reaction, actually confused two separate modes of selection: namely, selection for; a) a narrowing of the range of variation in the population, and for; b) canalisation, or a tightening of developmental regulation. However, if the cause of a broad spread of phenotypes in the

dependent mode of development described earlier. The great evolutionary importance of the development of regulatory mechanisms was continually emphasised:

> In the process of evolution, the entire morphogenesis (i.e., the entire reaction apparatus) together with all its adaptive reactions *is endowed with regulating mechanisms which protect the processes of individual development against possible disturbance* by changing the accidental influences of external environment. Autoregulation is characteristic of all adaptive modifications. It distinguishes them, as processes with a long antecedent history, from morphoses which represent reactions without a historical past (1949a, p. 10; authors emphasis).

Such regulating mechanisms were instituted, of course, by the agency of stabilising selection.

4.3.3. The Role of Internal and External Factors.

In his analysis of the interactions between, and relative importance of, internal and external factors, Schmalhausen supported of the "well established facts" of the continuous interaction of nucleus and cytoplasm (p. 27). With Schmalhausen's emphasis, the cytoplasm was the "*specific substrate of ontogeny* in which occur all interactions that control determination and differentiation," including all the modifications dependent upon the external environment (p. 28). As regards the role of the nucleus, "only under its influences does the cytoplasm change and differentiate." Nevertheless, it was only by conceiving the cell as an integrated whole that we were to avoid contradictions (ibid.).[25]

It is in the context of his ideas regarding internal and external factors, that evidence appears against the characterising of Schmalhausen as a supporter of the gradualism of the synthetic neo-Darwinism. Gilbert, for example, has recently maintained that Waddington believed canalisation and genetic assimilation could

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population of a labile species is uncanalised development, then surely selection modes a) and b) are in fact identical.

[25] Schmalhausen's discussions of nuclear-cytoplasmic relations show that Gilbert is correct in emphasising this as an important point of similarity between Schmalhausen and Waddington. Hence Waddington wrote of nuclear-cytoplasmic relations: "It has frequently been argued that genes control only the later-developed and more superficial characters of animals and that the development of the basic plan of the body is controlled, not by them, but by the cytoplasm of the egg; and this contention has been hotly disputed by geneticists who seem to feel that it disparages the importance of their subject. We realise now, as in so many such controversies, both sides are in the right. . . . Thus for embryology the cytoplasm is as fundamental as the genes" (Waddington 1956, p. 348).

account for macro-evolutionary novelty, whilst Schmalhausen believed that stabilising selection could not.[26] The evidence begins with Schmalhausen's denial that nuclear-cytoplasmic interactions are sufficient to explain ontogenesis. Several higher levels of interaction are required. Regulatory development emerges when interactions of parts of the organism, at a higher level than that of the nucleus and cytoplasm, play the major role in ontogeny. Such interactions are mediated by information-carrying gradients of morphogens, or by induction systems (such as the neural organiser extensively studied by Needham and Waddington *et al*).[27] In Schmalhausen's view, these systems "determine quality, time, place, and size of certain tissues," and hence the "general basis of organisation." He was particularly interested in the possibility of adaptive hereditary variations in these systems (p. 29). His question was whether, through their effects upon these systems, "genic mutations and chromosomal rearrangements can produce a fundamentally new differentiation in the process of organic evolution" (p. 30). Could truly new organisations arise from simple changes to the norm of reaction?[28]

Schmalhausen began this enquiry by stating that phenogenetics "has accumulated extensive material indicating that the mutation process affects all types of morphogenetic interactions." Hence the connection between simple gene mutations and changes to the higher levels of organisation was, for Schmalhausen, fully experimentally established. First, he enumerated the ways in which such higher

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[26] Gilbert has recently asserted that Schmalhausen "was insistent that genetic stabilization should be made part of the population genetical model evolution. For him, embryological evidence did not fall outside the current definition of evolution; it fell nicely within it. Unlike Waddington, who stressed that genetic assimilation could give new types of organisms, Schmalhausen emphasised that "in these circumstances of adaptation, nothing new actually arises." (Gilbert 1994, p. 153; see my section 3.3.2.).

[27] See sections 1.3.1 and 1.3.2. for discussion of the Cambridge research programme into discovering the chemical nature of the amphibian organiser substance, or "evocator," and that programme's significance for the subsequent development of Waddington's synthesis of embryology, genetics and evolution.

[28] Mutations are defined in *Factors* as changes to the norm of reaction. In fact Schmalhausen states that "in contrast [to modification], a mutation is a *change in this reaction norm*; this is the most complete definition of any mutation whether it be visible or physiologic" (1949, p. 10; author's italics). However, since mutations were viewed equally to be the foundation of both dynamic selection (altering the norm), and stabilising selection (preserving the norm), and since dynamic and stabilising modes of selection could sometimes be combined, this definition appears problematic. It also provides support to Kirpichnikov's and Lukin's misgivings over stabilising selection's supposed separate status from neo-organic selection.

level morphogenetic systems can vary.[29] He had regard for Goldschmidt's rate-gene theory, saying: "Goldschmidt maintains that all these variations are the result of changes in the velocity of certain chemical reactions which are regulated by enzymes. This seems to be extremely plausible."[30] Yet Goldschmidt's full identification of genes and enzymes was thought to be "unproved and rather improbable," nevertheless it is apparent throughout that Schmalhausen, like Waddington, took the production and natural selection of fundamentally new differentiations for granted (p. 31). Furthermore, said Schmalhausen: "Heritable variations of the genotype with its norm of reaction must here be appealed to" (p. 32). Thus qualitatively new organisations did indeed arise from simple changes to the norm of reaction, appropriated by dynamic selection.

In Schmalhausen's own words, "participation of the external environment in formation of inherited structures and in their variation is an undisputed fact" (p. 34). More strongly, the evolutionary process was seen as a progressive internalisation of the external factors of development. This was characterised by the organism's progression from the dependent mode of development, through the *autoregulatory-dependent*, on to the *autonomous-mosaic*, and finally to the *autonomous-regulatory* mode, where the two autonomous modes were the most evolutionarily advanced. The first evolutionary transition, from fully dependent to autoregulatory-dependent development, produced an organism that, in Schmalhausen's words, "never submits passively to the influence of the external environment" (p. 35). Threshold reactions emerged at this first transitional stage. Thus in autoregulatory-dependent development, when the intensity of an external stimulus exceeds the lower threshold

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[29] Schmalhausen offered 5 ways in which changes can occur, in his terms, "in systems of morphogenetic correlation." Such were variations in: 1. Time and place of contact [of tissues]. 2. Time of appearance of morphogenetic substances. 3. Time of maturation of reacting tissues. 4. Upper or lower threshold of the normal reactivity of tissues. 5. The nature of the reaction itself (1949a, p. 31).

[30] Schmalhausen's and Waddington's appraisals of Goldschmidt's rate-genetical theory were both favourable, though both thought his quantitative enzyme notion of the gene implausible. Regarding Goldschmidt's belief that genes act by altering the rates of developmental reactions, Waddington believed this "fruitful idea" had happily led many geneticicsts to study development, producing much valuable work (Waddington 1941, p. 108) However, after re-vamping Goldschmidt in light of his own work, he noted of Goldschmidt: "In his recent Silliman lectures [Goldschmidt, 1940] he is still concerned to show that time is the one and only essence of the matter" (1941, p. 109; see also section 1.2.2.).

of a tissue's reactivity the reaction depending on it is completely and immediately expressed. The point is that between the upper and lower thresholds, there exists a wide range of possible variations in the intensity of external stimuli to which the organism will not respond. This, said Schmalhausen, "indicates a decline in importance of the external factor."[31] At the lower threshold, a chain reaction ensues of internal mechanisms determining morphogenesis, with the external stimulus merely determining which historically developed morphogenetic reaction, or canalised pathway, is "realized" out of all those that can occur at that time and place. Thus what Schmalhausen called the "usual" forms of adaptive modifications are always expressions of this type of dependence, having some degree of historical foundation.[32]

The next step of the progression towards the organism's full emancipation from environmental circumstances, was represented by the autonomous-mosaic mode of development. Here the role of external factors is further reduced, and internal factors assume fundamental significance.[33] It was rare, in Schmalhausen's view, in autonomous development for the control exerted by external factors to extend even as far as the larval stage, or metamorphosis (p. 38). Gradual complexification of the

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[31] Such a process would be entirely contrary to de Beer's understanding of ontogenesis. For de Beer, all processes of development had to be initiated anew under the influence of the external stimuli responsible for the development of each specific character. In other words, all development, even in higher animals, remained permanently a form of dependent development, with internal factors merely allowing processes to occur with some regularity. In both Schmalhausen's and Waddington's theories this was entirely reversed, with external factors merely triggering regular developmental processes in autoregulative development, before, in autonomous development, becoming superfluous (see de Beer 1930, p. 18, and my section 1.4.).

[32] Clearly, the transition to autoregulative dependence described the move towards Waddington's internalisation, or genetic assimilation, of triggers which determine the choice between developmental pathways (Waddington 1941, p. 109 [points 1 to 5]; and 1940, p. 49). For Waddington, this movement progressed under the influence of canalising selection. Schmalhausen also provided some entertaining examples: "Many types of autoregulative dependence are known in plants. In *Polygonum amphibium*, the mechanism forming aerial leaves is replaced at a certain degree of moisture by a mechanism producing floating leaves, which frequently have a different form and structure. . . . In animals, however, organization is not so greatly affected by such reactions. Seasonal color changes [temperature-dependent reactions] are very widespread and have a definite autoregulative character" (1949a, p. 36).

[33] Corresponding closely to Waddington's actual genetic assimilation event (Waddington 1942, p. 565).

emancipating regulative mechanisms of development continues through this evolutionary stage.

The most evolutionarily advanced mode of development was the autonomous-regulatory mode, where internal regulatory processes become even more important. At this stage, adaptive modifications are principally of whole organs and systems. Thus, stated Schmalhausen, they were "with few exceptions . . . the result of functional activity of the organ itself" (ibid.). Adaptability has, by this stage of evolution in higher organisms, been fully internalised, such that only one morphotype with extensive adaptability develops per organ. Schmalhausen's combined functionalist and morphological approach to evolution is evident as he states that "the fundamental form [of an organ] is transformed into an almost endless number of harmonious and adaptive variants." Lamarckist sympathies also appear to be expressed, as Schmalhausen asserts that "the use and disuse of organs becomes a matter of great importance" (ibid.). Furthermore, the external environment influences the makeup of the organism, not so much in the form of the physical stimuli from the inorganic environment, as in the form of "biocenotic" conditions which affect primarily the behaviour of animals in acquisition of food, and in defence against enemies (p. 39).[34] This is an important landmark in Schmalhausen's thesis. The complexity of developmental regulation arrived at in higher organisms facilitated, in his view, explosive adaptive radiation. The force behind this proliferation of adaptive forms was the use and disuse of organs, prompted by the organism's appetitive and competitive drives. This evolutionary mechanism, the hereditary fixation of acquired modifications via stabilising selection, is at least formally neo-Lamarckian. Schmalhausen clearly presented this as a mechanism--most explicitly of all in relation to the evolution of higher vertebrates--for the actual and not merely apparent inheritance of acquired characters.[35]

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[34] Schmalhausen's biocenotic factors closely resembled Osborn's "neuro-genetic" and "psycho-genetic" factors in the production of further ontogenetic variation upon coincidently selected variations: that is, in Baldwin's organic selection *sensu stricto*. However, whilst Schmalhausen regarded organic selectionism as a genuine possibility, he also saw the process as totally unrelated to his stabilising selection of adaptive modifications, for reasons already discussed (see sections 2.5, 2.6.2., 4.2.).

[35] Eliot Sober recently made an interesting distinction between causal and formal Lamarckism: "Lamarckism, like most *isms*, is a family of doctrines, often imprecisely formulated. The portion of it pertaining to the mechanism of inheritance provides a two-part thesis, one

There were several important consequences of the emergence of autonomous-regulatory development. Firstly, the stability and integration of such development produced independence from the standard norms of reaction of the lower, dependent modes of development. Hence, the phenotypic variability found in labile, environmentally dependent populations would no longer occur. Secondly, many slight mutations are not expressed in the stable organism. However, in Schmalhausen's words, when mutations are expressed "they are always phenotypically less stable than the ancestral normal type," and reveal pre-existing mutations, for reasons explained in my section 4.2.

Throughout this evolution towards autonomous development, the selection of adaptive modifications was seen to be of vital importance--a point often repeated by Schmalhausen in language reminiscent of his neo-organic selectionist compatriots. If, Schmalhausen very logically stated, natural selection is the basic factor in evolution, "then the concrete expression of individual characteristics under given environmental conditions is of decisive importance in this process." It was therefore, he added, "impossible to ignore the significance of 'noninherited' variations or modifications" (p. 44). If adaptive, they determined the survival of their possessors and influenced their further existence and evolution. On the face of it, this view was not incompatible with neo-organic selectionism. However, the placing of "noninherited" in quotation marks, emphasised Schmalhausen's dismissal of the notion of a non-hereditary plasticity of the phenotype. In Schmalhausen's view, as in Waddington's, genes underpinned all reactions involved in the production of the phenotype, including those producing adaptive modifications.[36]

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describing a pattern, the other prescribing a causal process that connects the elements of that pattern. First, there is the idea that characteristics that are 'acquired' within the lifetime of a parent may become 'genetically encoded' for its progeny. Second, there is the thesis that the trait is genetically encoded in the offspring *because* it was advantageous in the lifetime of the parent. Weismannism and the "central dogma of molecular biology" that is its successor . . . contradict the claim about process, but not the claim about pattern" (Sober 1984, p. 106; authors emphasis). If we apply Sober's generously wide criteria for causal Lamarckism--namely, that an acquired character becomes heritable simply by cause of its being adaptive and not, as Weismann would have required, by its blueprint being imparted to the germinal material via some direct instructional mechanism--Schmalhausen's mechanism of autonomisation appears much more than formally Lamarckian. (See my discussion of neo-Weismannism and epigenetic inheritance in section 5. 1.).

[36] In response to Mayr's characterisation of organic selection as a non-genetic plasticity of the phenotype governing the evolution of the genotype, Waddington replied: "a plasticity of the

4.4. Elementary Processes of the Variation of an Organism and of its Historical Development.

With regard to the two major theories contesting the true mechanism of adaptive evolution--a contest Dobzhansky had described in 1937 as "the real issue"--Schmalhausen clearly saw fault with both.[37] It was his contention that "the origin of adaptability is an insufficiently studied aspect of evolutionary theory," since "Lamarckians based their theory upon the premise of an already existing individual adaptability and did not examine its origin while the Neo-Darwinians regarded it as unimportant since they assumed that the results of individual adaptability, being non-heritable, have no evolutionary value" (p. 175). In Schmalhausen's estimation, by contrast, knowledge of how the organism's system of adaptive reactions developed--that is, understanding the origins of adaptability--was "very important in understanding the laws of evolution" (ibid.).

Schmalhausen began his analysis of the subject by restating that "it is a well known fact that the expression of many mutations depends upon variations in the external environment" (ibid.). A series of examples of the quantitative environmental dependence of mutations was given by him from work on *Drosophila*, especially examples of humidity and temperature dependence of expression. These mutations likewise showed a qualitative dependence of expression upon the internal, genetic environment. Here, then, was an important piece of supporting evidence for stabilising selection; namely, the very sensitive dependence, both quantitative and qualitative, of mutant expression upon the external and genetic environments. In Schmalhausen's analysis, such sensitivity was "dependent upon slight changes in the genotype, i.e., the combinations of small mutations--modifiers" (p. 178).

Schmalhausen attempted to use these empirical data as support for the complete relativisation of gene expression. Thus he maintained that "many experiments demonstrate the effectiveness of artificial selection in strengthening or weakening the effects of mutations." Yet his real interest was in the possibility of completely

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phenotype cannot be 'non-genetic'; it must have a genetic basis, since it must be an expression of genetically transmitted potentialities" (Waddington 1959, p. 390; see section 2.5.)

[37] See section 2.1. for Dobzhansky's discussion of "the real issue" in the modern synthesis' study of adaptive evolution.

altering the nature of the dependence of gene expression upon the external environment. If this were possible, completely reversed developmental responses to the environment could, if adaptive, quickly become hereditary via the stabilising selection of already existing genes in the population. Such radical developmental plasticity would provide an explanation of the origins of adaptability that was neither neo-Lamarckian, nor strictly neo-Darwinian. Kamshilov had apparently done a series of experiments on the *Drosophila* mutation eyeless, providing, in Schmalhausen's words, "the experimental proof that a reaction can be completely reversed."[38] Not only could environmental dependence be reversed by selection--in eyeless from the requirement of a moist to a dry culture medium--but it could also be destroyed, so that a uniform and stable expression occurred regardless of environment. It is clear, both from Schmalhausen's descriptions of the mechanism of stabilising selection and of his evidences for it from nature, that he viewed this example as an experimental demonstration of its mechanism in action.[39] Yet, after describing Kamshilov's work he commented reservedly: "The significance of this phenomenon will be discussed subsequently. Here, it is enough to note that the reactions of mutations to variations in the external environment may be transformed by selection, so that harmful effects resulting from this dependence may be either suppressed or altered and may acquire a different, perhaps even beneficial, expression" (p. 181). It followed, said Schmalhausen by way of support for his concept of morphosis, that "favourable modes of reaction to environmental factors are not a priori properties of the organism," but a product of its developmental history, and natural selection (ibid.).

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[38] Kamshilov's work showed that full expression of the *Drosophila* gene eyeless, typically dependent on a moist substrate, can be produced on dry medium by artificial selection of a strain with reversed dependence. Thus, said Schmalhausen, "In the original strain, low humidity was associated with large eye size (diminished expression) but, in the experimentally produced strain, low humidity diminished the number of facets (intensified expression of the mutation). Hence artificial selection has produced strains in which the dependence of the morphogenetic process (development of the eyes) upon the external environment (moisture of the substrate) is different from the dependence present in the ancestral form" (1949a, p. 180).

[39] Kamshilov's experiments provided a more dramatic and less controvertible demonstration of the polygenic basis of stabilisation (or canalisation) than Waddington's 1952 crossveinless experiment. Should Waddington have displayed a similar reversibility of expression of the major gene(s) Bateman thought responsible for the assimilation of crossveinlessness, he may perhaps have convinced her, and his other Edinburgh colleagues, of the validity of the canalisation hypothesis. (See section 3.1.2. for discussion of the Edinburgh controversy over canalisation).

Having thus found experimental genetic demonstration of the potential for transforming morphoses into adaptive reactions by stabilising selection, Schmalhausen returned to studying the phylogenetically established forms of such selectively generated adaptive reactions. The developmental effects of these he split into three categories. Firstly there were *general physiologic modifications*, for example, variations in growth rate dependent upon nutrition, humidity, and temperature. Secondly, *physiogenic modifications*, which consisted of specific adaptations of the organism or of its parts to variations in the physical environment. Thirdly there were *functional modifications* of organs, described as "indirect responses of the organism to variations in the external environment" (p. 184). These corresponded closely to the above mentioned dependent, autoregulative-dependent, and autonomous-regulative modes of development respectively. The third category, functional modifications, specifically concerned higher vertebrates, and were "always determined by the role of certain tissues and organs in the vital activity of the organism as a whole" (p. 188). Examples included the familiar functional hypertrophy of neurones and skeletal muscle in response to increased loads, and vascular reorganisation in response to neuromuscular changes (p. 189).

A close similarity can be seen between Schmalhausen's evolutionarily important physiogenic and functional modifications, and the neo-Lamarckian palaeontologist Cope's "physiogenetic" and "kinetogenetic" modifications.[40] Delage and Goldsmith believed that for Cope, kinetogenetic modification was "by far the most important in animal life." This, they added, was a view "in perfect accord with the Lamarckian viewpoint" (Delage and Goldsmith 1912, p. 254).[41] In Schmalhausen's discussion of

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[40] As Cope said in 1896: "I propose to cite examples of the direct modifying effect of external influences of the characters of individual animals and plants. These influences fall naturally into two classes, viz., the physico-chemical (molecular), and the mechanical (molar) . . . . To the two types of influence which thus express themselves in evolution, I have given the names Physiogenesis and Kinetogenesis." As an example of physiogenetic modifications, Cope related that "By exposing the pupae of butterflies to low temperatures material changes in the coloration of the mature insects can be produced." Schmalhausen's only examples from animals were also temperature dependent colour changes. Cope continued: "In the vegetable kingdom it is quite evident that evolution is more usually physiogenetic than kinetogenetic. In the animal kingdom we may reasonably suppose that kinetogenesis is more potent as an efficient cause of evolution than physiogenesis." (Cope, 1896, pp. 225-230; in Delage and Goldsmith 1912, pp. 252-253).

[41] Bowler has made an historical point about physiogenesis which relates directly to the disputed concept of morphosis. Many Lamarckians in the 1890s professed the non-adaptive nature of

functional modifications, their most important attribute was that they connected structure, function, and evolutionary development, in an ever closer causal relation. The strongly Lamarckian tone of the following passage, and the ubiquitous role of stabilising selection, are evident:

> Thus it is assumed that the origin of new functional differentiations is always based upon the vital activity of the organism itself. The new division of function is accompanied by the formation of new structures as a result of the functional activity of the organism. *Functional differentiations arise under the influence of function itself*; in the course of evolution, they are stabilized and incorporated into the *autonomously developing structures* through a change in the morphogenetic factors. The evolution of active functional structures thus becomes fully comprehensible. (Pp. 189-190; author's emphasis).

This fascinating passage illustrates the depth of functionalist and progressivist sentiment at the heart of Schmalhausen's morphological synthetic theory. It may be that that this still only constitutes a formal, and not a causal Lamarckism, yet it comes perilously close to the latter. The stabilization and hereditary incorporation of functionally produced novelties is simply the phenomenon of Lamarckian use-inheritance. For Schmalhausen, at least in higher vertebrates, it was the fixation of changes in *morpho*genetic (that is, epigenetic) factors, not genetic ones, that brought about the hereditary fixation of functional differentiations. What is more, in higher organisms, such changes arose "*under the influence of function itself.*" These specific hereditary changes--that is, the morphogenetic changes initially supporting the novel differentiation--were then rapidly underpinned by the non-specific hereditary changes incorporated by stabilising selection. In other words, small and often deleterious mutations are rapidly selected, within a few generations, to underpin the newly acquired developmental pathway. Here, then, was "direct adaptation" functioning not at the genetic, but at the epigenetic level.[42] The time-worn example

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many physiogenic changes, says Bowler, "as it allowed them to use the existence of non-adaptive characters as evidence against selection" (Bowler 1983, p. 64). Unfortunately, this undermined what Bowler calls "the more optimistic image of Lamarckism, which rested on the assumption that acquired characters are normally adaptive" (ibid.). Schmalhausen may well have been aware of the perceived difficulties with Cope's categories among neo-Lamarckians. Nevertheless, for Schmalhausen, normal characters were nearly always adaptive by definition. Only a temporary mutational disruption of the norm, or a temporary need to react to abnormal environmental stimuli, led to the physiogenic production of non-adaptive morphoses (and only then as a necessary preamble to their selective stabilisation, within the continuing adaptive evolutionary cycle).

[42] In discussing the neo-Weismannian understanding (and dismissal) of direct adaptation at the strictly genetic level, Waddington stated: "It has been usual indeed, to consider this suggestion

of callous formation in birds and mammals, is given as an example of a common functional adaptation. Schmalhausen concluded that functional adaptation "is considered very important in the origin of new differentiations in the course of evolution of the higher vertebrates." He also believed this mechanism shed light on "the very origin of the capacity for functional modifications," that is, on the origin of adaptability itself in higher organisms (p. 190).

4.4.1. The Significance of Adaptive Modifications in Evolution.

The evolutionary significance of adaptive modifications was firmly at the heart of Schmalhausen's argument for stabilising selection. On the history of this subject, he believed:

> The significance of adaptive modification in evolution has been evaluated by Charles Darwin. Some subsequent Darwinists however, regarded his statement regarding this problem as merely unnecessary concessions to Lamarckism. Nevertheless, the works of Lloyd Morgan, Baldwin, and a number of other Darwinian animal psychologists show an excellent and hitherto unexcelled analysis of the evolutionary importance of adaptive modifications from the Darwinian point of view. Unfortunately, the more recent advances of genetics have prompted the spread of neo-Darwinian concepts. Moreover, adaptive modifications generally have not been accorded any place among the factors of evolution. Only recently has this problem been rescued from oblivion by a number of Soviet investigators [here referring directly to Kirpichnikov, Lukin, and himself]. However, the evolutionary importance of adaptive modifications still has not been studied in all its aspects. *Nor has it been properly evaluated.* Here, therefore, an attempt will be made to indicate the fundamental direction of the future analysis of this problem. (1949a, p. 198; emphasis added).

If this passage can be taken at face value, then it is clear that Schmalhausen held the Darwinian analysis of this problem in high regard, and neo-Darwinian dismissals of the problem--along with neo-Darwinism itself--in somewhat lower regard.[43] Thus Schmalhausen would probably have agreed with Waddington's negative view of Soviet biologists' contributions to the problem in the 1930s and 1940s. Waddington was extremely scathing of the "Russian" work, believing it to be merely neo-

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as the only possible alternative to the opposed view that environmental effects have no hereditary consequences, the phenomena of adaptation being solely due to natural selection of chance variations." Waddington felt that his own work suggested the epigenetic alternative described here but, in his 1952 paper, yet he made no mention of Schmalhausen's 1946 views (Waddington 1952a).

[43] See footnote 3 above on Schmalhausen's evident capacity to stand up for his genuinely held scientific opinions despite the hostile political environment within Soviet biology in the 1940s.

Mendelian gene selectionism repackaged.[44] It was, after all, the analyses of Lukin and Kirpichnikov that prompted Schmalhausen to conclude, prior to his own analysis, that the problem had still not been properly evaluated.

Schmalhausen's illustrated the value of adaptive modifications via a discussion of *modificational eurybionty*, or adaptation to more than one biotope (local biotic environment). This adaptive capacity led to decreased mortality due to physical factors, which in turn helped maintain the hidden reserves of genetic variability. Until this introduction of the biotic environment, the effects of stabilising selection were described by Schmalhausen either in the context of its visible effect on populations; that is, increasing normalisation, or in terms of its internal developmental mechanism; that is, increasing autonomisation. He now added the ecological description of increasing "specialization or the transformation of eurybionty into *stenobionty*"; literally, the constriction of a species' environmental range (ibid.; emphasis added). Should local or seasonal environmental changes become permanent, the organism was already adapted and, said Schmalhausen, "the adaptive norm, which previously was of secondary importance, may become the principal or even exclusive norm" (p. 200). With regard to the transition from eurybionty to stenobionty, Schmalhausen stated:

> This type of organic adaptation proceeds very rapidly--in the course of one generation--and is followed by a hereditary transformation of the organism in correspondence to its new position in the external environment. The hereditary transformation occurs gradually as a result of stabilizing selection. In this case, the adaptive modification acquires fundamental importance, since the specific adaptive modifications shape the course of further evolution . . . . in all these instances of adaptation, *nothing new actually arises*. The organism merely responds to variations in the external environment by means of definite reactions. The capacity for these already had been acquired during the preceding evolution of the organism in a variable environment. (Ibid.; emphasis added).

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[44] With respect to Waddington's designation "neo-Mendelian" to the synthetic theory, Lovtrup makes the following useful observation: "The use of the expression 'Neo-Darwinism' as the name of the ruling theory of evolution has been criticised because it was adopted by Weismann at the end of the last century to represent his particular version of Darwinism. It seems that today very few biologists are familiar with this historical fact, and therefore this objection may be safely neglected. Of much greater importance is that . . . there is a difference between Darwin's theory and 'Neo-Darwinism' so fundamental that it is a mistake to associate the latter theory with Darwin's name. The currently accepted theory is more correctly called *Mendelian population genetics*; for convenience I shall here employ the name 'Neo-Mendelism,' as suggested by Waddington" (Waddington 1975, p. 168; in Lovtrup 1987, p. 6).

The phrase "nothing new arises," is important in two senses. Firstly, stabilising selection was radically divergent, in Schmalhausen's view, from the neo-organic selectionism of Kirpichnikov and Lukin. Thus Schmalhausen had never suggested the subsequent fixation of any novel hereditary imitation of an original "non-hereditary" modification, *as part of the mechanism of stabilizing selection.* However, he accepted the reality of such a mechanism as an expression of "common dynamic" selection (as defined in my section 4.2.). As the term "stabilisation" itself clearly indicated, there is only ever the original modification whose phenotype, if adaptive, received gradually increasing genetic support due to natural selection. Hence "nothing new rises" in stabilisation, because its mechanism did not allow for any neo-organic selectionist phenovariant-genovariant distinction. Hence genetic stabilisation could come about relatively rapidly in comparison to dynamic selection, since thanks to Kamshilov's experiments we now know that genes under selection are radically alterable in their phenotypic effects. Gene expression is fully subordinated to the organism's stringent adaptive requirements, most especially when in the service of higher functional modifications.[45]

There is, of course, a second significance to Schmalhausen's phrase "nothing new arises." Gilbert also quotes from p. 200 of the *Factors* as he contrasts Schmalhausen's supposed gradualism with Waddington's acceptance of saltationism. Thus Gilbert states: "Unlike Waddington, who stresses that genetic assimilation could give new types of organisms, Schmalhausen emphasised that 'in these instances of adaptation, nothing new actually arises" (Gilbert 1994, p. 153). Yet Gilbert overlooks the immediate context of Schmalhausen's phrase. Nothing new actually arises, in the transition from eurybionty to stenobionty, because eurybionty is characterised within the population by a *pre-existent* broad selection of relatively uncanalised local adaptive norms. It is from these pre-existent adaptive reactions that stabilising selection chooses the most adaptive, when one set of environmental circumstances comes to predominate. The statement that nothing *adaptively* new arises in the transition to stenobionty, cannot therefore be construed as a judgement

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[45] In an echo of Conn's Simian illustration of classical organic selection, Schmalhausen suggested as an example that "forest dwelling mammals may find protection in trees so that the extremities become adapted for climbing. Hence fundamental new adaptations may arise on the basis of functional modifications" (ibid.).

about the *kinds* of variant forms available for stabilisation within the eurybiontic population; that is, whether microvariations or novel macrovariations. Gilbert has tried to generalise Schmalhausen's phrase in order to portray him as an evolutionary gradualist, and supporter of Dobzhansky's population genetical contribution to the synthetic theory. Yet to accept this portrayal would entail having to deny too much good evidence to the contrary, not least Schmalhausen's frequent avowals that fundamentally new structures may arise on the basis of his functional adaptations. Other reasons need to be invoked for us to explain Dobzhansky's considerable support of the theory of stabilising selection.

Like Waddington, Schmalhausen also focused on what he called the "striking example" of the fixation and ontogenetic acceleration of callosities; specifically the soles of the feet in humans, and the elbows of the wart hog.[46] Thus Schmalhausen concluded that "callosities which first arose as modifications in response to a local stimulus have subsequently begun to develop at the same locus in the absence of the external stimulus. Thus a new structure which first was produced by the direct differentiating action of a functional stimulus has become stabilized" (p. 204). Having commended Darwin's successors on their analysis of adaptive modification; namely, Lloyd Morgan, Baldwin, and the "other Darwinian animal psychologists," Schmalhausen significantly added a denial of the uniqueness of the neo-organic selection mechanism proposed by Lukin:

> It is known that the action of stabilizing selection is based upon a selective advantage possessed by the adaptive norm (including also new adaptations) over all deviations from it. It operates by the accumulation of all mutations which do not bring the phenotype beyond the limits of the established norm. It may be assumed that *common dynamic selection* operates simultaneously in the same direction in which the modification of the organism is proceeding; that is, on the basis of the selective advantage of further deviation over the established norm. This is possible if the modifications are inadequate, unstable under the given conditions, or occur late in the ontogeny of the particular form. This replacement of modifications by inherited variations with definite advantages has been studied extensively by Lukin (1935, 1936, 1940). There is no doubt of the existence of these processes. *However, they do not constitute a special form of natural selection.* Since, in this case, selection is based upon advantageous

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[46] With respect to the link between stabilising selection, canalising selection, and selectionist supports for recapitulation, see my chapter 1 section 1.1. Schmalhausen states that Leche (1902) had demonstrated the accelerated appearance of callosities into embryonic stages of development (Schmalhausen 1949a, p. 203).

> hereditary variations whose probability is rather limited, the process of dynamic selection is very slow. (P. 204; emphasis added).

This second paragraph, focusing on Lukin's "substituting" (coincident) selection (see section 2.6), could just as easily have been referring to Simpson's soon to be published "Baldwin effect." As discussed in my section 2.5. Simpson was in agreement with Schmalhausen over the infrequency of the dynamic selection of coincident hereditary variations--stage 3 of the Baldwin effect.[47] Their views were also aligned in the belief that this did not constitute a special form of natural selection. Yet their writings fundamentally disagreed, for reasons that are now made clear, over Simpson's characterisation of coincident selection as a particular example of "the broader principle" of stabilising selection.[48]

4.4.2. The Origin of Regulatory Mechanisms of Morphogenesis.

Having described the mechanism by which natural selection stabilised adaptive modifications--a process leading to the production of a new and stable adaptive norm--Schmalhausen discussed in his terms the "mechanisms which preserve the norm during variations of the external, and, partly also, of the internal factors of development" (p. 206). The genetic means of preservation were principally genic balance and the all-important factor of hidden genetic variability (p. 207). Although linkage helped create and maintain stable combinations of genes, of much greater value, said Schmalhausen, "are the regulating mechanisms which consist of the phenomena of diploidy, genic balance (regulating genomic correlation), dominance of the norm, and morphophysiologic regulation" (ibid.).[49]

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[47] As discussed in my chapter 3, Simpson provided his own three part definition of the Baldwin effect (Simpson 1952a, p. 112; see my section 2.3.2.).

[48] In his 1953 paper, Simpson wrote as though Lukin, Kirpichnikov, Gause, and Schmalhausen, were all in agreement that organic selection was simply a mode of stabilizing selection. Hence Simpson quite misleadingly asserted: "Schmalhausen and some others (mostly Russian) speak of 'stabilizing selection.' Noting that stabilising selection was sometimes equated with Baldwin's organic selection, Simpson then added: "Stabilizing selection applies to any mechanism tending to fix an adaptive type . . . *The Baldwin effect is one such mechanism,* but not the only one and not (even in Schmalhausen's opinion) the most important" (Simpson 1953, p. 112; emphasis added).

[49] As a measure of the importance Schmalhausen the morphologist placed upon genetic systems, diploidy and genic balance received between 10 and 20 lines. Dominance received a mere 3 lines. Yet, as we emerge into the epigenetic levels, phenogenetic systems received 11 pages of discussion, and morphophysiologic systems (including development of morphogenetic regulations), received a further 11 pages.

Schmalhausen focused on the morphogenetic significance of "genohormones" (morphogenetic substances) in vertebrate embryonic development.[50] Normal development that is complex, with correlation of development between parts (such as in skull development in the chick), depended upon the genotype as a whole. In such cases, he added, "the role of the individual genes is reduced to the level of modifiers" (p. 219). The final and most significant means for preserving the stability of the norm were, of course, morphogenetic. It is in this context that Schmalhausen focuses much less on genetics, and more directly upon embryogenesis. Thus he stated that: "As the systems of correlations become more complex, they lose their genetic character; in other words the effects on [sic] individual genes can no longer be distinguished (more precisely their disruption by mutations has lethal consequences). Morphophysiologic interrelations and their systems may be regarded as entities that are not capable of analysis in genetic terms" (Ibid.) Put another way, such physiological systems are so deeply canalised that genetic disturbance will only visibly effect the organism should such disturbance be lethal.

Schmalhausen created two higher categories of morphophysiologic correlations, existing above the purely physiological level. These functioned at the "ergontic" level, and the evolutionarily highest or "morphogenetic" level. Ergontic correlations--for example the variable formation of bone under the action of muscle--are described as a "contingent result of the existence of functional interrelationships" (p. 220). In other words, ergontically produced structures were essentially by-products of the mode of function of working organs--by-products that stabilising selection had been able to act upon. The morphogenetic category was characterised by the loss of any such contingency. At this highest level, said Schmalhausen, "the interaction of parts of a developing organism may be a *direct cause* of morphogenetic processes." Morphogenesis becomes "not an incidental but a fundamental effect of the interaction of two or more parts" (ibid.; emphasis added). Yet practically, drawing sharp

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[50] In the case of invertebrates, the works of Ephrussi, Clancy and Beadle (1936) on diffusible eye colour determinants in *Drosophila* are discussed. Also Kuhn's similar investigations into diffusible pigment-forming substances in *Ephestia Kuhnellia* from 1935.

boundaries between these very abstract categories of correlation was admitted to be impossible.[51]

This transition, from ergontic to morphogenetic correlation, recalled Schmalhausen's other descriptions of the evolution of regulating mechanisms of morphogenesis: namely, the transitions from dependent development to autonomisation, and from eurybionty to stenobionty. At least the connection with autonomisation was made explicit, by his observation that the ergontic-morphogenetic transition "apparently resembles the processes involved in the formation of autoregulation in the ontogeny of forms dependent upon external factors" (p. 222). In another expression of strong (in Sober's sense of causal) neo-Lamarckist tendencies, Schmalhausen's mechanisms for both the acquisition and inheritance of new morphogenetic correlations are so closely connected, as to be virtually indistinguishable. In open advertisement to the morphologist's evolutionary ascendancy in these matters, Schmalhausen proclaimed: "The problem of the origin of new morphogenetic correlations does not present any difficulties from the point of view of a morphologist. The appearance of new differentiations in the course of evolution is simultaneously accompanied by the formation of new interrelationships *in the form of internal factors determining the heritability of these differentiations* (the processes of integration are a necessary condition for hereditary determination of differentiation)" (p. 221; emphasis added). Thus it seemed that the activity-dependent causation of new differentiations, the necessary functional integration of the new structures thus produced, and their resultant heritability, are all but different aspects of a single mechanism of heredity. In other words, a necessary condition for new differentiations to occur at all in phylogeny, was the simultaneous appearance of fully functional *and heritable* relations to the rest of the organism. Unfortunately, Schmalhausen provided no empirical examples from actual development with which to ground the reader, leaving her once again with a sense of floating in a sea of

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[51] As with many of Schmalhausen's concepts, the need for clear explanatory examples was never quite fulfilled. Although he noted that it is "clear that many transitions exist between physiologic, ergontic, and morphogenetic correlations," only an obscure embryological analogy is provided to help the reader clearly identify the three processes. Thus he stated: "In the embryo in which almost all the energy is expended in morphogenetic processes, ergontic correlations determine the interrelationship between those forms of vital activity which characterize embryonic life. Here the correlations acts as specific morphogenetic interrelationships" (1949a, p. 220).

terminological abstraction. Such correlation of variations had, of course, long been accepted by biologists as a requirement for the organism's survival.[52] However, what appears decidedly unorthodox in Schmalhausen's views, is the notion that it is the very mechanisms of these relations themselves that constitute their specific hereditary basis. The carriers of heredity, at the morphogenetic level, become nothing other than the very structures that facilitate the function of new differentiations. Put another way by Schmalhausen, "the mutual relationships of parts, which become more complex in the course of evolution, act at each stage of development as factors determining the further course of development" (ibid.)

In describing such regulative morphogenetic development due to "the mutual relationships of parts," Schmalhausen reiterated that the terms of geneticists are no longer sufficient. Hence he maintained: "The terms genic balance, dominant genes, double reserve of genic activity, etc. employed by geneticists merely serve as approximate expressions for describing complex phenomena. Behind these terms are hidden extremely intricate interactions, not between genes, but firstly, between the processes of intracellular metabolism and, secondly, between the more complex physiologic and morphogenetic processes" (ibid.). This had also to be true, then, of the explicitly genetic lower levels of protection of the norm (as described by him in a mere three lines, see footnote 47 above). Schmalhausen therefore justified his use of these lower level categories, as being a convenient means of illustrating the emergent inadequacy of formal genetics. As he explained, "our distinction between genetic and morphogenetic systems reflects the increased complexity of the interrelationships which at first were amenable to analysis by genetic methods but which have become unanalyzable in the course of further evolution" (ibid.).[53]

The clearest similarities between Schmalhausen's evolutionary mechanisms and Waddington's, emerged in Schmalhausen's discussion of these higher, morphogenetic means of protecting normal development. Three general mechanisms were involved: a) extension of the thresholds of normal reactivity of tissues, b) decrease of

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[52] An appropriate example in this context would be Weismann's concept of "intra-selection," which Alister Hardy mistakenly identified with Lloyd Morgan's coincident selection (section 2.3., footnote 15).

[53] Indeed, throughout chapters 1 and 3 of *Factors*, there is an abiding impression of the secondary importance to the author of the Mendelian genetic level of description and analysis.

specificity of morphogenetic substances, and c) complexity of morphogenic correlations. In mechanism a), both the quantitative and qualitative variability of morphogenic substances, made extension of the thresholds of normal tissue reactivity to accommodate these fluctuations extremely important.[54] Yet morphogens do sometimes transcend upper and lower thresholds of target tissue reactivity, even during crucial aspects of development. Such excesses, said Schmalhausen, "appear at once either as large mutations or as lethals, if they affect vitally important morphogenetic processes" (p. 224). Morphogens can also shift their time of appearance beyond the window of a tissue's competence, preventing a reaction and its dependent reactions. This mechanism explains why small mutations only have a visible effect upon the late developmental stages, when the vital processes of morphogenesis are completed (p. 225).

Turning to mechanism b), here stabilising selection for the individuals least responsive to changes in the morphogenic substances occurs. Evolution thus freed development from the contingencies of the organisms own internal environment. Hence both qualitative and quantitative aspects of morphogens, said Schmalhausen, "lose their importance in the course of evolution parallel with the development of a definite normal tissue reactivity" (pp. 225-226). Hence we now possess a morphogenetic explanation of the evolutionary transition--described in such varied ways by Schmalhausen--from dependent, through autoregulative, into autonomous modes of development.[55] Without exception, Schmalhausen believed, "all the

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[54] Schmalhausen provided as an example Goldschmidt's work on the development of intersexes in *Lymantria dispar*, where "The morphogenetic effect is normal, and almost independent of the concentration of morphogenetic or inducing substances" (1949a, p. 223).

[55] In a passage very reminiscent of Waddington *circa* 1942, Schmalhausen explained: "We have seen that in the autoregulatory type of individual development the factors of the external environment lose their determining importance and merely become stimuli which release an autonomous sequence of morphogenetic processes, and, that in the course of the progressive autonomization of ontogenesis, the internal morphogenetic factors also lose their specificity and are finally reduced to the level of stimuli which release an autonomous sequence of morphogenetic processes (self-differentiation)" (1949, p. 226). In 1941, Waddington likewise began with a loss of external stimulus (for example, friction for the production of a callous) specificity when, due to canalisation: "the action of the external stimulus is reduced to that of a switch mechanism, simply in order that the optimum response shall be regularly produced." Next, and effectively replacing Schmalhausen's "internal morphogenetic factors" with concrete "evocators," Waddington described loss of specificity at the internal level: "But switch mechanisms may notoriously be set off by any number of factors. The choice between the alternative developmental pathways open to gastrula ectoderm, for example, may be made by the normal evocator or a number of other things." Finally, said Waddington, "once a

experiments of reciprocal transplantation of pieces of tissue from one embryo to another show that the specificity of a morphogenic reaction is determined by the properties of the reacting tissue itself." Holtfreter's, Needham's, and Waddington's experiments, on the inductive effects of a variety of embryonic tissue extracts, were cited as evidence.[56] Such loss of specificity means that morphogenesis has acquired a maximum degree of protection from any destructive influences. However, this does not mean that induction itself has become irrelevant, since it determines rate, timing, and co-ordination of developmental reactions (ibid.)

Lastly, in mechanism c), the complexity of morphogenic correlations, is found the most sophisticated in this long list of systems protecting the norm of reaction. It consisted in the gradual development, under stabilising selection, of the underlying conditions necessary for all the previous systems. Schmalhausen concluded that all morphogenetic interactions form a very complex integrated system. He added: "Each individual reaction is assured by an entire aggregate of concurring factors; each factor separately may undergo extensive variations without seriously affecting the dependent reaction." Thus Schmalhausen has progressed from Braus's "double assurance" to what might be called "multiple assurance," increasing markedly the stability of normal morphogenesis (p. 230).[57]

4.4.3. Evolution of Individual Adaptability and Morphogenesis.

In a very interesting passage, Schmalhausen conceded that the question of the relative importance of dynamic and stabilizing selection was, as yet, unanswered: "At

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developmental response to an environmental stimulus has become canalized [Schmalhausen's autoregulation, see 1949a, p. viii] it should not be too difficult to switch development into that track [by an] even more regularly acting gene" (Waddington 1942, p. 565). Hence Schmalhausen's autonomisation and Waddington's genetic assimilation appeared almost synonymous, but for Schmalhausen's insistence upon the insufficiency of the genetic mode of description, especially at morphogenetic levels of developmental regulation (See section 3.1.2., footnote 29).

[56] In my chapter 1, I discuss the importance to Waddington's evolutionary thought of his acceptance of reacting tissue specificity, as opposed to evocator specificity, as stimulated by this research. The developmental mechanisms responsible for producing reacting tissue specificity in Waddington's theory were very similar to those producing autonomization in Schmalhausen's. (For Waddington's retrospective views on evocator versus reacting tissue specificity, see Robertson 1977, p. 598).

[57] For the significance of Braus's notion of *Dopelte Sicherung* (double assurance) to Spemann's, and particularly to Waddington's research, see Saha 1991, p. 101; Horder and Weindling 1986, p. 191; and Waddington 1940a, p. 49.

present, we do not know to what extent evolution has been due to direct selection of new types of reactions (dynamic selection) and what has been the role of differentiation of existing reactions into more specialized reactions, with the ensuing establishment of a hereditary foundation through stabilizing natural selection. A discussion of this subject at the present state of our knowledge would not be profitable" (p. 237). This clearly suggested a tactical withdrawal from his earlier position that stabilising selection was the prevalent mechanism of all adaptive evolution. The question, just as it had been for Hardy in the early 1940s, was an empirical one for which there was not, as yet, insufficient evidence. It also reinforced the view that Schmalhausen, contrary to received opinion, was no neo-Darwinian supporter of a one-sided dependence upon common dynamic selection, as he indeed indicated he was not in his Preface and Chapter 1. A strong suggestion of Schmalhausen's leanings over this question were provided by his remark: "It is, however, an indisputable fact that only the sex cells are inherited directly (ibid.).[58]

In his summarisation of these processes of autonomization, Schmalhausen re-emphasised the level of functional adaptations, believing it to be of fundamental importance for determining the continuing course of evolution. Hence, he emphasised, "the burrowing paw of a mammal can develop only in a burrowing animal" and "a flipper can arise only in an actually swimming animal"--a point many staunch neo-Darwinians would surely accept, but on very different (neo-Mendelian and strong selectionist) grounds to Schmalhausen's functionalist developmentalism. The converse process, he believed, was inconceivable; "a flipper cannot develop in a terrestrial animal" (p. 240). Thus Schmalhausen again appeared to suggest that the

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[58] In other words, there could be no absolute causal separation of directly transmitted or so-called "hereditary" characters (Weismannian blastogenic characters), and acquired or so-called "non-hereditary" characters (Weismannian somatogenic characters), except in the very obvious case of the direct donation of the blastomeres themselves. And synthetic neo-Darwinism's suggestion that such a separation is possible, merely highlights that movement's historical focus on the abstraction Mather characterised in 1943 as "the characteristic expression of the gene." Thus for Schmalhausen, the genetic and epigenetic factors needed to produce adaptive modifications were as inherited as those needed for the production of hereditary variations. Put alternatively, the phenotypic expression of variations was as much a question of development and stabilisation as was the phenotypic expression of adaptive modifications. Given these facts, made explicit by many, including Goodrich in 1924 (and of course Waddington), Schmalhausen used the *reductio* about germ cell transmission to intimate that only the theory of stabilising selection, with its acceptance of the phylogenetic significance of adaptive modifications, could provide an adequate conceptual scheme for adaptive evolution.

activities of higher organisms are directly causally related to novel differentiations in a Lamarckian fashion. Yet at all times, of course, he stressed the absolute importance of stabilising natural selection to autonomization, saying confidently: "All these changes have been the result of stabilizing selection. Hence, stabilizing selection is the most important agent altering the factors of individual development, determining the continuous process whereby individual adaptations are gradually incorporated into the normal organization, and consequently, transforming all of ontogeny by progressively raising the regularity of normal morphogenesis and the stability of the adapted norm" (p. 242).[59] Finally, we are reminded that the stabilisation of ontogeny--stimulated by the environment, and effected by natural selection--is an accelerating force behind progressive change. In other words, the relatively rapid action of stabilising selection, as opposed to slower classical dynamic selection, increases in importance proportionately as evolutionary progress continues to advance (ibid.)[60]

4.5. Discussion.

Not surprisingly, Simpson at the end of his review of *Factors of Evolution* said:

> The book as a whole is exceptionally difficult. This arises in part from the complexity of the subjects treated, for few can bring to the reading such broad knowledge and such comprehension of abstruse details as are

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[59] Schmalhausen rejected any suggestion of a reduction in evolutionary plasticity as a result of continuous stabilising selection (Beurlen's suggested "congelation of form"). "On the contrary," Schmalhausen noted, "attention is called to the increasing plasticity of organic forms" (1949a, p. 242). It appears counter intuitive that the mechanisms of stabilisation should produce lability at the level of the general reaction norm. Yet, Schmalhausen strongly asserted: "Simultaneously with the continuous stabilization of special types of reaction . . . there are also acquired entirely new reaction forms. And the capacity for individual adaptability, including the capacity for adaptive modifications, is based upon these new reaction forms. The capacity for more extensive adaptation is an important acquisition which leads the organism into new paths of progressive evolution" (p. 243). Williams (1966) produced a similar argument to Buerlen's against Waddington's genetic assimilation; and Jablonka and Lamb (1995) partly supported Williams' objection that development of a stimulus-independent response causes a reduction in phenotypic and genetic flexibility. However, Jablonka and Lamb defended Waddington, adding that "selection for a stimulus-independent phenotype could affect the frequency of alleles at additional loci. It could lead to functional interdependence between previously independent developmental pathways; as a consequence, the production of the modified character would involve a larger number of interacting loci than previously. Genetic flexibility might actually increase, not decrease as a result of genetic assimilation." (Jablonka and Lamb 1995, p. 36).

[60] For a discussion of the extent and significance of Waddington's own staunch progressivism, see Hahlweg 1981.

> possessed by the author. The difficulties are, however, partly semantic and organizational and might have been avoidable either in the original or in the translation. A few special terms of the Russian school of morphogenesis are explained in the foreword, but others strew the rough path of the English reader. The translator may be to blame for some infelicities (Simpson 1949, p. 322).

Infelicities notwithstanding, as a developmentalist synthesis of all the processes relevant to adaptive evolution in plants and animals, nothing remotely comparable to *Factors* existed by the end of the Second World War. Waddington's 1940 monograph *Organisers and Genes*, apart from being more modest in size, contained the relevant material only within one or two chapters. This, then, provides us with the first and most obvious reason for Dobzhansky's choice of Schmalhausen over Waddington: that at the time of publication of the *Factors* in 1946, no other major work provided Dobzhansky with the synthesis' "missing link."[61] Waddington had yet to publish anything of book length on the canalisation and hereditary fixation of adaptive modifications. This fact Waddington wryly attributed to the intrusion of the Second World War.[62]

In 1959, Waddington wrote to Dobzhansky suggesting that Schmalhausen had conflated two types of selection: "stabilising selection type 1," which Waddington believed held the gene pool constant, and "stabilising selection type 2" which, in Waddington's words, "built up genotypes which determine developmental pathways, which exhibit what you [Dobzhansky] call homeostasis and I call homeorhesis" (Waddington 1975, p. 96). But in December of 1952, Waddington had published the following much fuller account of his criticisms:

> The idea of the "canalization" or "buffering " of development (Waddington 1939, 1940) which underlies the theory of genetic assimilation, is also closely related to the concept of homeostasis, which has recently been introduced in genetical theory. This word has been used in two senses, which should be distinguished. Lerner . . . has applied it in connection with the tendency of the gene frequencies in a population, after disturbance by

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[61] Gilbert makes the observation that, "Like Dobzhansky, Waddington also used the "missing link" trope to describe the absence of embryology from the Modern Synthesis," adding in parentheses: "interestingly, this trope is Haeckelian; only if there is a linear chain can there be a missing link" (Gilbert 1994, p. 146).

[62] Tongue in cheek Waddington tells us that: "Before the grain of thought which originally led to the formulation of these ideas had proceeded very far it was unfortunately broken off by some of the more pressing business that demanded ones' attention at that time (in point of fact, an ecological study of predation between aircraft, U-boats and ships became for a time more engrossing even than Nature red in tooth and claw") (Waddington 1957, p. 73).

> artificial selection, to return, under the influence of natural selection, to an equilibrium state. This may be called "homeostasis of gene ratios" or "genetic homeostasis." The aspect of natural selection concerned in maintaining it is what I have called "normalising selection" (Waddington, 1953). Dobzhansky and Wallace . . . use the term in quite a different connection; an organism is said to be homeostatic when it adjusts itself to recurrent environmental changes in such a way that its function continues unimpaired." This might perhaps be called "developmental homeostasis." But the word homeostasis is perhaps an unfortunate one, since it seems to imply a stationary state, whereas development essentially involves change in time. It is for this reason that I have preferred the words canalization or buffering, which refer to an equilibrium sequence of states rather than to one unchanging equilibrium state. For the aspect of natural selection concerned with setting up such buffered developmental systems, I have recently (1953) used the term "stabilising selection," which was introduced by Schmalhausen (1949) who, however, does not clearly distinguish it from normalising selection. But again, this is perhaps not a very satisfactory expression, since the stabilisation of development would seem to imply that change had been brought to a standstill. Probably the best expression would be "canalizing selection", derived from the word used in the original discussion of the concept. (Waddington 1953b, pp. 386-387).[63]

However, Waddington's criticisms of Schmalhausen, made here within a reply to Simpson's "Baldwin effect" paper of the same year, had already been made by Simpson in his 1949 review of the *Factors*--a fact which Waddington later pointed out in his 1961 genetic assimilation review paper. In his account, Simpson first described Schmalhausen's categories of dependent, autoregulatory, and autonomous development, adding in very general terms: "A role of stabilizing selection is that it tends in the course of evolution to transfer developmental processes progressively from the first to the last of these categories" (Simpson 1949, p. 323). Yet, after giving an example of autonomisation in mammalian development (in this case, the embryonic fixation of callosities in baboons), Simpson then introduced the underlying theme of his review: "In this sense, 'stabilizing selection' is most strictly defined and is narrowly equivalent to the 'organic selection' of Baldwin and others down to Gause." After this highly contentious assertion, Simpson immediately continued: "Schmalhausen, however, also uses 'stabilizing selection' in at least two other senses, without clearly explicit distinction. In some passages it seems merely to mean selection in favour of wild type, or of an established norm, what is sometimes called 'centripetal selection'" (ibid.). This, then, is probably the stimulus for Waddington's

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[63] Waddington clearly makes a direct claim here for priority over what he described in *The Strategy of the Genes* as stabilising selection "*sensu stricto*" (Waddington 1957, p. 73).

own subsequent objections, with the precedent of "centripetal selection" setting the stage for his own invocation of normalising selection.[64]

Turning first to address the question of centripetal, or normalising, selection. Clearly, Schmalhausen often stated that stabilising selection effected its results through the elimination of phenotypes marginal to the adaptive norm. As Waddington himself later explained, "it is a commonplace to point out that the primary effect of natural selection is to eliminate deviant forms" (Waddington 1953c, p. 192). However, to suggest that this phenomenon indicated the action of a separate *kind* of selection which, in Waddington's words, "holds the gene pool constant," was either to indulge in stating the commonplace, or merely to describe an obvious consequence of stabilising selection, with respect to major genetic disruptions to the norm. Put differently, Schmalhausen's stabilising selection is an ongoing process. Given some stringent environmental requirement for the regularisation of an adaptive character, then of course stabilisation necessitates the elimination of, firstly, individuals with a grossly deviant morphology from the population. This will be necessarily be followed, in accordance with selection pressures, by elimination of somewhat less deviant individuals, due to their possession of a somewhat more stable morphogenesis. To suggest that the first phase of this process does not represent selection for more stable morphogenesis, simply because it could be defined in terms of Lerner's genetic homeostasis, was to suggest--against the whole thrust of Waddington's developmentalism--that the elimination of some genes can be morphogenetically insignificant.[65] At the very least, then, Waddington's objection

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[64] Several others, including Mather, Lerner, and Dobzhansky, somewhat uncritically accepted Simpson's viewpoint as veridical. For example Lerner stated: "The rejection by natural selection of the extreme deviates is a process referred to by Schmalhausen (1949) as *stabilizing selection* (in one of his usages of the term; see Simpson, 1949)" (Lerner 1954).

[65] Adams, who has extensively studied Soviet evolutionary morphology, seems to be the only commentator to appreciate the distinction between the deep morphogenetic effects, and surface phenomenal consequences, of the singular causal mechanism of stabilising selection. Thus, differentiating the phenomenal consequences of stabilising selection from those of dynamic selection, he states: "Schmalhausen distinguishes . . . *dynamic* selection, which tends to move the population mean for a given trait directionally . . . from *stabilizing* selection, which eliminates extremes from the norm and tends to maintain the population mean" (Adams 1988, p. 282). Then, addressing the deep morphogenetic effects, he immediately adds: "In Schmalhausen's view this stabilizing selection has two important effects: it leads to the integration of the genic complex and to the development of tightly interwoven developmental and autoregulatory mechanisms, and it leads to the build-up of a 'reserve' of hidden variability that can, under certain conditions, be 'mobilized' (ibid.).

violated the principle of parsimony, at most it violated his own express principles of evolutionary developmentalism.[66]

Moving to Simpson's third perceived sense of the way in which stabilising selection was being used, he continued: "Elsewhere, and more frequently, it means selection favouring and, in a sense, producing 'internal regulating mechanisms which counteract the harmful influences of the external environment, or of disadvantageous mutations and other disintegrating factors. Among the mechanisms of this sort discussed at some length are diploidy, dominance of wild type [Schmalhausen's dominance of the norm], balanced genetic systems, determination of morphogenesis by the genome as a whole, wide range of normal tissue reactivity, and complexity of morphogenetic correlations" (ibid.). Simpson's list is, of course, immediately recognisable as corresponding to Schmalhausen's lengthy discussion of mechanisms for protecting the norm of reaction, culminating in the complex "multiple assurance" of development (Schmalhausen 1949, p. 230; my section 4.4.2.). For Simpson, it was only in relation to his own understanding of neo-organic selectionism (which he later designated the "Baldwin effect"), that the phenomenon of stabilising selection was undoubtedly real. Hence he continued:

> Stabilizing selection in the narrowest sense, or 'organic selection' of genotypes coincidental with adaptive induced modifications, is doubtless a real phenomenon. It seems to have been established experimentally by Gause and to be the most probable explanation of some observed cases of adaptation. It is also of considerable interest in its bearing on some of the test cases of neo-Lamarckism. There is, however, room for question whether it merits such extreme emphasis, aside from the ideological struggle which evidently stimulated some of these studies. That it is really of relatively minor importance is suggested by the fact that when Schmalhausen is discussing broader problems and general historical aspects of evolution *he hardly ever uses "stabilising selection" in this sense, but*

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[66] Waddington described normalising selection, as selection for "the elimination of phenotypes *directly* dependent on the presence of abnormal genes" (Waddington 1953c, p. 192; emphasis added. This was contrasted to stabilising selection "*sensu stricto*" (that is, canalizing selection), which selected against phenotypes "whose disadvantage is due to the relative instability of their genetic system.") (ibid., author's emphasis). However, when applying Waddington's own strictly developmentalist principles, based upon Goodrich's dictum (see section 2.5.), deviant phenotypes "directly dependent on the presence of abnormal genes," were *a priori* phenotypes "whose disadvantage is due to the relative instability of their genetic system." Hence, in every other debate Waddington had with modern synthesis geneticists (particularly those supporting neo-organic selectionism), he always emphasised the direct dependence of the phenotype upon the *epi*genotype, whether the genes involved might be described as abnormal or not. It was only in relation to the question of whether Schmalhausen's stabilisation was actually better defined as Waddingtonian normalisation, that he temporarily ignored a radically epigeneticist story on the role of genes in development.

> *almost exclusively in the sense of the development of regulating mechanisms* (Simpson 1949, p. 323; emphasis added).[67]

Thus, for Simpson, the indubitably legitimate sense in which stabilising selection was being used--that is, in signifying the Baldwin effect--was so insignificant as to be the one which Schmalhausen hardly ever used. In fact, a closer examination of the *Factors* might have shown that it was one which the author *never* used, and one which he both implicitly and expressly denied on several occasions (Schmalhausen 1949a, pp. 198, 204, and 237). This was because, for Schmalhausen, the neo-Mendelian interpretations of organic selection of Lukin, Kirpichnikov, and Gause, were merely one mode of action of "common dynamic selection": dynamic selection, or the classical form of natural selection, having been graphically defined in antithesis to stabilising selection in Chapter 2 of *Factors*. Indeed, with regard to neo-organic selection's being reducible to a minor mode of action of classical natural selection, Simpson and Schmalhausen were in complete accord. Thus it was Schmalhausen's postulation of the existence of a separate, causally antithetical, and evolutionarily highly significant kind of selection, concerned with the autonomisation of acquired modifications, which was the major issue that separated the two morphologists Simpson and Schmalhausen. An issue, furthermore, which threatened to leave them at complete odds over Dobzhansky's "real issue," and hence the status of the neo-Darwinian synthetic theory.[68]

Interestingly Waddington--who's 1942 theory bore strong resemblance to Schmalhausen's (in its focus upon canalisation, indifference to "normalisation," and distinction from Huxley's neo-organic selection), nevertheless appeared to concur with Simpson's negative analysis of Schmalhausen's monograph. In fact, Waddington clearly attempted in 1953 to claim priority for his concept of canalisation, employing direct support from Simpson's analysis. Thus in his paper

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[67] Interestingly, Simpson confuses throughout his writings Baldwin's organic selection *sensu stricto*, that is, the further adaptive modification of previous coincident variations, with Lloyd Morgan's original concept of coincident selection (closely related to stage 3 of Simpson's own Baldwin effect). This was distinction which Baldwin and Lloyd Morgan devised, and Osborn concurred with, by 1897 (See section 2.5.1., footnote 43).

[68] In the 1937 and 1941 editions of *Genetics and the Origin of Species*, Dobzhansky wrote: "No coherent attempts to account for the origin of adaptations other than the theory of natural selection and the theory of the inheritance of acquired characteristics have ever been proposed. Whether or not these theories are adequate for the purpose just stated is a real issue." (Dobzhansky 1941, p. 187; see my section 2.1.)

"Epigenetics and evolution," and after identifying Simpson's three versions of stabilising selection, he commented:

> The lack of precision in the use of the term makes it difficult to decide how far Schmalhausen had realised the causal connexion which, it is argued here, exists between the canalization referred to in his second use of the term and the genetic assimilation involved in the third. Simpson (1949) appears to believe that Schmalhausen thought of assimilation taking place only by the spread through the population of chance mutations which happen to produce the same effects as the environmental stimulus, and he claims (as does Huxley, 1942) that this is the strict meaning of the older idea of organic selection. The essential point of the idea which is being advanced here is that the canalization of the response to an environmental stimulus so moulds the general genetic background that it becomes almost inevitable that a gene or system of genes will appear which can adequately substitute for the external stimulus (Waddington 1953, pp. 195-196).

After a detailed analysis of *Factors of Evolution* such as undertaken above, it becomes difficult to see how anyone could have construed Schmalhausen as failing to understand the causal connection between canalisation and genetic assimilation. Waddington certainly could not agree with Huxley's and Simpson's interpretation of the evolutionary significance of adaptive modifications, and must equally certainly have recognised a very close relationship between his own synthetic theory and Schmalhausen's. It might be argued, then, that Waddington felt an imputation of confusion within Schmalhausen's own understanding of stabilising selection, would leave clear the opportunity to claim priority for his own canalisation theory of evolutionary morphogenetic stabilisation. At least, Schmalhausen's monograph positively influenced Waddington's revision of the original 1940 concept of the genetic supersession of an external stimulus, changing it into "stabilising selection type 2."

Finally, a difficulty that seems to be overlooked in contemporary Western criticisms of Schmalhausen's thesis, is the problem of maintaining a distinction between classical and stabilising selection based upon the dynamics of their relation to the norm of reaction. This difficulty becomes acute when Schmalhausen attempts to maintain a dynamic aspect to stabilising selection, stating that its action does not necessarily diminish future adaptability (Schmalhausen 1949, p. 243). On occasions, Schmalhausen in fact retreated to the position that stabilising selection produces only minor changes to the norm of reaction. However, since mutations are themselves defined as alterations to the norm, and since stabilising selection depends upon the accumulation of many mutations, whatever their effects, the difficulty remained.

In conclusion, Waddington and Schmalhausen still stood very much together over the evolutionary mechanisms for the fixation of adaptive modifications, and very much apart from attempts to incorporate their views within a classical dynamic selectionist framework. The epigenetic or morphogenetic bases of their theories, and the roles they saw for embryology and genetics within an adequate modern theory of adaptive evolution, were broadly equivalent once Schmalhausen's work had been assimilated into Waddington's scheme. It is clear, at least to this author, that Waddington's assent to the views of new synthesis supporters, suggesting that Schmalhausen's concept of stabilising selection was confused, relate primarily to Waddington's priority concerns over the true mechanism for evolutionary morphogenetic stabilisation. Finally, for both men, the only escape they saw from the adaptationists' dilemma was a genetically enlightened evolutionary developmentalism--which, at a time of hardening selectionism within the synthesis, they alone were fully qualified to provide. The issue of the relationship between neo-Lamarckism and Schmalhausen's and Waddington's syntheses, will be addressed at length within my concluding Chapter 5.

Chapter 5.

Summary Conclusion: A Modern Developmentalist Synthesis.

> To be sure, little time now needs to be spent on the neo-Lamarckian theory that hereditary adaptation arises by *direct* interaction of organism and environment. This theory was, I think, surely correct in designating organism-environment interaction as the cause of adaptation and adaptation as the main orienting force in evolution (which, incidentally, Lamarck himself did not believe). The neo-Lamarckians did great service to evolutionary theory by insisting on this relationship and by producing a great deal of evidence for it. There is, however, no longer any real doubt that they mistook the nature of the interaction, which does not produce adaptation directly but through the mediation of genetical selection. The postulated neo-Lamarckian mechanism for direct transfer of modification to a genetical system does not exist, and all the evidence for its action as well as much evidence it could not possibly explain can be wholly accounted for by the indirect mechanism of selection.[1]
>
> George Gaylord Simpson.

5.1. Embryology, Epigenetic Inheritance and Evolution: "Old Terminology" Versus "New Terminology" in the Modern Synthesis.

Synthetic neo-Darwinism endeavoured to leave behind the late nineteenth and early twentieth century's most persistent evolutionary doctrines: strong recapitulationism and neo-Lamarckian heredity. These two central components of the "Old Synthesis" in evolutionary biology, had worked together since the rise of Haeckel's biogenetic law. Lamarckian inheritance was central to Haeckelian recapitulation, because evolutionary change by terminal additions to ontogeny was as crucial to Haeckel's adaptationism and progressivism, as it was to the recapitulatory acceleration mechanism itself (section 1.1., see also Bowler 1983, p. 68). Furthermore, although Haeckel championed *Darwinismus* in Germany, he in fact ranked Goethe and Lamarck as Darwin's equals in the origination of a transmutationist theory. Therefore Haeckel's own views on evolution constituted, in

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[1] Simpson 1953b, p. 266.

Gould's words, a "curious and inseparable mixture" of these three men's insights (Gould 1977, p. 80).

The "phylogenizing" of post Darwinian morphology was a very successful research programme, at least in terms of its longevity and intensity. During the period from publication of Haeckel's 1866 *Generelle Morphologie* until Garstang's important and damaging 1922 critique of the biogenetic law, embryology was transformed by recapitulationism. Yet the new power Haeckel had apparently imparted to evolutionary embryologists; namely, to directly view the lineage of ancestral adult forms by analysing an organism's embryonic stages of development, had many reverberations far beyond embryology itself. In Conklin's words, recapitulation "promised to reveal not only the animal ancestry of man and the line of his descent but also the method of origin of his mental, social and ethical faculties" (Conklin 1928; in Gould 1977, p. 116). Hence Gould has discussed five areas of the human sciences deeply influenced, if not deeply traumatised, by unbridled Haeckelian recapitulationism.[2]

However, the late nineteenth century's expedient relativisation of the biogenetic law, with its untenable "adult stage" recapitulationism, initiated the description of relative rates of ontogenetic acceleration for individual organs and structures. This obviated the strict Haeckelian view which had funded the doctrine's most obvious and widespread abuses; namely, that embryology was essentially a series of frozen adult forms (also see Mayr on Meckel, section 1.2.)[3] Nevertheless, despite the fact

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[2] Just three of Gould's examples suffice to make the point. In ethnology, recapitulation was employed to link the transitory behaviours of children of "higher" races with the fixed habits of adult "savages" (Chamberlain 1900; in 1977, p. 117). Again, in criminal anthropology, normal children were believed to pass through a "savage" phase, and were therefore predetermined "criminals" at one stage of their development. But whilst the normal adult achieved civilisation in later life, the "born criminal" remained trapped at the brute stage (Parmelee 1912; in 1977, p. 121). In psychoanalysis, the trained biologist and staunch recapitulationist Freud believed: "Each individual somehow recapitulates in an abbreviated form the entire development of the human race (Freud 1916; in Gould 1977, p. 156). For example, in Gould's words, Freud "linked the infant's oral and anal sexuality to a quadrupedal ancestry before vision became a dominant sense and eclipsed a previous reliance upon smells and tastes" (1977, p. 157).

[3] Gould speaks at length on this dismantling of the strict Haeckelian doctrine: "The obvious alteration involved a simple shift of perspective. If organs are accelerated at different rates, then each organ must be considered separately, for each still repeats the stage of its own evolution. . . . Cope and Weismann developed this alteration [and] it quickly became the methodological focus of nearly all serious work in comparative embryology. Recapitulation was preserved--indeed, it was strengthened--by accommodation" (Gould 1977, p. 174). He

that the exclusively selectionist Weismann was himself an organ and structure recapitulationist, the anti-Lamarckian and anti-recapitulationary forces within neo-Darwinism increased in strength. In the light of this ongoing agenda within the synthetic theory, the evolutionary syntheses of Waddington in the West and Schmalhausen in the Soviet Union were indeed radical alternatives, and not just footnotes to its completion. As phenogeneticists, embryologists and morphologists, Waddington and Schmalhausen both believed in an actual, and not merely an apparent, inheritance of acquired characters. Stabilising selection, properly understood, could never have been accepted into the emerging synthesis of the 1940s, no matter how well it may have been founded in good science and the "impeccable logic" of its exponents.[4]

Furthermore, Waddington the palaeontologist was a strong organ and structure recapitulationist, with a belief that genetic assimilation provided its explanation (section 1.2.2.). Likewise, Schmalhausen's evolutionary synthesis of morphology and genetics was by no means incompatible with the recapitulationist morphology of his mentor Severtsov.[5] Because of the general perception in the 1930s and 1940s that strong recapitulationism had finally been discredited, very few people were looking for selectionist explanations for recapitulation. Those who were, stood in opposition to T. H. Morgan's passive explanation of recapitulation, as merely the causally insignificant survival of ancestral characters in descendent embryos (See

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adds: "Haeckel's reading fell from favour and his law, refractory as ever to empirical criticism, retained its popularity through a redefinition in terms of individual organs" (1977, p. 175).

[4] As Simpson related in his review of *Factors of Evolution*, Dobzhansky had spoken of the "impeccable logic" of Schmalhausen, just as Schmalhausen had spoken of the "impeccable logic" of Charles Darwin himself.

[5] Ghiselin has commented: "To many it has seemed enigmatic that morphology contributed virtually nothing to the synthetic theory of evolution. Beyond the accumulation of more phylogenetic data and the elucidation of long-term trends, it seems to have existed in another world. One might conjecture that there was something about morphologists that led them to dislike selection theory" (Ghiselin 1980, p 181). Similarly Coleman States: "Morphology made no concrete contribution to the synthesis, but rather the reverse: the synthesis had an impact on the field of morphology" (Coleman 1980, p. 173). Waisbren has made reply to this opinion with a review of the work of the Oxford trio of Goodrich, Huxley and de Beer (Waisbren 1988). Yet as we have seen, only Goodrich positively stimulated a genuine integration of morphology into the synthesis. However, Ghiselin is justifiably impressed with the contributions made to evolutionary morphology by Schmalhausen's teacher, Severtsov. Therefore I hope that a reappraisal, in the light of the present history, of the contributions made to a genuine synthesis by Waddington's embryology and Schmalhausen's functionalist morphology will stimulate fresh discussion in this area.

Rasmussen 1991, p. 61, and also T. H. Morgan 1932, pp. 174-175; in Rasmussen 1991, p. 82). Thus in the West at the time of the selectionist hardening of the synthetic theory, only Waddington's ideas, based on Morgan's genetics, provided such an explanation. Waddington's alternative synthesis was unique, both in the embryologically developed basis of its developmental approach, and in its direct threat to the neo-Darwinists' rejection of strong organ and structure recapitulationism. In 1930, with de Beer's discrediting job done and with Haeckelian recapitulation and neo-Lamarckian heredity jointly offered the *coup de grace*, the founders of the synthetic theory believed that they could ignore embryology, and continue unhindered to investigate Dobzhansky's true mechanism of the origin of adaptations.

Yet at Cambridge in the 1930s, chemical embryological studies of the processes that caused the series of tissue differentiations in vertebrate ontogeny, showed how embryology had become the furthest thing possible from an irrelevance to the synthesis. These processes, when viewed as internal aspects of the phenotype just as subject to selection as the external and behavioural morphotype, brought otherwise marginally interesting processes, in particular Braus' and Spemann's "double assurance," to assume a new adaptive evolutionary significance (sections 1.3.1. and 1.3.2.). Powerfully, then, Waddington's twin concepts of reacting tissue specificity in embryonic induction, and selection for increased tissue "competence" (that is, the ability to react very sensitively and invariantly to the evocator stimulus causing that induction) led to a truly synthetic explanation of the genuine inheritance of acquired adaptive characters. They led, in other words, to the concept of "genetic assimilation" (section 1.3.2.). Once Waddington had identified evocatory substances with primary gene products, the natural selection for ever greater competence efficiencies formed an empirical and theoretical conduit strongly linking population genetics and embryology. Furthermore, the idea that selection for greater competence efficiences would necessarily cause a migration of induced adaptive characters to earlier stages of development, synthesised Waddington's embryo-genetics and the selectionist explanations for recapitulation given by F. M. Balfour and Fritz Muller (section 1.2.2., see also Gould 1977, p. 101) For Waddington, all these empirical findings and theoretical developments led him to call for a nexus of disciplines, under the general rubric of "diachronic biology" (section 1. 2.1.).

The difference between his concept of diachronic biology and the recently consolidated synthetic theory, enabled the maverick Waddington to publish deep reservations over the emergent neo-Darwinian orthodoxy in the early 1940s. Unlike the staunchly neo-Darwinist de Beer, Waddington had no ideological commitment to toppling neo-Lamarckism and the biogenetic law (section 1.4.). Furthermore, Waddington's embryological theory could, as mentioned above, just as easily accommodate Haeckelian recapitulation as it could Garstang's paedomorphic retardation.[6] Most importantly, Waddington's mechanism explaining the hereditary fixation and acceleration of acquired characters threatened to undermine Morgan's, Garstang's, and de Beer's supposed deductive disproof of Haeckel's biogenetic law, by showing how external factors of development could indeed become internalised.

Waddington's embryological synthesis had, then, served to answer de Beer's rhetorical question regarding the basis of recapitulation in neo-Lamarckian heredity. De Beer had asked, concerning one reputed example of the accelerated inheritance of acquired characters, whether anyone could suppose that friction wearing down the upper molars of the adult dugong "has anything to do with the origin of the internal factor which controls the resorption of the tooth in the unborn embryo?" Waddington's strategic response was to state that "it certainly seems very far-fetched to attempt to explain such phenomena without bringing in the fact that the environment might be expected to produce similar effects" (See Waddington 1953c; reprinted verbatim 1975, p. 30). Moreover, Waddington addressed the issue within the language of de Beer's "new terminology," rather than the "old terminology" of the traditional Lamarckism debate (section 1.4.).[7] In fact, Waddington's explanation of recapitulation whole-heartedly embraced the new opportunity, presented by de Beer, for a terminological break with the late nineteenth century's narrow obsession

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[6] De Beer's eight modes of heterochrony were convincingly reduced by Gould to just two; ontogenetic acceleration and retardation (Gould 1977, p. 228). Both these processes could be explained by canalisation (section 1.2.2., footnote 32).

[7] As discussed in my Chapter 1, de Beer asserted in 1930 that "the question--Are acquired characters inherited?--has no meaning, and what the questioners really mean is--Can external factors become internal" (de Beer 1930, p. 15). Thus the question was shifted from what he characterised as "the old terminology" of the inheritance of acquired characters, to the more precisely phrased question of whether or not the external forces acting upon ontogenetic processes can become "internalised" (1930, p. 18). Such a move was perfectly accommodated within Waddington's strategy of discrediting both neo-Lamarckian and neo-Darwinian mechanisms of adaptive evolution, as conceived by Weismann (section 5.2.).

with the hypothetical mechanism of somatic induction.[8] Both Waddington and Schmalhausen, from the early 1940s, were much happier with the broader question of whether or not a genuine inheritance of acquired characters occurred: that is, with whether or not external factors, known to be responsible for the stable and regular unfolding of ontogenetic development, could become internalised and phylogenetically fixed.

Turning to the question of neo-Lamarckian heredity in modern synthesis historiography, attitudes to the syntheses of Waddington and Schmalhausen have, to date, been entirely conservative. It is usually the opinion of modern historians that Waddington and Schmalhausen (and most especially Waddington), were acceptable to the prevailing neo-Darwinian orthodoxy, but of minor significance to the emerging modern synthesis. Jablonka and Lamb's recent book, though challenging in many other respects, clearly adopts this received view of history. Thus Jablonka and Lamb assert that although the evolutionary processes forwarded by Waddington and Schmalhausen could be regarded, in their words, as "having a Lamarckian outcome," they only had such in the sense of Medawar's "weak" form of Lamarckism.[9] As the authors explain, "Waddington and Schmalhausen did not suggest, as is required in the

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[8] The neo-Darwinian equation of neo-Lamarckism with somatic induction was a result of the extremely exacting demands of proof, originally made by Weismann, laid upon the proponents of neo-Lamarckian heredity. These demands were readily adopted by the neo-Weismannian supporters of the synthetic theory. Yet, as Mayr has stated, neo-Lamarckists tended also to accept orthogenesis, as well as "Geoffroyism" (which ascribed evolutionary change to the direct influence of the environment). In Mayr's words, "The product of this [direct] induction is transmitted to future generations, by means of an inheritance of acquired characters" (Mayr 1980, p. 5; see also section 3.3.1. footnote 56).

[9] In Medawar's "weak" form of Lamarckism, "Modifications acquired in each member of a succession of individual lifetimes, as a result of recurrent responses to environmental stimuli, may eventually make their appearance in ontogeny even when the environmental stimuli are absent or are deliberately withheld" (Medawar 1957, p.83). To this, Medawar added the recapitulatory tenet that "the age of appearance of these modifications in ontogeny will eventually anticipate the age at which environmental stimuli could in any case have been responsible for them" (ibid.). This, Medawar's "purely descriptive" weak form had a specific statement of genetic cause added to it to give Medawar's formulation of the "strong" form, where: "The repeated induction of character-differences within the lifetimes of individuals of successive generations *is accompanied by* a genetic change in each individual, the change being such as eventually to reproduce the character-difference elicited by environmental stimuli even when those stimuli are withheld" (1957, p. 91; emphasis added). Hence for Medawar, unlike for Weismann, no particularly strong causal connection between external stimuli and genetic change (viz. somatic induction) was insisted upon as evidence for the strong form, since the phrase "is accompanied by" allowed equally for somatic, direct, and parallel induction mechanisms.

'strong' form of Lamarckism, that the acquired characters were accompanied by the origin of adaptive genetic changes in the individuals in which they were induced" " (Jablonka and Lamb 1995, p. 37). For Waddington and Schmalhausen, therefore, "the environment effects the expression of genes, not the genes themselves" (ibid.).

Jablonka and Lamb here witness to the continuing dominance of the late nineteenth and early twentieth century conceptual framework--the framework of de Beer's "old terminology"--for debating the mechanism of the origin of evolutionary adaptations. In fact, using this framework, Mayr, Simpson, and many other neo-Darwinians in the 1950s (including de Beer), dismissed suggestions of the inheritance of acquired characters as failed attempts to legitimate the "strong" Lamarckian mechanism of somatic induction. Since adequate evidence for the existence of a mechanism for somatic induction had never been forthcoming, the neo-Darwinian selectionism of the synthetic theory could continue hardening unchallenged. However, real difficulties for the hardening synthesis, caused by its total dependence upon this narrow justification for the exclusion of the inheritance of acquired characters, were presented by the problem of the hereditary fixation of adaptive modifications. These difficulties, so vividly identified by Simpson in the early 1950s, necessitated a dismissive approach among synthesis supporters to the evolutionary significance of phenotype-genotype interactions. The debate over the evolutionary significance of adaptive modifications to the phenotype was always haunted by fears, openly expressed by Simpson, that it still left the decision between neo-Darwinian and neo-Lamarckian heredity to be made (section 2.3.2.).

Yet many evolutionists, writing from the early years of the twentieth century, had fully understood that the equation of Lamarckism with some mechanism of somatic induction, was simply a result of the doctrinal extremities of Weismannism. Delage and Goldsmith noted in 1909 that due to his "too narrow and too exclusive" concept of heredity, Weismann would only accept somatic induction as evidence of neo-Lamarckian heredity (Delage and Goldsmith 1912, p. 197). He therefore rigidly excluded as evidence the sometimes adaptively directed alteration of the germ plasm by an environmental stimulus, so as to produce the heritable facsimile of a somatic modification produced by the same stimulus (namely, parallel induction).[10] *A fortiori*, in Delage and Goldsmith's words, Weismann excluded "all cases in which an action is exerted simultaneously on the soma and on the germ cells," regardless of whether an adaptive modification precedes the production of an adaptive germinal variation: that is, both the closely related mechanisms of parallel and direct induction (ibid.).[11] Regarding this demarcation between somatic induction and other mechanisms, the authors wisely commented that "the line is very hard to draw in the majority of cases and the evidence demanded from the Lamarckians is very difficult to produce, for the two actions are not easily dissociated in real life" (1912, p. 198). And even if this were possible, they added tellingly, "it would only have a theoretical bearing on Weismann's theory of the germ plasm; *it would have no bearing at all on the question of the heredity of acquired characters as a factor in the evolution of species*" (ibid., emphasis added).[12]

Likewise in 1923, Dendy shrewdly recognised that the demarcation between somatic and other forms of induction, was rooted directly in Weismann's highly problematic distinction between "somatogenic" and "blastogenic" characters. In his 1893 *The Germ-Plasm: A Theory of Heredity*, Weismann identified somatogenic characters with acquired characters, writing: "By *acquired* characters I mean those which are not preformed in the germ, but which arise only through special influences

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[10] Dendy describes parallel induction using the following general example: "We know from the study of hormones . . . that almost infinitesimal quantities of specific chemical substances are able to produce very conspicuous and very definite effects upon the animal body . . . but no permanent modification of the germ plasm is effected, and, hence, there is no true inheritance. It is a case of what is sometimes called 'parallel induction,' in which the body and the germ cells are exposed at the same time to the same stimulus, but in the case of the germ cells, of course, the effect is delayed until the development of a new individual takes place" (Dendy 1923, p. 210).

[11] Delage and Goldsmith offered the following example of direct induction: "Paul Bert tried to acclimatise some Daphnae to salt water by gradually adding salt to the aquarium. At the end forty-five days, when the water contained 1.5% of salt, all the adults had died, but the eggs in their brood chambers had survived, and the new generation arising from these flourished well in the salt medium. Packard, a Lamarckian, who cites this case from Cuenot, sees in it evidence of the heritability of a modification, but Thomson, a Weismannian, regards it merely as an instance of the direct modification of the germ cells or of the embryos" (Delage and Goldsmith 1912, p. 198).

[12] Delage and Goldsmith nevertheless added that the distinction "assumes a certain importance in the case of characters resulting from the use or disuse of organs and generally localised," although the detailed basis for this assertion was not given (ibid.).

affecting the body or individual parts of it. They are due to the reaction of these parts to any external influences *apart from the necessary conditions of development*" (Weismann 1893; in Dendy 1923, p. 201; first emphasis author's). Such characters Weismann called somatogenic, "because they are produced by the reaction of the body or soma." These Weismann contrasted with blastogenic characters, which were defined as "those which originate solely in the primary constituents of the germ ('keimesanlagen')" (ibid.). Dendy immediately homed in on the most problematic phrase in Weismann's distinction:

> The expression "apart from the necessary conditions for development" clearly indicates a difficulty with which Weismann was faced in endeavouring to draw an absolutely clear-cut line of demarcation between somatogenic and blastogenic. It is obviously impossible to make any sharp distinction between the influences of the environment upon the developing organism, which in fact constitute the necessary conditions of development, and those environmental stimuli to which the adult is exposed, just as it is impossible to draw a sharp distinction between the period of development and that of adult life. (Dendy 1923, p. 202).

Thus, as Denby made clear, Weismann's distinction can only be arbitrarily made since (as others such as Goodrich later reiterated) every character is necessarily the combined result of internal and external influences. Therefore, the extent to which external influences may become internalised, by becoming a fixed part of the "necessary conditions of development" of so-called blastogenic characters, was always an extremely vexed empirical question. More importantly, it is thereby made the *only* important question, when deciding whether acquired adaptive modifications, produced as a response to such external influences, can themselves become, to use de Beer's 1930 term, "internalised" (section 1.4.). It was an irony of the development of synthetic neo-Darwinism that Weismann's blastogenic-somatogenic distinction had, by turns, been both too strong and too weak to support its ends.[13]

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[13] The arbitrary polarity of Weismann's categories lay at the roots of the deepening adaptationists' dilemma. At one extreme, de Beer's early modern synthesis campaign against Haeckel's phylogenetic causes forced him to weaken the preformist heredity of the blastogenic-somatogenic distinction. Supporting Dendy's and Goodrich's views, de Beer insisted that: "Each ontogeny is a fresh creation to which the past contributes only the internal factors by means of heredity" (de Beer 1930, p. 18). However, such a softening of Weismannian heredity proved too dangerous a concession to an epigenetic view of development, and hence possibly to neo-Lamarckian heredity, during the later synthesis period. Therefore in 1953 Simpson cautioned those neo-Darwinians seemingly seduced by organic selectionism either there was or was not a causal connection between adaptive modifications and subsequent genetic changes in a population. If there were, then neo-Lamarckism was "as much supported as supplanted" (Simpson 1953, p. 115; section 2.3.2.).

With regard to the blastogenic-somatogenic distinction, Schmalhausen in 1946 offered the superficially banal but important insight that "it is, however, an indisputable fact that only the sex cells are inherited directly" (Schmalhausen 1949a, p. 237; section 4.4.3.). This simple *reductio* of Weismannian heredity clearly made the point that, from the beginning of ontogeny, no structure beyond the zygotic blastomere itself has the privileged status of being exclusively blastogenic in origin. Nevertheless, the substitution of "somatogenic" characters for supposed adaptively and morphologically equivalent "blastogenic" characters--that is, neo-organic selectionism--still appeared acceptable to Schmalhausen. In other words, the hypothesis of the coincident selection of hereditary variations was, for him, a plausible (if slow and insignificant) mode of classical dynamic selection, as it was for leading supporters of the modern synthesis, such as Huxley and Simpson.

Yet the somatogenic-blastogenic distinction was not, for the most part, acceptable to Waddington. For him, the whole concept of coincident selection--especially when held as a universal theory of adaptive evolution to replace both neo-Darwinism and neo-Lamarckism--concealed a fallacy: namely, the fallacy exposed by Dendy and Goodrich, that any character could be either completely inherited or completely acquired. With respect to the second part of the fallacy, Mayr's notion of a "non-genetic phenotypic plasticity" (1951), suggested to Waddington the view that acquired modifications to the phenotype had no hereditary basis, and therefore no possible phylogenetic significance (section 2.5.). With respect to the first part of the fallacy, extreme concepts such as Gause's "substituting selection," suggested to Waddington a view that the hereditary fixation of adaptive environmentally induced modifications was merely apparent. For the Soviet neo-organic selectionists, particular Gause, with his appropriation of Chetverikov's 1926 genovariant-phenovariant distinction, held especially rigidly to the blastogenic-somatogenic distinction (section 2.6.1.).[14]

Both Waddington and Schmalhausen, and particularly Schmalhausen, described field evidence of the actual, and not merely apparent, hereditary fixation of adaptive modifications via stabilising selection. Unfortunately, although such evidence

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[14] Gause's resurrection of Geoffroy Saint-Hilaire's "principle of compensation" is testimony to the strength with which he held to this view. The initial modification and the substituting variation were necessarily materially distinct because of Geoffroy's principle.

appeared plentiful, what it signified had traditionally remained equivocal, at least as far as neo-Darwinian critics were concerned. The anti-Lamarckian Thomson had long before demonstrated that the amassed evidence for the inheritance of acquired characters was, though very extensive, rarely if ever decisive.[15] There was, perhaps, little to distinguish Jordan's and Kellogg's examples of the apparent inheritance of the effects of environmental influences from 1921, and Schmalhausen's theoretical examples of the transition from dependent to autoregulative development from 1946 (section 4.4.3., footnote 32).[16] Unfortunately, it was still the case that their mechanisms for these undoubtedly real phenomena remained radically underdetermined by theory; notwithstanding that the explanatory power of that theory had increased greatly, as had its consilience with physiological genetics and experimental embryology.

Nevertheless, after the Second World War, Waddington attempted to experimentally determine the causes of his genetic assimilation. Yet, from the point of view of observing supporters of the synthetic theory, the 1952 crossveinless experiment was irrelevant to the mechanism of adaptive evolution, because Waddington had chosen to demonstrate the genetic assimilation of a phenotype with zero adaptive value (3.1.2.). Waddington fully realised that objections raised against his total reliance upon artificial selection were invalid, as long as selection effectively linked surviving phenotypes and descendent genotypes.[17] One might also have

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[15] In 1926, Thomson listed a long series of supposed examples, under nine headings, illustrating what he called the major "misunderstandings as to the question at issue." However, he formulated the question in the old terminology of somatic induction (and hence the rigid blastogenic-somatic distinction), in such a way as to leave room for direct and parallel forms of induction: "The precise question is this : *Can a structural change in the body, induced by some change in use or disuse, or by a change in surrounding influence, affect the germ-cells in such a specific or representative way that the offspring will through its inheritance exhibit, even in slight degree, the modification which the parent acquired ?* (Thomson 1926, p. 174; author's emphasis).

[16] Jordan and Kellogg ended their example-packed chapter on the inheritance of acquired characteristics thus: "To sum up, there is no convincing evidence that the direct influence of environment is a factor in the separation of species, except as its results may be acted upon by natural selection. We have no proof to show that the environment of one generation determines the heredity of the next--and yet perhaps most naturalists feel that the effects of extrinsic influences work their way into the species, although a mechanism by which this might be accomplished is as yet unknown to us. (Jordan and Kellogg 1921, p. 210).

[17] This was perhaps a point that many Darwinians might have been expected to recognise from having read the *Origin of Species*, and noted the significance imputed to artificial selection by

expected a more favourable response from modern synthesis supporters for other reasons. Surely, Waddington's employment of mal-adaptive phenodeviants and artificial selection for the verification of canalisation, added a certain mechanistic and reductionistic authenticity to his experiments.[18] Such protocol would undoubtedly have appealed to Waddington's own dialectical affinity for both the mechanistic and reductionist systems of laboratory genetics, and the process-morphological implications of the canalisation doctrine.

Waddington's difficulties with the genetic assimilation research programme, came not from want of results, or failure in experimental design, but from a deepening of the very problem of under determination that the experiments had been designed to resolve. Far from coming to a resolution, the problem appeared to have become entrenched at the detailed genetic level of interpretation. No one doubted that the genetic fixation of chemically induced phenocopies occurred in these experiments. Nor, in fact, did his colleagues at Edinburgh doubt that several genes were often (though neither always, nor indubitably) collectively responsible for this fixation. Yet nobody, inside or outside Edinburgh, shared Waddington's view that canalisation of the phenotype was a prerequisite for genetic assimilation. Without canalisation, however, Waddington's theory had nothing obviously new to offer evolutionary biology. The contrary views of his Edinburgh colleagues that selection for major genes, whether pre-existent or spontaneously occurring, fully accounted for genetic assimilation, were played down by Waddington as incidental divergences of opinion, rather than evidence of the completely alternate and deeply canalised pathways of opinion that they were. Probably in Bateman's view, and certainly in

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Darwin himself. Furthermore, as Provine reminds us, its significance had not altered by the time of the impending synthetic theory: "In 1925 it was still true that the best evidence for natural selection in nature came from its similarity to the efficacy of artificial selection, the evidence for which (as in the experiments of Hopkins, Castle, Sturtevant, Payne, and others) was overwhelming" (Provine 1986, p. 234). However, Waddington showed that he was not insensitive to these criticisms. At a late stage during the genetic assimilation research programme, experiments were carried out on the assimilation of a quantitative adaptive modification; the enlargement of anal pappilae in *Drosophila* larvae in saline conditions. These experiments were completely dependent upon natural selection. As Waddington remarked: " The experiments which have been described so far have dealt with characters which (a) would not be adaptive in Nature, and (b) the production of which involved threshold phenomena. Both these limitations have been removed in a recent experiment" (Waddington 1959, p. 1654).

[18] The term "phenodeviant" was first used by Landauer in his experiments to investigate the nature and causes of Goldschmidt's phenocopy phenomenon. (Landauer 1957, 1958).

Alan Robertson's, the canalisation hypothesis was entirely unproven, and unnecessary. The "genetic assimilation" of Waddington's Edinburgh colleagues would have amounted to little more, in Waddington's mind, than coincident selectionism: that is, Simpson's "Baldwin effect." In short, Waddingtonian canalisation was not an acceptable working hypothesis to developmental geneticists in Great Britain at the time of the synthesis, at least not in Edinburgh in the early 1950s, and certainly not in Birmingham.

With the rejection of Waddington's canalisation, the language of genetic assimilation could more easily be adopted by modern synthesis evolutionary geneticists. Thus genetic assimilation became merely a handy term for the process which had been known since the mid 1890s as organic selection. Waddington's mechanism for the genuine inheritance of acquired characters, validating neo-Lamarckist phenomenology whilst bypassing the Weismannian demand for evidence of somatic induction, was dismissed as at best unverifiable, and at worst completely fanciful. The canalisation term also became an equally handy expression, describing the results of orthodox processes of physiological and genetic homeostasis, honed under classical Mendelian gene selection. Waddington's perceived experimental failure to convince the orthodox establishment of its deeper phylogenetic significance, had rendered it no serious threat to the neo-Darwinism of the synthesis. Worse still for Waddington in the 1950s, Dobzhansky's support for Schmalhausen, combined with his deafening silence over Waddington's theory, even undermined Waddington's hopes that his "canalising selection" would be adopted ahead of Schmalhausen's stabilising selection (sections 3.3. and 3.3.1.).

The debate over the Lamarckian inheritance of acquired characters was, however, only one issue raised by modern synthesis developmentalism. There was also deep concern over whether evolutionary trends were the results of acceptably contingent and externalist constraints upon the direction taken by natural selection, or unacceptable internalist teleological constraints. Among the former, acceptable mechanisms were included subsidiary historical restriction; especially Baldwin's organic selection, and dominant historical restriction; namely Plate's orthoselection. Among the latter, unacceptable mechanisms were all but the weakest forms of orthogenetic restriction, thus including Eimer's definitely directed evolution, or Julian Huxley's dominant orthogenetic restriction (section 2.3.3.). At the deepest level, the unacceptability of internal developmental constraints to the synthesis in the 1940s, was similarly a consequence of strong selectionism. Therefore, the rejection of Waddington's and Schmalhausen's syntheses of selectionism and developmental constraint, needs to be discussed.

5.1.1. The Strong Selectionism of Post-War Developmentalist Syntheses: Adaptationism and Local Developmental Constraint.

I turn now to some broader issues raised by the present history of modern synthesis developmentalism. In the spirit of Gould's words from the epigraph to the Introduction (head of section 0.1), Amundson has recently attempted to support the existence of a clean historical division between developmentalists and adaptationists. He characterises this division in terms of "adaptation-versus-constraint disputes" which, he says, run continuously throughout 19th and 20th century biology and traverse the categories of evolutionism versus creationism.[19] Thus for Amundson, the big question is: "Why does accommodation between adaptation and constraint seem so difficult?" On some descriptions, he adds, "they sound merely complementary, but debates persist."[20] The answer, he believes, lies in the opponents "dramatic difference in explanatory strategies and assumptions" (Amundson u.d., p. 3). However, in modern synthesis developmentalism, a strict application of the adaptation-versus-constraint divide breaks down: both Waddington's and Schmalhausen's theories provided a developmentalist solution to the adaptationists' dilemma, and incorporated a strong selectionist explanation of local developmental constraints upon the phenotype. Nevertheless, Amundson's idea is useful for

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[19] For example, says Amundson, in pre-evolutionary biology Paley's *Natural Theology* (1802) represented "an extremely influential codification of adaptationist British natural theology. Meanwhile French and German Unity of Type concepts represented the "constraint-style theories [which] gave non-adaptationist explanations of organic form, and therefore did not provide support for an inference to a supernatural adaptation-producing designer" (Amundson u.d., p. 7).

[20] Amundson also discusses Maynard Smith *et al's* important distinction between "local" developmental constraints, and "universal" constraints. Developmental constraints are generally defined as "biases on the production of variant phenotypes or limitations on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system" (Maynard Smith *et al* 1985, p. 266). Amundson paraphrases the local/universal distinction, stating that the former are "specific to particular related groups of organisms (e.g. mammals)," whilst the latter involve "general laws of nature (e.g. the principle of the lever)" (Amundson u.d., p. 10).

providing an explanation for the historical shepherding apart of Schmalhausen's conception of evolution from Waddington's; that is, for explaining the historical legitimisation of stabilising selection, and de-legitimisation of canalising selection.

The concept of local developmental constraint is centrally important to the history of modern synthesis developmentalism. Waddington's contest with Schmalhausen, for priority over discovery of the true mechanism of evolutionary morphogenetic stabilisation, directly reflected the paucity of such developmental constraint approaches to evolution in the 1940s and 1950s. Tremendous scientific capital was potentially involved in being the sole instigator of a genuine developmentalist synthesis. Such nominal syntheses of development and evolution as had existed just after the second war, either failed to accept Morgan's theory of the gene, as had Goldschmidt's, or failed to forge a genuine synthesis of, in Provine's words, "positive or logical unification" between experimental embryology and genetics, as had de Beer's (Shapere 1980, p. 390). However, another aspect which unified Waddington and Schmalhausen's syntheses was their strong selectionism. Consequently, the debates between Waddington and Schmalhausen's champion Dobzhansky, the criticisms of Schmalhausen from Western supporters of the synthetic theory, and the debates between Schmalhausen and the Soviet neo-organic selectionists, all centred upon the status of the natural selection of adaptive modifications.

It is important to recall these selectionist debates, since Waddington and Schmalhausen's theories were primarily attempts to resolve the adaptationists' dilemma. Firstly, Schmalhausen's concept of stabilising selection was consistently misunderstood, and unfailingly misappropriated (sections 2.5., 2.6., 2.6.2., and 4.5.). The main objections from Western critics to *Factors of Evolution*, had been over its lack of clarity (due to rushed production under deprived conditions), poor translation, and the more dubious suggestion that its central concept lacked a single meaning. Hence Simpson complained that stabilisation was being used in at least three separate senses; namely, coincident selection, selection for the wild type, (or centripetal selection), and selection for the development of regulating mechanisms in morphogenesis. Waddington passively concurred, adding personal though unwarranted doubts that the third and, for him, solely legitimate sense had even been properly understood by Schmalhausen (section 4.5.). It was Simpson's third sense which synthesised adaptive changes with the emergence of local developmental constraints. Thus, by the time of Waddington's publishing *The Strategy of the Genes* in 1957, Schmalhausen's supposed third sense, describing his mechanism for the evolution of morphogenetic stabilisation, had been characterised by Waddington as stabilising selection "*sensu stricto*." Furthermore, after summarising Schmalhausen's concept of the autonomisation of development, Waddington stated: "For a series of events of this kind, the name "genetic assimilation" may be suggested" (Waddington 1953a, p. 125).[21]

Neither Simpson nor Schmalhausen promoted the proliferation of kinds of natural selection. Simpson rightly said that in the context of the historical aspect of evolution (that is, virtually throughout the important sections of *Factors*), Schmalhausen discussed stabilising selection "almost exclusively in the sense of the development of regulating mechanisms"; in other words, in the sense of local developmental constraints (Simpson 1949, p. 323; section 4.5.). It is surely safe to conclude, therefore, that Schmalhausen did not overlook the independent existence of a third form of natural selection, to be defined in purely population genetical terms. As discussed in my Chapter 4, the genetical basis for developmental stabilisation became progressively less important to Schmalhausen, as the language of genetics becomes less adequate to description of the evolutionary process of autonomisation (Schmalhausen 1949a, pp. 219-222). Schmalhausen was too much a classical Darwinian morphologist, and too little a Mendelian population geneticist, to have seen the need to further proliferate kinds of selection. Hence, the phenomena explained by Simpson's "selection for the wild type" and Waddington's "normalising selection" were undoubtedly recognised by Schmalhausen, but only as a necessary external consequence of selection for the stabilisation of morphogenesis (section 4.5.).

However, the absence in Schmalhausen's *Factors* of talk about universal developmental constraints, was very favourable to those who, like Dobzhansky, wished to tailor Schmalhausen's morphological insights to the synthetic theory.

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[21] Interestingly, this paper's extensive discussion of Schmalhausen's ideas did not appear in Waddington's 1975 collection of reprints, *The Evolution of an Evolutionist*. Schmalhausen had likewise maintained, in the preface to *Factors*, that Waddington's "genetic assimilation" corresponded to his own "autonomization" (Schmalhausen 1949a, p. viii; see section 3.3.1.).

Hence stabilising selection--more so than Waddington's genetic assimilation and canalisation--could be readily deployed within the synthetic theory. Effectively, Schmalhausen's stabilising selection was seamlessly translated by supporters of the synthetic theory into "*dynamic* selection for the stabilisation of ontogenetic development, via improved mechanisms of homeostasis." Such a process could comfortably bear the title stabilising selection, whilst remaining causally identical with the classical selection of synthetic neo-Darwinism. Thus Schmalhausen's own express intentions to elaborate stabilising selection's deeper phylogenetic significance could be ignored; conveniently mired, as they were to remain for half a century, in the conceptual morass of *Factors of Evolution.* Also, Schmalhausen's local developmental constraints--producing his local "adaptive norms"--could be construed (at least from the English translation of *Factors of Evolution*) as simply the result of continued dynamic, or even neo-organic, selection for random genetic variations in the population.

By contrast, many of Waddington's concepts from the mid 1950s displayed an overt emphasis upon more universal developmental constraints. These concepts would have surely convinced the emerging orthodoxy--which allowed only for subsidiary historical restrictions upon the direction of selection--that his theory was unacceptable to the modern synthesis (section 2.3.3.). A prime example is provided by Waddington's teleological notion of the "creode" or "necessary path," as visually expressed in the mystical metaphor of the epigenetic landscape.[22] Waddington also multiplied the number of constraining forces acting in evolution to four. These included the familiar mutational and natural selective forces, plus his own less familiar "exploitive" and "epigenetic" forces. Each of these four was connected in a "circular and not merely unidirectional causal sequence," and which guide the pathway of development (1960, p. 400). These terms, in particular the creode, actually added little to the teleological impact of the epigenetic landscape, with its topographical representation of both present and future constraints upon morphology. They described technically what the landscape could quite readily, after a brief explanation,

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[22] See Waddington 1957, pp. 30-38, for an extended discussion of the epigenetic landscape in relation to his 1950s notions of the creode and homeorhesis. The original notion of a temporal series of secondary competencies grew, as discussed in section 5.1., out of Waddington's Cambridge work on the chemical nature of the vertebrate evocator in the mid 1930s.

be seen to depict (section 1.3.2.). Yet these notions of Waddington's were certainly not a reaction against modern synthesis adaptationism (ibid.) Empirically, the exploitive system was no more than a coadaptationist notion of feedback between organisms, their neighbours, and the physical environment. It provided a fuller, ecological explanation of the causes of Waddington's exogenous adaptations (section 1.3.2. footnote 50, and section 5.4.).

Clearly, an increasingly teleological dimension to Waddington's theorising in the late 1950s, expressed his ever-present leanings towards universal developmental constraints in explaining adaptive evolution. These were to resurface throughout his later career. For example, in his 1959 letter to Dobzhansky, Waddington discussed experiments he was undertaking to "demonstrate a mechanism which makes it easier for selection to continue for long periods in the same direction, as in the lineages one used to call 'orthogenetic.'" This proclivity in Waddington, and its attendant anti-reductionism, was epitomised by his positive attitude towards Rene Thom's catastrophist mathematics from the 1960s, for modelling the choices made at developmental branchpoints in ontogeny and phylogeny.[23]

5.1.2. Current Notions of Local Developmental Constraint: The Continuing Controversy over Waddingtonian Canalisation.

Just as in the 1950s, contemporary neo-Darwinism does not recognise Waddington's synthesis of adaptation and developmental constraint. Furthermore, his evolutionary thinking has continued to be misrepresented, for reasons directly related to those in evidence at the time of the synthesis.

A good example of Waddington's misrepresentation is given by Maynard Smith *et al.* In a collaborative 1985 review paper, "developmental constraints and

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[23] Looking for a way to mathematically model the development of a few well-defined macrostates (as are produced during canalisation), Waddington displayed his anti-reductionist and anti-atomist tendencies within a summary of the I.U.B.S. symposia, stating: "Many of our discussions have [been] explorations of ways of handling simple macrostates without having to break them down into an unmanageable plethora of vastly complex microstates. One of the most fully developed approaches has been by way of Rene Thom's theory of catastrophes. This is a general theory about discontinuities, which may divide a multi-variate phase-space into regions which have a definite identity, since they are bounded against eachother by the catastrophe surfaces. We have here a conceptual framework which is not atomistic, but which provides clear-cut boundaries and precludes interpenetration of entities, features which are two of the major aids to clarity of thought which atomism has provided in the past" (Waddington 1972, p. 284).

evolution," the authors elaborated on the distinction between universal constraints, or those which "do not depend upon any distinctive features of organisms," and local constraints, which, "in contrast, are confined to particular taxa" (Maynard Smith 1985, p. 267). The authors' examples of local constraints would undoubtedly have been characterised by Waddington as examples of the effects of canalising selection. Yet canalising selection is separately discussed, within a short section representing local constraints due to orthoselection. Canalisation is, then, in the authors' terms, a special case of the power of natural selection to "limit the morphological and behavioural variations adequate to the task of living" (1985, p. 270). However, the author's also make unqualified use of the term stabilising selection, undoubtedly intending Simpson's selection for the wild type, rather than either Schmalhausen's own intention, or Waddington's stabilising selection *sensu stricto* (see sections 3.3.1., and 4.5.).[24] That the authors did intend such an interpretation is clear from the context, with its subordination of any selection-driven mechanism for the progressive autonomisation of morphogenesis, to classical selection for the normal type. Thus Maynard Smith *et al* state, regarding Waddington's observations of the morphological uniformity of the wild type: "Waddington (1957) suggested that the reason for this . . . is that the typical 'wild type' pattern has been exposed to many generations of stabilizing selection, whereas the mutant pattern has not. According to this view some developmental constraints are themselves the result of [classical] selection, *and are not the automatic consequences of the structure of the developmental system.* Various experiments support Waddington's view by showing that stabilizing selection can reduce the variability of mutant phenotypes" (ibid., emphasis added).

Here, then, is both a source of corroboration for Amundson's viewpoint, and a familiar obfuscation of the intended meaning of stabilising selection (4.2.). It is also a clear misrepresentation of Waddington's experimental intentions. Whilst for the historicist and externalist Waddington, developmental constraints were trivially the

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[24] Both Maynard-Smith and Kaufmann attended what Waddington described as a "series of Symposia on Theoretical Biology," organised by him on behalf of the International Union of Biological Sciences, at the Rockefeller Foundation's Villa Serbelloni at Bellagio, Italy, beginning in 1966. Both would therefore have been intimately acquainted with Waddington and his canalisation theory (see the Preface to Waddington 1972).

result of natural selection, still for the structuralist and internalist Waddington *all* developmental constraints were *necessarily* the "automatic consequence of the structure of the developmental system." Waddington's canalising selection, properly understood, supports the bridge between adaptationism and developmental constraint which is here being dismantled. Though in fact, it was Schmalhausen's concept of stabilising selection which built that bridge.

The extent of the debt owed by modern developmentalism to Waddington's concepts, although not that owed to Schmalhausen's, has nevertheless been acknowledged by reviews contemporary to that of Maynard Smith *et al*, such as Stewart Thomson's. Focusing upon Bonner (1980), Goodwin (1983), and Raff and Kauffmann (1983), Thomson observes, especially in the editions of Bonner and Goodwin, that "a wholeheartedly epigeneticist view takes over." Thus the works of Hall and Horder (Goodwin 1983), and Maderson and Alberch (Bonner 1982), explicitly see the epigenetic nature of development as, in Thomson's words, "a prime feature in its evolutionary potential." Furthermore their theories, he adds, "follow directly in the tradition of Waddington . . . whose influence still dominates the whole subject" (Thomson 1985, p. 229). Thomson ended his review with a query over adaptation, motivated by contemporary structuralist views. From a traditional externalist view, he said, adaptation is shaped by selection, and an adaptation's cause is contained within external independent factors. By contrast, internalist and structuralist approaches restrict selection to what he calls a "purer" role in acceptance or rejection of the results of autonomous internal processes (1985, p. 231-232). Yet, under determination of the structuralists' anti-adaptationist thesis reveals, for Thomson, the lack of understanding of internal evolutionary mechanisms in their environmental context. In addition to the genetic origins of particular changes, he asks, what are the ecological factors? How are internal and external environments related? In Thomson's view, "this brings us back to Waddington and the whole question of genetic assimilation" (ibid.). Thus, although Schmalhausen's place is not mentioned, the historical importance of Waddington's four "circular and not merely unidirectional" constraining forces is accepted by many within current developmentalism. Therefore many, like Thomson, see Waddington's insights at the time of the modern synthesis as still uniquely valuable, and as necessarily informing any more complex synthesis of adaptation and developmental constraints.[25]

It is therefore no coincidence that the most extreme examples of developmental internalism, such as Brian Goodwin's process structuralism, are expounded by the intellectual descendants of Waddington's Edinburgh research programme (sections 3.1. and 3.1.1.). Present day structuralists, with an anti-genocentric focus upon evolutionary laws of form, concentrate their investigations of evolutionary change towards fully universal developmental constraints. Obviously, such a programme represents one canalised pathway leading away from the developmental branchpoint of Waddington's genetic assimilation research. The subordination of gene expression to higher level epigenetic plasticity, was an integral aspect of Schmalhausen's and Waddington's theory in the 1950s. Within the process structuralist conceptual scheme, however, there is virtual elimination of formal genetics from the evolutionary picture.

Goodwin, Waddington's Ph.D. student, is also deeply anti-historicist, holding to purely formal and structural criteria for determining homologies. For Goodwin, "homology is an equivalence relation on a set of forms which share a common structural plan and are thus transformable into one another" (Goodwin 1984, p. 101). It is, he adds, "therefore a logical relation, independent of any historical or genealogical relationships which the actual structures may have" (ibid.). However, Goodwin's supervisor took completely for granted the historical and genealogical view of homology, which a Whiteheadian process-philosophical world view necessarily required. Hence, with respect to neo-Darwinism and its offspring, the modern synthetic theory, Goodwin asserts that "it is this persistent attempt to understand biology in historical terms, and thus to stress the role of particulars, of contingencies, and of genealogies, which is the source of current tensions in the subject." Whereas, by contrast, "workers in various disciplines are rediscovering and

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[25] For example, Ho and Saunders state: "There have always been critics of the neo-Darwinian synthesis: independent thinkers who steadfastly refused to lose sight of the fundamental problems of evolution which the theory does not address. The most influential among the critics were undoubtedly Waddington, Goldschmidt, and D'Arcy Thompson, who did much to keep the real issues alive throughout the period of the grand synthesis. Their writings continue to inform the present evolutionary controversy, though they were not sufficient by themselves to bring that about" (Ho and Saunders 1984, p. 3).

emphasizing evidence of regularity, of constraint, of order in their empirical material which resists assimilation into an historical interpretation of biological process of the type which characterizes Weismannism and the modern synthesis" (Goodwin 1984, p. 99). Goodwin thus rejects almost all of Waddington's footholds in the synthetic theory; namely, Darwinian historicism, strong selectionism, and the central importance of Morgan's genetics. What, of course, has remained an important inspiration to process structuralism from within Waddington's work is the canalisation concept--though in its static aspect as a universal developmental constraint, rather than as an historically and selectively developed effect. Thus, in the context of criticising historical explanations of variation, Goodwin writes that "anyone who accepts such explanations as satisfactory has, at the very least, lost sight of more basic questions such as why it is that mutations give rise to only certain categories of morphological disturbance. . . . These are questions relating to organization, to invariance, and to transformation, which cannot be answered in terms of historical processes and inheritance" (1984, p. 104).[26] It is quite interesting, however, that two central motifs throughout Waddington's career in evolutionary biology--namely, process and assimilation--still find their way into Goodwin's anti-historicist prose.

5.2. General Conclusion: A Genuine Inheritance of Acquired Adaptive Characters.

Jablonka and Lamb's words encapsulate the received view with regard to British and Soviet modern synthesis developmentalism, when they state: "Waddington's and Schmalhausen's explanations of the inheritance of acquired characters were very much within the traditional neo-Darwinian framework. In fact, from the 1940s to the 1980s, there were few real challenges to neo-Darwinism, or to

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[26] As Waddington remarked in his autobiographical note in 1969, "I wanted to return to Morgan's idea that the only 'potencies' it is meaningful to talk about are the potential activities of genes. So did several people who were primarily geneticists, but who had become interested in development without having actually worked on it very much" (Waddington 1969a, p. 79).

the assumptions on which it is based" (Jablonka and Lamb 1995, p. 37).[27] As Jablonka and Lamb would undoubtedly agree, an over-simplistic neo-Mendelian and pan-selectionist approach to adaptive evolution, combined with a rigidly Weismannian approach to heredity, became the cause of serious theoretical difficulty for supporters of the modern synthesis during the 1940s and 1950s. Yet, quite contrary to their opinion, Waddington and Schmalhausen's conceptions of adaptive evolution were at the forefront of these difficulties. Indeed, it is testimony to the historiographical efficiency with which modern synthetic neo-Darwinism has absorbed Waddington's and Schmalhausen's developmentalism that many, including Jablonka and Lamb, now view their syntheses as essentially orthodox.[28] To contradict Simpson's statement from the epigraph to the present chapter, the "postulated neo-Lamarckian mechanism for direct transfer of modification to a genetical system" emphatically did exist. It simply did not conform to Weismannian criteria; and neither, as many Darwinians have often reflected throughout his century, did it have to.

The present history has therefore focused on attempts, made by prominent supporters of the synthetic theory, to cover over specific difficulties issuing from modern synthesis evolutionary embryology and developmental genetics. These difficulties culminated during the 1940s and 1950s, when the hardening selectionism of the synthesis brought back late nineteenth century concerns, over the degree of evolutionary significance to be accorded adaptive modifications to the phenotype. The recurrence of this issue in the 1940s and 1950s I have described as the

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[27] Jablonka and Lamb's Chapter 2, where the concepts of Waddington and Schmalhausen are explicitly dealt with, is aptly entitled "Neo-Darwinian explanations of the inheritance of acquired characters."

[28] That this historiographical reconstruction, which began in the 1950s within the subsuming campaigns of Simpson (Chapter 2) and (to a less certain extent) Dobzhansky (Chapter 4), was as effective as I claim, is made apparent by Jablonka's and Lamb's opinion that: "For some people, any lingering doubts about the adequacy of the neo-Darwinian interpretation of certain types of evolutionary change were dispelled by the kind of ideas developed by Schmalhausen and Waddington. These ideas were not completely new, having been foreshadowed by those of Baldwin, Lloyd Morgan and Osborn at the end of the nineteenth century. In 1896 each of these biologists had independently suggested an evolutionary mechanism that, they believed, helped to reconcile the Lamarckian and Darwinian positions. The mechanism became known as the 'Baldwin effect' or 'the principle of organic selection'" (Jablonka and Lamb 1995, p. 31). For further evidence of the broad acceptance of this view in the historiography of the modern synthesis, see Continenza's work on Waddington and organic selection (1986, 1987).

adaptationists' dilemma. Partly as a result of the historical consequences of this dilemma, notable observers of the synthesis--among them strong supporters of its central tenets--have registered an awareness that its development unfolded more through the exclusion of potentially troublesome biological disciplines, rather than by their inclusion into the fold (sections 0.3 and 0.4.). However, In the synthetic sense of logical entailment described in the Preface, post second world war developmentalism in Great Britain and the Soviet Union offered a genuine synthesis of embryology, genetics, and evolution.

Garstang's and de Beer's nominal syntheses had merely attempted to justify the theoretical coexistence of embryology, developmental genetics, and neo-Darwinian evolution. They had concentrated on description of the possible modes of heterochronic change, and on their proximate causation, within the framework of the synthesis between neo-Mendelism and neo-Weismannism. They had also sought to completely deny any direct phylogenetic significance to developmental changes going on within individual ontogenies, to prevent the re-emergence of Ernst Haeckel's fearful phylogenetic heresy. For evolutionary morphologists such as Garstang in 1922, as for embryologists like de Beer in 1930, there were indeed external influences upon ontogeny which had come into existence during phylogeny, but definitely none that had been internalised and become hereditary. That is, none that had become phylogenetic causes of development in the Haeckelian sense. Phylogeny was no cause of ontogeny. The external and non-hereditary causes involved in producing these ontogenetic changes were certainly not be allowed any adaptive hereditary effect upon a descendant organism's development. The hereditary material passed on to descendants was to remain hermetically sealed away from any such influences, as Weismann had strictly dictated. On the contrary, then, individual ontogenies were the direct cause of phylogeny--a phylogeny which was, in turn, simply their passively accumulated by-product. Thus, in the context of the hardening synthetic neo-Darwinian theory, although ontogeny was instructionally determined, phylogeny became, ever more strictly, selectively determined.

Schmalhausen's and Waddington's syntheses undermined this entire theoretical edifice. They showed, as Waddington explicitly claimed, that this rigid instruction-selection dualism of modern synthesis neo-Darwinism was no longer sustainable. The seeds for its collapse had already been sown by the powerful new genetics of interaction which had emerged in the 1930s. By the late 1930s it was clear, to all who were interested, that the complete epigenetic plasticity of gene expression relative to the organism's genomic, physiological, and biotic environments, allowed for the actual, and not merely apparent, hereditary fixation of adaptive modifications in populations under natural selection (see Mather and Waddington, on the work of Muller, Ford, Stern, and Goldschmidt; section 3.2.).

To illustrate the early consequences for synthetic neo-Darwinism of this new understanding, we need only review the challenge that Waddington's synthesis posed to Garstang's and de Beer's disproof of recapitulation. As we have seen, de Beer's rejection (based on Garstang's earlier Weismannian analysis) of the existence and action of phylogenetic causes, forced de Beer into an implausibly strong denial of the power of internal hereditary factors to effect morphogenesis *ab initio*. Waddington's embryologically founded mechanisms of canalisation and genetic assimilation therefore directly challenged de Beer's views at several levels. Firstly, they provided an account of precisely how, couched in de Beer's new terminology, the necessary external causes of development could indeed become internal and phylogenetic. Secondly, they showed how those internalised heritable causes became independent of the original external stimulus: that is, how once genetically assimilated, they became sufficient causes of the development of adaptive characters in precisely the fashion de Beer sought to deny (section 1.4.). Thirdly, the observational and theoretical basis for Waddington's challenging mechanisms had come directly from chemical embryology: specifically, from the search for the chemical nature and developmental action of the amphibian primary evocator. Therefore, to draw such pro-recapitualtionist and anti neo-Darwinian conclusions, and to construct an alternative synthesis claiming a genuine inheritance of acquired characters, all from the results of experimental embryology research in the 1930s, would surely have been perceived as nothing less than a series of heresies to de Beer. Lastly, what had served to legitimate Waddington's account was precisely de Beer's own renunciation of the archaic nature of the debate surrounding the issue of neo-Lamarckian inheritance. As de Beer's proposed new terminology indicated, the real issue over the inheritance of acquired characters was not whether it had a basis in the material transformation of internal factors. At issue was, simply, whether a *functional* basis existed for internalising the epigenetic effects of externally produced stimuli. In other words, could any of the external and contingent causes of development have their specific effects transferred to function within Weismann's internal and "necessary conditions of development," causing the inheritance of adaptive modifications?

Both Waddington and Schmalhausen resoundingly affirmed the existence of such a functional basis, from within the evidential confines of experimental embryology, functional morphology and phenogenetics. For Schmalhausen, epigenetic changes (most effectively as a result of his "functional modifications" in higher organisms), constituted what he called the *specific* hereditary basis for evolutionary change. Epigenetic inheritance, for Schmalhausen, was necessarily primary. As he stated in *Factors of Evolution*: "The appearance of new differentiations in the course of evolution is simultaneously accompanied by the formation of new interrelationships in the form of internal factors determining the heritability of these differentiations" (1949a, p. 221;. Section 4.4.2.). Crucially, Schmalhausen saw those simultaneously formed interrelationships as occurring above the genetic level; that is, as occurring between *morpho*genetic hereditary determinants. Evidence for this is provided by Schmalhausen's emphatic rejection of the sufficiency of the genetic level of description to the causative processes in adaptive evolution (ibid.). What was more, this insufficiency did not reflect any particular paucity of explanatory power in 1940s gene theory *per se*; that is, within its own narrowly defined domain. Rather it reflected, in Schmalhausen's expressed opinion, the fact that behind the terms of formal genetics lie hidden extremely intricate interactions between complex metabolic, physiologic and morphogenetic processes (ibid.).[29] Genetics, then, in all but the simplest organisms, described the *non*-specific hereditary basis of adaptive evolution, acting via the mechanism of stabilising selection. Thus, over a relatively short number of generations, stabilising selection got hold of already functioning and *heritable* modifications, as stimulated by and replicated within the organism's physical and ecological (biotic) environment,

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[29] Hence, at evolutionarily lower levels of morphogenetic complexity (for example, in the protista, where genetic and morphogenetic levels remain in closer proximity) the terms of formal genetics still, in Schmalhausen's view, retained some explanatory value. Yet, he maintained, as evolution progressed, "Our distinction between genetic and morphogenetic systems reflects the increased complexity of the interrelationships which at first were amenable to analysis by genetic methods but which have become unanalyzable in the course of further evolution" (ibid.).

and provided the non-specific hereditary supports for endorsing an "autonomisation" of the adaptive phenotype.[30]

Waddington was equally committed to the epigenetic and ecological basis of adaptive evolution. Hence, the "epigenetic" and "exploitive" forces of his evolutionary paradigm, described a very similar ecologically oriented approach to the genuine inheritance of acquired characters. In the late 1960s, Waddington stated of the long-running controversy over the hereditary fixation of adaptive modifications: "Any paradigm which omits the effects of environments in altering phenotypes would seem to make it difficult, if not impossible, to deal with this (leaving it to 'random mutation' is not dealing with it.) It was only by taking this factor into account that a solution could be found, in the form of genetic assimilation" (Waddington 1969b, p. 109). However, as his career in evolutionary genetics progressed, Waddington's attacks on the synthetic neo-Darwinian paradigm became more ambiguous, and more concessionary (section 3.1.1.). By 1969, Waddington ended his usual attack upon the mathematical formalisms of Haldane, Fisher, and (to a lesser extent) Wright: "The comments made above do not in any way imply that we should abandon neo-Darwinism ; they only suggest that some of the simplifications on which the mathematical theory has been based have outlived their usefulness and should be revised" (1969b, p. 110).[31]

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[30] For Schmalhausen, then, replication of the specific (morphogenetic) hereditary basis for evolutionary change, was supported by the stable replication of the organism's external (biotic) and internal (genetic) environments. Or, put in terms of the stabilising selection process, replication of external (biotic) structures, combined with the more or less stable replication of internal specific hereditary (morphogenetic) structures, allowed time for stabilising selection to genetically underpin a genuine inheritance of adaptive modifications. Such autonomisation would, therefore, only occur in the direct descendants of those members of the population already possessing the most nearly autonomous development. For Schmalhausen, this stabilising selection mechanism was much faster than the classical dynamic selection of synthetic neo-Darwinism, which had to wait for precisely the right imitating major gene mutation to occur, facilitating a merely apparent fixation of adaptive modifications.

[31] We may note here that Waddington confused the issue of the acceptability of his old conceptual adversary, synthetic neo-Darwinism, still further in his late career. In reply to Maynard Smith's critical comments on his alternative evolutionary paradigm, Waddington again rejected "*neo-D*" within a series of definitions intended to ensure commensurability in the debate: "By *neo-D* I mean the view that Weismann's doctrine--that there is no influence of the phenotype on the genotype--can be transferred from the individual level to the population level, and that an adequate theory of evolution can be formulated in which 'fitnesses' are attributed to genotypes. John slides altogether too easily between the Weismannist point that the environment of an individual does not affect the heredity he transmits, and the quite different argument that the environment of a population does not affect what they transmit. I maintain

This statement can be readily contrasted with the morphologist Schmalhausen's much stronger view that "the mathematical analysis of evolutionary transformation . . . involve[s] extreme abstraction and a withdrawal from concrete reality" (Schmalhausen 1949a, p. 141; section 4.1.). Waddington in the 1950s was principally a geneticist: A very different professional commitment from his paleontological morphology of the 1920s, and his chemical embryology of the 1930s (3.1). The difficulty with which he had gained professional status in genetics, only served to strengthen his commitment to that profession, and, therefore, his desire to be acknowledged for genuine contribution to genetic understanding of adaptive evolution.[32] Hence Waddington's language surrounding morphogenetic stabilisation (especially his term for its hereditary fixation; namely, genetic assimilation), was very consciously constructed from the terms of deterministic Mendelian genetics. Acceptance of "genetic" assimilation, would certainly have ensured his adaptive evolutionary theory recognition and respectability within the recently emerged discipline of evolutionary population genetics (section 3.1.2., footnote 32).

Unfortunately, however, the synthetic theory's hardening selectionism, necessitated an uncompromisingly deterministic one-gene-one-character approach from its supporters toward the adaptationists' dilemma. Waddington's mechanism, coming as it did from a geneticist aspiring to the status of a modern synthesiser, had to be "assimilated" to the existing, neo-Darwinian synthesis. Endless arguments over the theoretical nuances differentiating genetic assimilation from Huxley's and Simpson's neo-organic selection, merely increased the tensions within Western

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that a population's environment does influence, quantitatively, what they transmit, because natural selection acts on phenotypes which are partially environment dependent" (Waddington 1969b, p. 127). Yet this reply to Maynard Smith (who had defined Weismannism as, "roughly, if the phenotype of an individual is altered by an altered environment, this will not cause that that individual to produce offspring with the new phenotype"), was still ambiguous (Maynard Smith 1969, pp. 124-125). It was left unclear just how population genetics and canalising natural selection could be combined to undermine "*neo-D*," and render Waddington's paradigm acceptable. Waddington needed to explain Weismann's arbitrarily narrow criteria of evidence for the inheritance of acquired characters. That is, he needed to distinguish between uncorroborated genetic inheritance via somatic induction acting structurally upon single gene loci, and fully corroborated *epigenetic* inheritance via selection for adaptive morphogenetic interactions, supported by his own canalising selection (Waddington's paradigm).

[32] The proliferation of kinds of Mendelian gene selection in the 1940s and 1950s (particularly the empty proliferation of synonyms for both classical Darwinian and neo-organic selection in the West and the Soviet Union), might be a useful tool for analysis of the professional structure of evolutionary genetics in the modern synthesis period.

synthesis genetics; tensions which had to be, and were very successfully, absorbed. The fact that Waddington's conception of genetic assimilation was too intricate for most evolutionary biologists--including reactionary Darwinians potentially sympathetic to Waddington--to differentiate it from the coincident selection of hereditary variations which was organic selection, simply made Waddington appear contrary and stubbornly heterodox. Furthermore, as Gilbert observes, orthodox opinion was that the genetic assimilation term only conveyed the notion that physiological responses "could be readily fixed in the genome" (Gilbert 1991, p. 205). On the other hand, Schmalhausen's essentially morphological approach, primarily employing the language of developmental regulation rather than formal genetics, meant that he could much more generously and politically concede the legitimacy of both organic and neo-organic selection--whilst, nevertheless, strenuously promoting the far greater importance of his own stabilising selection (section 4.4.1.). After all, single gene alterations of the norm of reaction were not, in his view, adequate to the description of actual evolutionary processes. These considerations may have helped to ensure Schmalhausen's terminology achieved greater prominence within the later synthesis. It did not, however, achieve the phylogenetic significance Schmalhausen had intended it to.

5.3. Epilogue: Current Theoretical Supports for Modern Synthesis Developmentalism.

Finally, and as noted in section 5.1., several very recent works have shown a renewed interest in epigenetic inheritance and evolution. Jablonka and Lamb have offered a four point definition of epigenetic inheritance, which embodies a denial of the legitimacy of Weismannian extremism. In their terms, "The inheritance of an acquired character has occurred if: (1) the change in the character is induced by the environment; (2) the induced change is specific and repeatable, although not necessarily adaptive; (3) a specific change in hereditary information is involved; (4) the change is transmitted to the next generation" (Jablonka and Lamb 1995, p. 14). The authors add that the above conforms with Mayr's definition of soft inheritance, whilst avoiding his focus on the genetic material as DNA.[33] However, the examples of epigenetic inheritance given by the authors primarily relate to gene-level alterations, principally differential DNA methylation, found to be transmissible between sexual generations; that is, across the meiotic divide. Hence they remark: "The EIS [epigenetic inheritance system] on which most of our discussion is based is the chromatin marking EIS, since this seems to be the predominant system for transmitting epigenetic information in the cell lineages of multicellular organisms" (1995, p. 137). In other words, Jablonka and Lamb stay very close to the traditional Weismannian terms for discussing epigenetic inheritance, by limiting their discussion to structural alterations to the material gene itself. The pull of this traditional mode of discourse, is illustrated in the authors' discussion of the possibility that such inheritance systems may not "Mendelise." Hence, they state that "if transmitted between sexual generations, permanent chromatin marks (epialleles) should behave like chromosomal variations in DNA base sequence, and segregate in a Mendelian fashion at meiosis" (ibid.). Whilst such mechanisms may be effective, they are surely a far cry from Schmalhausen's suggestions of stable morphogenetic inheritance systems. In this context, Jablonka and Lambs EIS might be better labelled "perigenetic" rather than epigenetic.[34]

Testimony to the growing trend in acceptance of at least some degree of epigenetic inheritance, is given by neo-Darwinian Maynard Smith's recent elaboration of a similar "perigenetic" methylation mechanism. Maynard Smith asks: "Given that, at least occasionally, epigenetic states are sexually transmitted, what are the evolutionary consequences?" (Maynard Smith and Szathmary 1995, p. 247). The answer had already been provided in 1990 by his "dual inheritance system," which postulated a complex chain of genetic interactions, leading to the trans-meiotic labelling (deactivation), and un-labelling (activation), of developmental effector genes

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[33] Mayr defined "soft inheritance" as: "Inheritance during which the genetic material is not constant from generation to generation but may be modified by the effects of the environment, by use or disuse, or other factors" (Mayr 1982, p. 959; in Jablonka and Lamb 1995, p. 13). Hence, over forty years on, Mayr's concept still retains the germinal essence of the neo-Weismannian phenotype, when discussing Dobzhansky's "real issue" of the mechanism of adaptive evolution.

[34] According to Chambers (1993), *epi-* may denote "above" or "over," whereas *peri-* denotes "around" and "near."

by physiologically inducible labelling genes. Resembling Jacob and Monod's operon model for the regulation of gene expression in prokaryotes, the significant outcome, in Maynard Smith's terms, is that "evolution . . . requires only a single mutation altering the specificity of one of the labelling genes" (1995, p. 249). Perhaps predictably, he concludes: "An adaptation that originally occurred during development would have become genetic: this is precisely what Waddington (1956) had in mind when he coined the term 'genetic assimilation'" (ibid.). However, whether or not Waddington may have found this an interesting idea, it is most unlikely, for reasons already discussed at length, that Waddington would have accepted a trans-meiotic gene activation mechanism as capturing the essence of his concept.

It is clear from section 5.3. that Goodwin's process structuralism is openly accepting of epigenetic and morphogenetic inheritance mechanisms, and would, in all likelihood, be equally dismissive of both genetic and perigenetic ones. However, process structuralism's anti-selectionism, and its anti-historicist approach to evolutionary development, remains squarely in the tradition of ideal morphology. It is therefore too hostile to the reactionary Darwinism and functionalist morphology of Severtsov and Schmalhausen. Developmental systems theory, however, with its radically inclusive view of which structures may constitute inheritance mechanisms, appears far more conducive to the union of functional morphology and epigenetic inheritance. Griffifths has recently defended DST's extrapolating, "to its logical conclusion," the current dissolution of the idea that genes are the sole evolutionary replicators. For him, Dawkins' "'remarkable replicator' is neither the genome nor the zygotic package, but the entire developmental system" (Griffifths 1997, p. 474).

In Griffiths terms: "According to DST the stability of biological form can be explained by the recurrence of the same system of developmental resources in each generation. The idea that developmental information resides in the genes is a shorthand for the idea that if all other elements of the developmental matrix are held constant, changes in the genes are reflected in changes in the phenotype. But it is equally true that if everything including the genes is held constant, changes in other elements of the matrix are reflected in changes in the phenotype" (1997, p. 472). Thus a radical extension of the set of heritable developmental resources, quite capable of supporting Schmalhausen's specific morphogenetic inheritance mechanisms, is the hypothetical result. A close relative and rival of DST, is the "extended replicator theory." ERT, then, attempts to retain a causally privileged status for the genome in ontogenetic and phylogenetic development. However, in their 1996 paper, ERT proponents Sterelny, Smith and Dickison, illustrate a similarly radical extension of the replicator concept. Quoting from their paper, Griffiths observes:

> In many parts of their paper Sterelny et al show a clear grasp of just how much can be explained by the differential replication of variants, and just how far the replicator extends: "Nesting burrows are replicators. The causal relations between burrows and burrowers is like that between genes and their interactors. No gene makes an organism. But variance explains variance: a variable oystercatcher may be black rather than pied because it has one gene complex rather than another, even though no gene complex makes a colour pattern. Similarly, a variation in a burrow can cause a variation in a burrower: a particular penguin chick may be healthy and safe because its burrow has one site rather than another, even though no burrow makes penguin flesh." (Sterelny 1996, p. 397; in Griffiths 1997, p. 485).

Such a suspension of the evolving phenotype, between the external biotic and internal genetic developmental resources of the organism, dovetails well with Schmalhausen's approach to the evolving morphotype in higher organisms. Schmalhausen likewise causally suspended his specific inheritance mechanism or "replicator,"--that is, the morphogenetic system--between the external biotype and the genotype. Certainly, Schmalhausen recognised aspects of the biotic environment as replicated developmental resources of the organism, whether or not he would have balked at including such resources as burrows within the class of the organism's inheritance mechanisms. The proponents of DST, therefore, view ERT as lacking grounds for differentiating itself from DST, and regard Sterelny *et al*'s concerns over unmanageable holism as ungrounded. Hence Griffiths concludes: "The only elements of the developmental system that are not ERT replicators are the persistent resources [e.g. air, sunlight, atmospheric pressure], elements which DST has already said are not replicated in development and are not part of the unit of evolution" (1997, p. 487).

Intriguingly, ERT defends its vision of a far more limited array of replicators on adaptationist grounds; in fact, upon a design argument. For example, they argue "the genome is one of the *designed mechanisms* in virtue of which phenotypes and genotypes duplicate themselves," and within which adaptations to this function abound (Sterelny 1996, p. 387). This they believe to be the key to the privileged role of replicators in development. Hence only replicators exist, in the author's terms, by virtue of their function in production of the organism's "lineage phenotype," whilst non-replicator developmental resources exist for totally independent reasons (1996, p. 388). Schmalhausen's morphogenetic inheritance structures would, by this criterion, qualify as ERT replicators.[35]

As Keith Thomson has already observed, an overview of extant developmentalist traditions clearly illustrates their indebtedness to two indispensable resources. Namely, Waddington's attempt at a developmentalist reformation of Mendelian gene-selectionism, and the radical functionalist morphology of Schmalhausen. Waddington's and Schmalhausen's focus upon the radical plasticity of gene expression, relative to the external and epigenetic environments, has been a crucial springboard away from crude neo-Weismannian heredity for process structuralism, developmental systems theory, and extended replicator theory alike. Even the pressure-induced perigenetics of latter-day neo-Darwinism pays its inevitable lip-service to Waddington's genetic assimilation. As we have seen, Waddington's and particularly Schmalhausen's reactionary Darwinism took a pan-adaptationist approach to evolution for granted. In fact, the opportunity for their simultaneous calls to acceptance of a genuine inheritance of acquired characters--but for being drowned out by the neo-Weismannian imperative--arose directly out of the hardening selectionism of the modern synthetic theory in the 1950s, and the adaptationist dilemma which that engendered.

But their adaptationist strong selectionism was not, unlike that of 1950s synthetic neo-Darwinism, of a reductionistic variety. Both men, and most expressly Waddington, rejected the picture of populations of organisms ascending fixed peaks

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[35] Three years before his death, Schmalhausen published a formal paper on evolution and cybernetics in which much space is devoted to Watson and Crick's 1953 landmark discovery, and to advances in molecular genetics. Appropriately, then, his views appear more in line with modern extended replicator theory, and ERT's adaptationist defence of a unique role for genomic structures in heredity. Thus he wrote: "Transmission of hereditary information occurs only in the process of cell division. *All permanent cellular substances, both nuclear and plasmatic ones, have a role to play in this.* However, the existence of a strikingly exact mechanism of copying, separation and equal distribution of chromosomes in mitotic division clearly shows the key importance of this particular mechanism. . . . Although this topic needs much further elucidation, the general scheme is sufficiently clear to enable us to evaluate fully its biological significance" (Schmalhausen 1960, p. 509; emphasis added. See also section 1.2.1., footnote 27, for an interesting parallel with prevailing nineteenth century views on heredity).

in an adaptive landscape; the result of selection for fitness within pre-existing external environments. Hence Waddington's insistence that we consider the evolutionary system to involve "at least four major subsystems"; namely, the genetic, selective, exploitive, and epigenetic. For him, the synthetic theory's reductionist "heap of pebbles and gravel-sorter" approach to adaptive evolution was totally inadequate. On the contrary, we needed to think in terms of "circular and not merely unidirectional causal sequences," with the state of each of the four subsystems being "partially determined by the action of each of the other subsystems" (Waddington 1960, p. 400). Likewise, Schmalhausen was aware of the coevolutionary significance of feedback between the ecological effects of adaptive functions, and consequent changes in adaptive response to the biotic environment. Hence, the dialectical logic of both men's work--notwithstanding Adam's concerns about the possibility of overstating Schmalhausen's dialecticism (Adams 1987, p. 283)--necessarily entailed that they view organism and environment as coevolving, covarying developmental resources.

Finally, then, the relationship--which has been at the heart of this history--between modern synthesis developmentalism's holistic adaptationism, and the atomistic and crudely deterministic "one gene one character" adaptationism which seemed often to characterise strong selectionist defences of the synthetic theory, raises some deeper and more metaphysical issues over the adequacy of synthetic neo-Darwinism. As Lewontin has discussed, understanding the impact of Mendel and Darwin requires a deeper, historical understanding of the objectification of the organism. In Lewontin's view, Darwin and Mendel made organisms the objects of quantifiable forces, whose subjects were, firstly, the internal heritable factors, and, secondly, the external non-heritable environment. In this way, Lewontin says, "Mendel and Darwin brought biology at last into conformity with the epistemological meta-structure that already characterized physics since Newton and chemistry since Lavoisier" (Lewontin 1983, p. 274). This change, then, was "absolutely essential" if biology was likewise to become quantitative and predictive. Whilst molecular biology may have advanced under this epistemology, developmental and evolutionary biology have not. Rather, they are handicapped by their misguided attempts to apply outdated concepts to such a rich developmental phenomenology. In Lewontin's words, "Evolutionary biology suffers particularly because it is the nexus of all other biological sciences, so that a lack of progress in developmental biology, in ecology, in behavioural science, all are fatal to a proper understanding of evolution" (1983, p. 275).[36]

Thus, in the context of the present history, the somewhat crude genetic determinism which characterised all explications of the principles of neo-organic selectionism, combined with Weismannian restrictions upon the evolutionary significance of phenotype-genotype relations, provide two key historical examples of how the orthodox synthetic doctrine held back the developmentalists' contribution. In discussing the continuing prevalence of such genetic atomism and determinism in the evolutionary literature, and the chameleon-like nature of present day neo-Darwinists, Smith observes: "They will deny that these difficulties arise from *theoretical* tenets of neo-Darwinism while simultaneously perpetuating the problem with a focused pursuit of a narrow methodology. These 'ecumenical chaps' admit that the dissenters have a valid point, but do little or nothing to revise their research to correct the problems" (Smith 1992, pp. 432-433). As Smith quite rightly adds, "It is trivially easy to find bald statements of genetic determinism in the literature" (ibid.). Here, then, arises an explanation of an otherwise mystifying discrepancy, between the sophisticated theory on genetic interactions available from the 1930s on the one hand, and the doctrines of, for example, Simpson's 'Baldwin effect' and Gause's substituting selection on the other. The explanation being that the hardening selectionism of the synthetic theory was bound, during the most exclusionary stages of its development, to maintain (especially in its most combative literature) the extreme subject-object dichotomy Lewontin describes. This its founders had to maintain, in order to defend the epistemological meta-structure that also hardened its broader scientific credentials.

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[36] Lewontin was an avid supporter of canalisation, writing, "There are no more important experimental results for evolutionary biology than those of Rendel (1967) on canalization" (1983, p. 278). Lewontin also worked with Waddington, in the late 1960s, on the hypothesis that the rate of evolutionary advance was inversely proportional to the rate increase in genomic DNA (Waddington and Lewontin, 1968, p. 109). In a passage with all the hallmarks of the extended replicator concepts of DST and ERT, Lewontin also stated: "It might be objected that the notion of organisms constructing their environments leads to absurd results. After all, hares do not sit around constructing lynxes! But in the most important sense they do. First, the biological properties of lynxes are presumably in part a consequence of selection for catching prey of a certain size and speed, i.e. hares. Second, lynxes are not part of the environment of moose while they are of hares, because of biological differences between moose and hares" (1983, p. 282).

Theodore Roszak wrote that the ecological approach, as an alternative and sustainable "reality principle," was the only possible salvation for twentieth century science (Roszak 1972). Later, he expressed concern that it, too, was becoming atomistic and objectifying in its approach to ecological interactions, thereby failing to free science from what he characterised as the "single visioned" nightmare of scientific objectification (ibid.). Whether or not Roszak's broader fears were justified, the ecological approach might at least save evolutionary biology.

5.4. General Summary.

The following points serve as a general summary of the above thesis:

1. The synthetic neo-Darwinian theory of evolution sought to expunge the two central pillars of the "old evolutionary synthesis": namely, strong recapitulationism and neo-Lamarckian heredity. Although it is very doubtful whether a fully "pan-selectionist" position was ever held by any supporters of the synthetic theory, nevertheless natural selection rose to complete dominance as the sole accepted mechanism of adaptive evolution. This was achieved within a two-stage hardening process, that spanned, in the context of the present thesis, the period from 1922 to 1953.

2. The first stage of the above mentioned hardening centred upon the removal of embryology from its previously central causal role in the mechanism of adaptive evolution. This it had enjoyed during the period of dominance of Haeckel's "biogenetic law," again in the present context, from 1866 to 1922. The unification of phylogenetic and ontogenetic causation (that is, of ultimate and proximate causation) which was the hallmark of the old synthesis, was facilitated by the synthesis of strong recapitulationism and neo-Lamarckian heredity described in point 1. However, since recapitulation was an accepted fact, the essential discrediting of the biogenetic law had necessarily to focus upon disproof of the neo-Lamarckian inheritance of acquired adaptive characters.

3. There was a general acceptance in the early 1930s, that the neo-Darwinian embryologist de Beer had finally discredited both neo-Lamarckian inheritance and Haeckelian recapitulation. Thus in the 1930s, Julian Huxley and de Beer ushered in the formation of a modernised "two-tier" embryology which, in neither its

morphological and descriptive aspect, nor its proximate-causal and experimental aspect, was to be allocated any direct causal significance within the synthetic neo-Darwinian mechanism of adaptive evolution. These eventualities signalled, for most selectionists, the final demise of old synthesis evolutionary morphology. Nevertheless, spearheaded by the Needhams' and Waddington's investigations of vertebrate primary induction processes at Cambridge, embryology, in Waddington's view, only gained in significance to the mechanism of adaptive evolution, despite its exclusion from the new synthesis.

4. Adaptationism continued to be controversial among evolutionists, particularly among experimentalists, who saw the synthetic theory as still clinging unnecessarily to the old morphological and adaptationist approaches of Lamarck, Darwin and Haeckel. Hence the second stage of the hardening of modern synthesis selectionism, in the 1940s and 1950s, witnessed a revival the late nineteenth century "adaptationists' dilemma" of having to explain the hereditary fixation of highly determinate adaptive modifications, without any of the recourse to non-selectionist mechanisms that Darwin himself had employed. This, in turn, re-awoke concerns over the relative adequacies of neo-Darwinism and neo-Lamarckism, with some reactionary neo-Darwinians, who were sympathetic to the Lamarckists, calling for recognition of the actual predominance of late nineteenth century "organic selectionism" over classical Darwinian selection.

5. Ironically, the strategic defence of the synthesis against such neo-Darwinian dissenters, as well as against any resurgence of the traditional enemy of neo-Lamarckism, entailed an appeal to the findings of developmentalists whose disciplines had been excluded from any direct causal role in the synthesis. Specifically, Waddington's embryological theory of genetic assimilation, and Schmalhausen's morphological theory of stabilising selection, formed the basis of Simpson's defence of synthetic neo-Darwinism. Dobzhansky's saw Schmalhausen's morphology as completing the synthesis, and Schmalhausen's *Factors of Evolution* as its last major work. However, Waddington's and Schmalhausen's understanding of the all-important causal phylogenetic significance of their own work was ignored, and their mechanisms for the hereditary fixation of adaptive modifications identified with neo-organic selection, or Simpson's "Baldwin effect."

6. Waddington responded immediately, and very negatively, to Simpson's attempt to identify the core of his genetic assimilation theory, with the coincident selection of adaptive mutations; that is, with stage two of Simpson's Baldwin effect. Waddington's mechanism was specifically intended to validate an actual, and not merely apparent, inheritance of acquired characters. Since, from the point of view of 1950s strong selectionists, the only acknowledged mechanism for such proscribed inheritance was (long-since discredited) somatic induction, the radically developmentalist heart of Waddington's synthetic theory had therefore to be discredited also. Therefore Waddington's attempt to experimentally verify a universal canalisation mechanism for genetic assimilation, was widely construed to be a failed enterprise. To the extent that Waddington's own views were later discussed by leading supporters of the synthetic theory (with the exception of Julian Huxley), he was portrayed as a frustrated neo-Lamarckian, and as having failed to distinguish his own controversial mechanism of genetic assimilation.

7. The English translation of Schmalhausen's broadest and last book-length statement of evolutionary theory, his 1946 *Factors of Evolution*, also failed to support Simpson's strategy of subsuming organic selection to broader population genetical theory. Schmalhausen, like his teacher Severtsov, saw formal genetics as essentially inadequate to the description of morphogenesis, and therefore to the evolutionary morphogenetic stabilisation at the heart of his alternative synthesis. Furthermore, Schmalhausen saw his own stabilising selection as fundamentally distinct from classic Darwinian selection, and as based firmly on developmentalist principles, formally identical to those of Waddington's canalisation. He also tentatively assumed the predominance of his stabilising selection, and therefore the genuine inheritance of acquired characters, over classical Darwinian selection--though unlike Waddington, he deferred to the judgement of necessary further empirical investigation to settle this matter. Again, these elements of Schmalhausen's synthesis were downplayed by Simpson and Dobzhansky so successfully, that they completely failed to enter the general discourse of the modern synthesis. This exclusion was greatly facilitated by the obscurity of Schmalhausen's work, which was rationally reconstructed by Simpson and Dobzhansky to fit the hereditarian principles of the synthetic theory.

8. The scientific priority debate between Waddington and Schmalhausen (actually, between Waddington and Schmalhausen's champion Dobzhansky), is assumed to have been won by Schmalhausen. Many of the concepts of Waddington's later synthetic evolutionary thinking owed their existence to the stimulus provided by his reading of Schmalhausen's *Factors of Evolution*. Waddington's brief tactical alignment with Simpson, over the supposedly confused nature of Schmalhausen's stabilising selection, is seen as tantamount to "sour grapes" from Waddington over the prior publication of *Factors* (1946) to any definitive statement made by Waddington on genetic assimilation.

9. The developmentalist syntheses of Schmalhausen and Waddington are, therefore, unequivocally portrayed as alternatives to the present orthodoxy of synthetic neo-Darwinism, and not merely as historical footnotes to that theory's inevitable triumph. The radically inclusive nature of their theories of heredity, with their powerful dialectical feedback conceptions of the relationship between genetic, epigenetic, and external environmental factors of inheritance, have since been extrapolated by various extant forms of developmentalism; notably ERT and DST. All today's functionalist (adaptationist and selectionist) and structuralist (non-adaptationist and non-selectionist) developmentalist theories of evolution, owe much of their own development to the dissemination of Schmalhausen's and (particularly) Waddington's concepts.

10. Deeper metaphysical issues are discussed regarding the sufficiency of the synthetic theory to adaptive evolution, with its narrow selectionist focus on an abstraction which Mather called "the characteristic expression of the gene" (Mather 1943a, p. 68). Hence the relationship between developmentalist adaptationism and synthetic neo-Darwinian adaptationism at the time of the new synthesis requires some historical understanding of the objectification of the organism. To Lewontin, Darwin and Mendel succeeded in making organisms the objects of quantifiable forces, whose causally separated subjects were the internal heritable factors, and the external non-heritable environment. Hence, the synthesis of Mendelism and neo-Darwinism subsequently placed an absolute restriction, upon an organism's adaptive responses to the external environment becoming incorporated into those internal factors; that is, upon the inheritance of acquired characters. Yet such an objectivist sundering of organism from environment has limited evolutionary theory, because of

the lack of genuine causal integration with essential disciplines not conformable to such a reductionist methodology--particularly ethology, development and ecology. Thus synthetic neo-Darwinism has been a stumbling block to a proper understanding of the interactional complexities of evolution.

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Glossary.

ADAPTIVE MODIFICATION. According to the joint definition provided by Baldwin and Lloyd Morgan in 1897, a change of structure or function due to the adaptation of an individual organism to its environment. Strictly, adaptive modifications are the result of a process of "accommodation"; that is, they are produced as a result of the organism's own functional activities (as in Cope's *kinetogenesis*), rather than the direct agency of the physical environment (as in Cope's *physiogenesis*). Most importantly, however, adaptive modifications were non-heritable changes.

AUTONOMISATION. Schmalhausen's term describing the process whereby the transition from dependent individual development to autoregulatory individual development occurs. The factors of the external environment lose their determining importance, and merely become stimuli which release an autonomous series of morphogenetic processes. Furthermore, as autonomization progresses, the internal morphogenetic factors (including Mendelian genes) are also reduced to the level of stimuli triggering autonomous internal processes. Hence Schmalhausen's autonomisation and Waddington's *genetic assimilation* appear almost synonymous, but for Schmalhausen's insistence upon the insufficiency of the genetic mode of description, especially at what Schmalhausen described as the more evolutionarily advanced, or "morphogenetic," levels of developmental regulation.

BALDWIN EFFECT. Simpson's term for the neo-Mendelian interpretation of J. M. Baldwin's and Lloyd Morgan's original concept of *organic selection.* Paraphrased, Simpson's 3-part definition ran as follows: 1) Individual organisms interact with the environment producing behavioural, physiological, or structural *adaptive modifications.* 2) Genetic factors exist/arise by mutation in the population producing hereditary characteristics **either** similar to the modifications in 1), **or** having the same sorts of adaptive advantages. 3) The genetic factors of 2) are favoured by natural selection and may spread in the population over the course of generations. The net result only outwardly resembles neo-Lamarckism, or the inheritance of acquired characters.

BLASTOGENIC CHARACTER. Weismann's term defining those hereditary variations which originated solely in the primary constituents of the germ plasm. Contrasted with *somatogenic characters*, which were acquired by the somatic cells during ontogeny, through the reaction of the organism to those environmental influences which did not constitute what Weismann called "the necessary conditions of development." Somatogenic characters were therefore strictly non-heritable.

CAENOGENESIS. According to Gould, caenogeneses (sometimes spelt cenogeneses) are exceptions to the *palingenetic* repetition of phylogeny in ontogeny, within Haeckelian recapitulation. They are produced by heterochrony (temporal displacement), heterotropy (spatial displacement), or the production of specifically larval-stage adaptations in the life-cycle of the developing organism.

CANALISATION. Waddington's 1942 phrase, expressing his observation that developmental reactions are *epigenetically* regulated so as to bring about one definite end-result, regardless of minor variations in conditions during the course of the reaction. Canalisation corresponded with Schmalhausen's less graphic conception of the narrowing of the *norm of reaction* under the influence of *stabilising selection.* Should Waddington's *canalising selection* persist, then at some point along the canalised pathway of development of an *adaptive modification*, the phenomenon of *genetic assimilation* may occur. Waddington later coined the term homeorhesis to simultaneously describe both the homeostatic and temporal aspects of this regulation process.

CANALISING SELECTION. Waddington's separate form of natural selection promoting the deepening *canalisation* of specific adaptive organismic structures and/or functions. Waddington wrote in 1953 that only one reading of Schmalhausen's closely related *stabilising selection* corresponded to canalising selection, and that as such it should be called either stabilising selection "type 2," or stabilising selection "sensu stricto."

COMPETENCE. Waddington's term, describing a chemical state of indeterminacy, or readiness to react to certain evocatory stimuli, existing within a tissue and allowing it to be subsequently channelled into one of two or more alternative developmental pathways. For Waddington in the late 1930s, the competence of a tissue was causally connected with its future development, whereas the classical concept of a potency was unsatisfactory because non-causal. Competencies emerged at developmental branchpoints. The nature of secondary competencies, occurring at subsequent branchpoints, were thus dependent upon the response to earlier competencies.

CLASSICAL SELECTION. A term widely used to describe classical Darwinian natural selection, as opposed to various forms of selection purported to either imitate or validate the neo-Lamarckian inheritance of acquired characters. Synonyms include *direct selection* (Kirpichnikov), *external selection* (Hardy), and *dynamic selection* (Schmalhausen).

COINCIDENT SELECTION. Lloyd Morgan's term for the proposed natural selection of hereditary germinal variations which produce a similar phenotype to non-hereditary *adaptive modifications*. Sometimes used as a synonym for Baldwin's *organic selection*, which strictly only refers only to the selection of further adaptive modifications to some previously coincidently selected hereditary variant form of an adaptation. *Orthoplasy* was said to occur if the cycle of organic selection followed by coincident selection continued on to form an adaptive evolutionary trend.

DIRECT ADAPTATION. A near synonym for *parallel induction*, the use of which may serve to distinguish inductive processes which lead to the genuine inheritance of a specific *adaptive modification*, from others, like parallel induction itself, which by definition need only produce some heritable close facsimile of the original modification. Used by Waddington in 1952 to discuss Dobzhansky's apparent dismissal of the former mechanism: that is, of the genuine inheritance of acquired characters.

DIRECT INDUCTION. A theoretical mechanism for the inheritance of acquired characters. To the Lamarckians, its consisted in the adaptively directed alteration of the germ plasm by an environmental stimulus, so as to produce a germinal variation, in descendent generations, adaptive to that same stimulus. Related to *parallel induction*, where in addition a somatic *adaptive modification* is simultaneously produced by the same stimulus. Weismann accepted both direct and parallel induction, but dismissed both as evidence for the inheritance of acquired characters.

DIRECT SELECTION. Term used by Gause, in opposition to either *organic selection* or his own *substituting selection*, and as a synonym for classical Darwinian natural selection.

DOMINANT HISTORICAL RESTRICTION. Julian Huxley's term for a strong restriction placed upon the direction taken by natural selection. Caused by previously selected heritable variations in a specific adaptive direction, increasing the selective advantage of further heritable advance in the same direction. This was not *orthogenesis*, since no internal predisposition for further variation exists. Huxley adopted an ambiguous metaphor, analogous to Waddington's *canalisation*, and proposed that a specialised line comes to occupy the bottom of a "groove" cut for it by selection.

EPIGENETICS. The internal organization that links the genotype to the phenotype. It encompasses all the interactions--among genes, and between genetic, morpho-physiological, and external environmental factors--that produce the final phenotype. Waddington also coined the phrase the "epigenotype" to indicate that these interactions may constitute stable--that is, heritable--mechanisms of individual development.

(MODIFICATIONAL) EURYBIONTY. Schmalhausen's phrase describing the ability of a population to adapt to more than one "biotope," or local ecologic environment, at one stage of the adaptive cycle of *stabilising selection*. This developed adaptive capacity led to a decreased mortality rate due to external physical factors, which in turn helped maintain the hidden reserves of genetic variability, which in its turn continued to support the adaptability of the population.

EVOCATOR. Waddington's term describing the morphogenetically active chemical emitted by an *organizer*.

EVOCATION. The morphogenetic effect produced by an *evocator*: namely, the induction of cellular and tissue differentiation.

EXTERNAL SELECTION. Hardy's term for classical Darwinian selection of random heritable variations. Hardy controversially spoke of external selection as an entirely separate kind of selection to Baldwin's *organic selection*, which latter he identified fully with Waddington's *genetic assimilation*. Synonymous with Schmalhausen's *dynamic selection*, and with Gause's *direct selection*.

GENETIC ASSIMILATION. Waddington's name for the process by which acquired *adaptive modifications* become converted into inherited variations, via the process of *canalising selection*, acting over several generations on a population. Waddington viewed the mechanism as a true alternative to *somatic induction* for the genuine inheritance of acquired characters. Genetic assimilation was controversially demonstrated by Waddington in the 1950s, using artificial selection for the hereditary fixation of *phenodeviants* in fruit flies.

GENOCOPY. Medawar's 1951 term for what he called the "genetic imitation" of acquired phenotypic changes. Conceived by analogy with Goldschmidt's correlative term *phenocopy*, genocopying was designed to explain the apparent hereditary fixation of Medawar's "Class B" (Waddington's *pseudo-exogenous*) adaptations. For the neo-Darwinian selectionist, although functional change anticipated hereditary change in Class B adaptations, the neo-Lamarckist explanatory mechanism of *somatic induction* was to be rejected, and the genocopy mechanism substituted. (See also the original version of Baldwin's *organic selection*, Lloyd Morgan's *coincident selection*, Gause's *substituting selection*, Kirpichnikov's *Indirect selection*, and Simpson's *Baldwin effect*).

INDIRECT SELECTION. Kirpichnikov's term, later renounced by him on realisation that the phenomena he was studying were better described by Lloyd Morgan's classical concept of *coincident selection.*

NEO-ORGANIC SELECTION. A term generally signifying the neo-Mendelian reinterpretation of Baldwin's classical concept of *organic selection.* More specifically, a synonym for the *coincident selection* of hereditary variations, or stage 2 of the *Baldwin effect.*

ORGANIC SELECTION. Strictly, James Mark Baldwin's term for the behaviourally-driven acquisition of *adaptive modifications*, which further the developmental direction taken by earlier, inherited *coincident variations.* The term underwent a rapid semantic evolution during the period 1896 to 1897. Initially--and popularly--the term defined Baldwin's complete mechanism for the (merely apparent) hereditary fixation of adaptive modifications. Later, Baldwin more narrowly identified the term only with the initial stage of his full mechanism; namely, Lamarck's law of use and disuse in ontogenetic development. Finally Baldwin and Lloyd Morgan agreed, with Osborn's assent, upon the strict sense given first above.

ORGANISER. A part of an embryo which exerts a morphogenetic stimulus upon another part, bringing about determination and differentiation of cell and tissue structures in the latter, and also determining their morphological structure (a complete process Waddington called "individuation"). Thus embryologists differentiate between truly organ forming capacities of, for instance, intact blastopore dorsal lip tissue (the "primary" organiser), and the simple capacity of the primary *evocator* substance to induce differentiation.

ORTHOGENESIS. Eimer's "definitely directed evolution." Orthogenesis described the definite, though indeterminate, direction of the internal hereditary variations that produce evolutionary change . Anti-selectionist and radically anti-adaptationist, its supposed hereditary mechanisms are unknown. Lamarck's classical theory of a slow and gradual increase in the complexity of living matter, is also often described as orthogenetic.

ORTHOPLASTIC INFLUENCES. Baldwin's term, describing all those means of an organism's functional accommodation to its environment (such as organic plasticity, imitation, and intelligence) which may be considered as directing evolution through *organic selection.*

ORTHOPLASY. Baldwin's term describing the directive or determining influence of *organic selection* in evolution, where organic selection is used in its strictest sense. Sometimes used as a synonym for organic selection in its original and broadest sense, the terms orthoplasy and orthoplastic influence, suggest Baldwin and Lloyd Morgan saw a much more powerfully directive role for their theory, than that indicated by Huxley's identification of *organic selection* with a special form of *subsidiary historical restriction* upon selection.

ORTHOSELECTION. Plate's term, synonymous with Huxley's later *dominant historical restriction* upon the direction taken by natural selection. Although readily adopted by Huxley as orthodox, Plate's leanings towards the Lamarckian inheritance of acquired characters, and also towards orthogenesis, may cast some doubt over the neo-Darwinian credentials of the concept.

PALINGENESIS. In Haeckelian recapitulation, according to Gould, palingenesis represented the true repetition of phylogenetic stages in the ontogenetic stages of descendant organisms (cf. *caenogenesis*).

PARALLEL INDUCTION. To neo-Lamarckians, a theoretical mechanism for the inheritance of acquired characters. It consisted in the adaptively directed alteration of the germ plasm by an environmental stimulus, so as to produce the germinal facsimile, in descendent generations, of a somatic *adaptive modification* produced by the same stimulus in ancestral generations. Related to *direct induction* where, by contrast, no initial adaptive modification occurs. Weismann accepted both parallel and direct induction, but challenged whether the parallelism of the former ever obtained in actual cases, and dismissed both as evidence for the inheritance of acquired characters.

PHENOCOPY. Goldschmidt's concept describing the production of acquired modifications, which closely resemble the phenotypes characteristic of known genetic mutations. Produced experimentally via the use of physical and chemical agents which, In theory, mimic the disruption of developmental events caused by the identified mutant gene(s). According to Landauer, the actual point of external interference in the developmental pathway varied according to the genotype, the developmental stage at intervention, the kind and quantity of the external agent, and other less determinate factors. See *Phenodeviant.*

PHENODEVIANT. Landaur's term for sporadically occurring developmental abnormalities. They are the result of indeterminate epigenetic events, through which deviant pathways of developmental become manifest, and broadly include artificially produced *phenocopies.*

SOMATIC INDUCTION. The classical neo-Lamarckian mechanism for the actual, and not merely apparent, inheritance of acquired characters. According to de Beer, Somatic induction was the hypothetical mechanism whereby external environmental factors produced an *adaptive modification* in the structure of the body, which then in turn effected a change in the internal hereditary factors, such that the initial modification became an hereditary *blastogenic character.*

SOMATOGENIC CHARACTER. Weismann's term identifying those non-hereditary characters acquired during the ontogeny of the organism. As such, these were not preformed in the germ, but arose only through the reaction of the organism to those environmental influences which specifically did not constitute what Weismann called "the necessary conditions of development." However, as several commentators have noted, any strict distinction between necessary and casual environmental conditions with respect to development is a practical impossibility.

STABILISING SELECTION. Schmalhausen's term for a separate kind of natural selection from classical Darwinian (Schmalhausen's "dynamic") selection. Stabilising selection is based upon the selective advantage, under definite and especially, fluctuating conditions, possessed by the organism's normal organization over variations from the norm. Associated with the elimination of most variations, and the establishment of more stable mechanisms of normal morphogenesis. Waddington described this kind of selection as "stabilising selection type 2, or his own *canalising selection*.

(MODIFICATIONAL) STENOBIONTY. Schmalhausen's phrase describing the stable adaptation of a population to one "biotope," or local ecologic environment, at one stage of the adaptive cycle of stabilising selection. Literally, the constriction of a species' environmental range; the opposite of *modificational eurybionty*.

SUBSIDIARY HISTORICAL RESTRICTION. Huxley's term for a less stringent form of restriction upon the direction taken by natural selection than *dominant historical restriction* or Plate's *orthoselection*. Subsidiary historical restriction, of which *organic selection* was for Huxley a special case, only made it easier for selection to act in particular directions.

SUBSIDIARY ORTHOGENETIC RESTRICTION. Huxley's term for a less stringent form of *orthogenesis* than Eimer's "definitely directed evolution." As true orthogenesis, and not merely *orthoselection*, its mechanism depended upon some unknown internal restriction of the type and quantity of genetic variation. Yet whereas Eimer's concept prescribed the direction of evolution, subsidiary orthogenetic restriction only, in Huxley's terms, "limited its possibilities."

SUBSTITUTING SELECTION. Lukin's term for the *coincident selection* of hereditary variations. Appropriated by Gause's, who thought it to be synonymous with Baldwin's classical *organic selection*, Schmalhausen's *stabilising selection*, and Lloyd Morgan's coincident selection alike.