

Between Holism and Reductionism: Organismic Inheritance and the Neo-Kantian Biological Tradition in Britain and the USA, 1890-1940

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Submitted in accordance with the requirements for the degree of PhD

The University of Leeds
Centre for History and Philosophy of Science
Department of Philosophy
October 2011

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Acknowledgments

Several people, directly or indirectly, contributed to this work. First of all, I have to thank my supervisor, Gregory Radick, who, with his patient guide and enthusiastic support, made possible this feat from the beginning. I have also to thank all the staff of the Centre for HPS in the Department of Philosophy at the University of Leeds, which provided a beautiful, friendly, and productive environment throughout all my stay. I thank Graeme Gooday as being an inspiring source of 'subversive' insights and really efficient advisor for practical issues. A special thank also to Annie Jamieson, who rendered my 'Ital-English' proper English. This dissertation has also hugely benefited from several discussions and wise advices I have received from Jonathan Hodge, Steven French, Adrian Wilson, Jonathan Thopam, Chris Kenny, Dominic Berry, Thierry Hoquet, Richard Delisle, Efram Sera Shriar, Berris Charnley, Emanuele Archetti, Jan Sapp, Joe Cain, Gar E. Allen, Jane Maienschein, Manfred Laubichler, John Betty, James Strick, Mark Ulett and many others I have incidentally met at conferences and various meetings.

I owe a very special thank to the Scripps Institution of Oceanography in San Diego (CA) for its generous support. In particular, to the director of Scripps Historical Archives in La Jolla Peter Brueggeman, and the archivists Rebecca Smith and Carolyn Rainey. Yet, I am grateful to the staff of Bancroft Library at the University of California, Berkeley, with its superefficient David Kessler. Thanks to the staff of Woods Hole Historical Collection Archives (MA), in particular the assistant director Diane Rielinger and the archivist Lindsey Fresta. A great thank also to the staff of the University College London archives (UK); in particular the responsible of special collections Mandy Wise. And of course, I have to thank all the staff of the Brotherton Library and Boyle Library at the University of Leeds. I am grateful to the British Society of the History of Science, the History of Science Society, the International Society for the History, Philosophy, and Social Studies of Biology, the Arizona State University, and the Société d'Histoire et d'Epistémologie des Sciences de la Vie, for their generous support to my research.

Finally, a great thank to my parents, Enza Varriale and Corrado Esposito, who provided the essential psychological support for achieving the difficult job of writing a PhD dissertation in a foreign language.

Abstract

Anglophone biology at the start of the twentieth century tends to be remembered as ambitiously reductionist. Yet it was also a time that saw the flourishing of a now largely forgotten Kantian tradition. Drawing on archival as well as printed sources, this dissertation charts the dissemination and appropriation of Kant's bio-philosophy in the UK and the USA in the late 19th and early 20th centuries. It was a tradition flexible enough to change as it encountered new institutional and disciplinary contexts, yet stable enough to unite an international community of biologists who were often in contact with each other and endorsed each others' work. The lives and researches of some representative exponents of this community are examined in detail: among the British biologists, J. S. Haldane, D'Arcy W. Thompson, E. S. Russell and J. H. Woodger; among American biologists, F. R. Lillie, E. E. Just, C. M. Child and W. E. Ritter. These men not only accepted a number of core tenets characterizing organismal biology but appealed to them in criticizing Weismann's germ-plasm hypothesis, Mendelian genetics, and other forms of what they saw as naïve reductionism and simplistic mechanism. Moreover — and in contrast with the socially conservative fate of Kantian biology in its German homeland — their scientific views often became intertwined with support for progressive or leftist political doctrines, eugenics included.

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1.0: Introduction

...the assumption that the orderly course of a process can be represented by an analysis of it into temporal and spatial processes must be dropped. It is thus the concept of wholeness which must be introduced as well as into the field of physics as into that of biology in order to enable us to understand and formulate the laws of nature.

Max Planck (Letter to *Science*), 1931¹

1.1: Discussing Organicism at the Second London Congress of the History of Science

In late June 1931, W. E. Ritter, Professor of Zoology at Berkeley and Director of Scripps Marine Association² arrived in London in order to chair the third session of the Second International Congress of the History of Science. The title of that session was “Historical and contemporary relationships of physical and biological science” and participants included the physiologist J. S. Haldane, the zoologist E. S. Russell, the biochemist J. Needham, the engineer L. L. Whyte, the botanist B. Becking, the zoologist L. Hogben, the theoretical biologist J. H. Woodger and the physicist A. Yoffe.³ In general, as Ritter remarked in his critical summary of the papers,⁴ the discussion touched on diverse issues, including: the supposed difference between inorganic and organic nature; the possibility of a scientific synthesis of the whole of natural knowledge; the importance of Aristotle and his tradition for a renewed life science; the importance of observation and experiment in the bio-sciences;⁵ and the new emerging physics exemplified by quantum theory, which, as Lancelot Whyte put it, would transform “... certain aspects of

¹ Planck, 1931, p. 612. Planck was explaining that, with the introduction of quantum mechanics in physics, physical sciences were doomed to change radically. The notion of wholeness had to be introduced. This quotation was often employed enthusiastically by many organismic biologists (in particular J. S. Haldane and J. H. Woodger).

² See Chapter 6.

³ Yoffe, as Werskey recalls, was one of the most prominent and influential physicists in Soviet Russia. See Werskey, 1978, p. 138.

⁴ W. E. Ritter, 1933, October–December. A critical summary of the papers presented at this session. *Archeion*, 14(4), 497–502.

⁵ W. E. Ritter, W.E. 1933, pp. 497–502.

the traditional antithesis between physical and biological theory.”⁶ In sum, different generations of scholars with very diverse backgrounds, convictions, and views were discussing some of the most interesting scientific issues of the time. However, one of the central concerns coming up in almost all of these contributions was the allegedly peculiar status of biological science, as contrasted with the theories and practices of other disciplines. And yet, more generally, this concern forecasted and introduced the discussion to the problem of reductionism and holism in biological sciences.

The first speaker in the session, that June day, John Scott Haldane, was particularly concerned about the peculiarity of life sciences and its methods of enquiry. Indeed Haldane, a famous Scottish aristocrat who devoted all his life to physiology, argued that biology had to be considered an independent and irreducible science because, as he explained, “each example of life...can only be interpreted as the manifestation of a persistent and indivisible unity, recognised quite naturally and in common language as the life of the organism and the stock to which it belongs, and showing itself in endless coordinated details of form, environment, and the activity which express it.”⁷ Of course, Haldane was in good company; Ritter himself, and more junior participants such as Russell and Woodger, fully agreed, both in this session and elsewhere, that biosciences rested on a different theoretical basis than disciplines like physics and chemistry. In fact, Russell was even more extreme than Haldane in expressing his uneasiness with physical methods as applied to investigations into life and, in particular to his own discipline: animal behaviour. In a brief summary of his contribution he contended that the influences of physics on biology had been quite negative in preventing: “...the development of a real science of animal behaviour, and hence animal ecology”.⁸ Woodger readily agreed; the modern biologist should start thinking more in terms of whole systems (as the philosopher Ludwig von Bertalanffy was teaching) than in terms of elementary stuff: “...modern biology requires a complex system of entities standing in abstractly specifiable relations to one another. Perhaps the notion of ‘protoplasm’ or ‘living matter’ will also go the way of ‘hereditary substance’ when we learn to think of cells more in terms of systems, and less in terms of stuff.”⁹

⁶ L. L. Whyte, 1933, pp. 510–511.

⁷ Haldane, 1933, p. 502.

⁸ Russell, 1933, p. 506.

⁹ Woodger, 1933, p. 514.

Of course, not everyone agreed. For example the young Cambridge biochemist J. Needham objected to Haldane in that, between the physicist and biologist, there was a new, intermediate figure who should be regarded with interest by all scholars of biosciences; the crystallographer. As Needham asserted: “The crystallographer deals with a form of organisation which is quite different from, and very much simpler than, the form of organisation which the biologist studies, but it is nevertheless organisation, a kind of rigid drill to which the aimless perambulations of particles in liquid or gaseous phases are subjected”.¹⁰ If crystallography dealt with problems neither reducible to physics nor extensible to biology, Haldane’s argument – according to which life sciences reflected a specific worldview – this would imply that crystallography embodied a further irreducible worldview. As Needham ironically added: “Crystal phenomena can only be studied in crystals, but I should not myself be in favour of adding a crystalline view of the universe to the biological view and the physical view, although I can see no logical reason, on Professor Haldane’s side, for refusing this status to crystallography.”¹¹ In short, although different disciplines explained different aspects of the world, this did not imply that each discipline would be irreducible, in principle at least.

Others too disagreed with the position of Haldane and his close advocates; the Russian physicist Yoffe stated that there were already a wide array of biological phenomena studied through physical methods¹² and the zoologist L. Hogben praised the virtues of mechanism and materialism as applied to modern biology as: “...instruments for arriving at predictable conclusions about how organisms behave”.¹³ Be that as it may, the end of the discussion brought a veritable conclusion on which everybody agreed: as Planck himself had stated in a short letter addressed to *Nature* in the same year, in the light of quantum physics, the whole inorganic realm needed to be seen through a new perspective.¹⁴ Classical physics, as exemplified by the traditional worldview and methods of Descartes, Galileo and Newton, was inadequate to explain the atomic world as well as insufficient to shed any light on the organic realm. Indeed, the new

¹⁰ Needham, 1933, p. 509.

¹¹ *Ibid.* p. 509.

¹² Yoffe, 1933, p. 514.

¹³ Hogben, 1933, p. 511.

¹⁴ Planck, 1931, p. 612.

physics was instead based on systemic thinking and drew heavily on biological concepts.¹⁵ This was not a new position; Haldane himself, many years before the London Congress, during a presidential address at the physiological section of the British Association delivered in Dublin in 1908, had emphatically and famously concluded his talk by claiming: “That a meeting-point between biology and physical science may at some time be found, there is no reason for doubting. By we may confidently predict that if that meeting-point is found, and one of the two sciences is swallowed up, that one will not be biology.”¹⁶

However, in the 1930s, when all of these debates were ongoing, the idea that the biological science should have a special status (either ontological or epistemic) was losing credibility among the international community of biologists. The diplomatic conclusion according to which the inorganic and organic world had to be seen through the lens of ‘wholeness’ remained a very precarious and vague notion: a view easily forgotten by younger generations. In sum, despite Haldane’s authority, the wind blew towards reductionist approaches to biology. After the 1930s, the triumph of theories and doctrine perceived as reductionist (Morgan’s chromosome theory of heredity, molecular biology, and population genetics) challenged powerfully the purposes and prospects of ‘systemic’ thinkers. Yet, before the London congress, ‘system’ thinking had a very positive and widespread reputation; a reputation supported from a significant tradition in life sciences: the so-called organismic tradition. One of the aims of this thesis is to reconstruct such a tradition; to examine how it thrived during the late 19th century and how it changed in the 20th century. Indeed, we will see that the language, conceptions, and ideas discussed at the London congress had a long history — a history dating back to Kant. Therefore, in the following sections we will see how important Kant became for the formulation of an organismic program; how influential were some of his ideas and speculations on the nature of life on leading 19th and 20th century biologists; how relevant were his views on how organisms had to be perceived and studied: in other words, we will

¹⁵ As Whyte clearly argued: “...classical methods are essentially inadequate to deal with ordered structures, and an additional law of a new type is necessary. This new law is expressed by equations called the ‘Quantum conditions’, whose importance for this discussion lies in the fact that they refer directly to systems as a whole, and not to the individual parts or particles which make up the system. For example, classical theory could not account either for the stability or for any of the unitary characteristics of the set of electrons which constitutes a copper atom. But in the quantum theory the quantum conditions for a complex atom imply the recognition of the atom as a system with various definable characteristics possessed by the atom as a whole... Thus certain aspects of the conflict between the purely micro-analytical methods of classical physics and the organic concepts of biology have been eliminated at their root” (Whyte, 1933, p. 510).

¹⁶ J. S. Haldane, 1908, *The Relation of Physiology to Physics and Chemistry*, in *The New Physiology and other Addresses*, Charles Griffin and Company, London, 1919, p. 19 .

chart the ramifications, interpretations, and multiple diffusion of Kant's bio-philosophy in England and the US, without overlooking its circulation in other countries.

1.2: Origins of an Idea and its Diffusion

What is the source of the idea that the life sciences should be based on principles and methods different from those in physics or other related disciplines? In other words, when and how did the problem of biology as having a peculiar status first arise? Relatedly, whence come the idea that the organism is an individual unity, in which the parts reciprocally cooperate for the welfare of the whole, and in which causes and effects, stimuli and responses, are irreducibly interconnected? According to M. Beckner (1959, 1967) and D. Haraway (1976), most of these ideas and approaches characterised a new 20th century paradigm in life sciences: the organismic paradigm. Indeed, Beckner maintained that the distinction between mystical or vitalistic views and organismic approaches "...was drawn clearly only in the twentieth century. Organismic biology may be described as an attempt to achieve the aims of the murky organismic-vitalistic tradition, without appeal to vital entities."¹⁷ To Haraway, such a distinction could be explained in Kuhnian terms: the new organicist paradigm was the result of a period of crisis in developmental biology. In brief, she argued that the first half of the 20th century was a time where "...the age-old dichotomy between mechanism and vitalism was reworked and a fruitful synthetic organicism emerged, with far-reaching implications for experimental programs and for our understanding of the structure of the organisms"¹⁸. In particular, she pointed to Driesch and his well-known experiments on sea urchin eggs as the event which highlighted an 'anomaly' within the 19th century mechanist paradigm in biology. To her, Driesch had shown that the extraordinary plasticity and regulative abilities of sea urchin embryos apparently defeated any mechanist or reductionist explanation. Thus, a new paradigm was required: a non-vitalist organicism.¹⁹

¹⁷ Beckner, 1967, p. 549.

¹⁸ Haraway, 1976, p. 2.

¹⁹ As she explained: "The strict atomistic, mechanist paradigm applied to organisms led Driesch in 1891 to expect the echinoderm egg to behave like a good machine. That is, the development should have been 'mosaic': the parts should have their fates fixed at the outset and simple interaction of atomic parts according to mechanical laws should be the essence of development. Regulation was not an admissible occurrence within strict mechanist

However, drawing on Ritterbush's *Art of Organic Form* (1968), Haraway recognised the importance of pre-holistic and pre-organicist traditions stemming from Kant and Goethe's bio-philosophical thought. But, because she genuinely believed in the 'new-paradigm' thesis, she was unable to see any relevant historical tie between the late 18th and 19th century holism and 20th century organicism. More recently, A. Harrington has established this connection. According to her, some expressions of German holism in the 20th century heavily drew on Kant's aesthetic view of the organic world and Goethe's Romantic conception of 'wholeness'. Analyzing the life and career of four leading organicists, controversial figures such as the neurologist C. Von Monakov (1853–1930), behaviourist J. J. von Uexküll (1864–1944), psychiatrist K. Goldstein (1878–1965), and the psychologist M. Wertheimer (1880–1943), she illustrates how much 20th century holism owes to the Kantian and Romantic world. In addition, she makes another profound and fascinating connection: some holistic discourses and approaches in Germany backed and supported fascist and Nazi ideologies. As she emphatically recounts, the romantic idea of wholeness was deliberately translated into practical policies by some National Socialist enthusiasts. In fact, one Nazi biologist, H. J. Fuerborn, intended to use the holist doctrine for didactical purposes. As Harrington reports: "...the core of all biological education in the Nazi schools could be found in three basic principles: the doctrine of biological wholeness (the whole as greater than the sum of its parts), the theory of biological development (the dynamic creation of organismic wholes), and the teachings of heredity (the transmission of the qualities of the whole across generations)".²⁰ We will see that almost all of the figures that I will consider in this thesis supported and proposed very similar ideas, although with very different purposes and results.

Thus, with Harrington, and contrary to Beckner and Haraway, I will argue that organismic or organismal biologies have a very long pedigree, a history that can be linked to Aristotle's zoology, Kant's bio-philosophy (as it was largely articulated in his *Kritik der Urteilskraft* published in 1790) and that of

paradigm. Driesch formed his expectations in such allegiance to the paradigm that he was certain his experiment of killing one of the first two blastomeres resulting from the first cleavage of sea urchin eggs would result in half-embryos. The appearance of whole little animals in his dish precipitated a practical and philosophic crisis of the first rank in embryology. The old paradigm seals its own fate by the operation of its own dynamic (Haraway, 1976, p. 6).

²⁰ Harrington, 1996, p. 177.

his Romantic followers.²¹ However, in contrast to Harrington, I will tell a different and original story. I will track the diffusion and uses of Kant's bio-philosophy in the UK and the US from the 19th century and the different impacts it had on specific institutions, a range of individuals, and the international ramifications. Through the analysis of textbooks, books, articles, and archival resources (letters and unpublished papers), we will view the unexpected emergence of an international community of scientists; British, American of course, but also French, German and Italian — all committed to spreading and supporting organismic and holistic views in biology and society. An entire intellectual continent will emerge; a partially forgotten world buried in dusty archives, and dark library stacks. We will discover that a sophisticated and original philosophy of biology was formulated, discussed and internationally accepted during the very first decades of the 20th century. This philosophy, we will see, was not rooted in well-known heroes such as Darwin, Spencer or Mendel; instead, it was rooted in and inspired by German embryologists, anatomists, and physiologists: people such as, von Baer, Cuvier, J. Muller, and R. Leuckart; influential philosophers such as H. Bergson and A. N. Whitehead. In other words, we will explore an almost pristine (or at least very partially-known) territory in the history of science.

Furthermore, I will explore the influence of Kant's bio-philosophy on some controversial views that many of these scientists held, on themes such as heredity, development and evolution. For instance, we will see that the strong opposition against Weismann's neo-Darwinism, and then against Mendelian genetics, was often based on holistic arguments and reasoning. Finally, I will show that many figures sharing organismic or holist approaches to biology, both in the UK and the US, were very far from supporting fascist, totalitarian or rightist ideologies or convictions. On the contrary, most of them were fully engaged in fostering progressivist or leftist causes; they genuinely believed that the 'organism as a whole' represented a powerful metaphor of a well-ordered, fair, liberal, and democratic society.

The chapter organisation is as follows. The second chapter explores some aspects of post-Kantian bio-philosophy, its diffusion and its transformations. In particular, I will show what kind of relations – historical, institutional, and philosophical – Kant has with 19th naturalists, and then 20th century biologists. In the third and fourth chapters I will illustrate the influence of neo-Kantian bio-

²¹ For a general introduction to Kant and Romantic bio-philosophy see next sections. For a general introduction to the debate about mechanism versus holism and organicism, see G. E. Allen, 2005.

philosophy in England during the 20th century as expressed by two generations of relevant British biologists: J. S. Haldane, D'Arcy W. Thompson, E. S. Russell, and J. H. Woodger. Finally, in the fifth and sixth chapters I will assess the impact of such a tradition in the US. In particular, I will analyse the work of W. E. Ritter, C. M. Child, F. R. Lillie, and his student E. E. Just, and demonstrate how it affected the agendas of whole institutions in which they worked or which they directed. Throughout each chapter, I will explore how the neo-Kantian tradition, transformed in organismic philosophies during the 20th century, was associated with current political and ideological doctrines. In the concluding chapter, I will draw some historical and philosophical conclusions about how organismal biologies relativised notions such as reductionism, holism, mechanism, and materialism.

1.3: Adopting a Historical Perspective on the Organismic Tradition

The philosopher D. C. Phillips argued in 1970 that there were five interrelated ideas which characterised the organismic stance. In his own words:

- (i) The Mechanistic approach, i.e., the analytic approach as typified by the physico-chemical sciences, proves inadequate when applied to certain cases – for example, to biological organisms or to society or even to reality as a whole.
- (ii) The whole is more than the sum of the parts.
- (iii) The whole determines the nature of the parts.
- (iv) The parts cannot be understood if considered in isolation from the whole.
- (v) The parts are dynamically interrelated or interdependent.²²

In what follows, we will see that Phillips' characterisation of organismic biology is essentially mistaken and superficial; it is highly abstract without rendering justice to the complexity and sophistication of the biologists advocating such an option. Firstly, not all organismic biologists believed that mechanism was inadequate; they only believed that the mechanist approach could be partial and insufficient if taken as the only and unique approach to scientific investigation. Secondly, not all organismic biologists thought

²² Phillips, p. 412, p. 1970.

naively that the whole was more than its parts; to many, the parts plus their interactions made the whole. The whole was not a mystical or transcendent entity. Thirdly, if the whole determines the nature of the parts, most of organismic biologists also maintained that parts determined the nature of the whole; all depended on the kind phenomenon to be explained. Fourthly, again, to most organismic biologists the parts could be studied in isolation in practice; what they questioned was that this strategy was always successful in principle. Indeed, as we will see, they aimed for a pluralism of strategies, not for a dogmatic epistemology. Fifthly, this is the only idea that really captured the view of almost every organismic enthusiast: in the living beings, parts were dynamically and temporally interconnected. As the influential philosophy of Whitehead taught during the first decades of the 20th century, the organism was not conceived as a thing or object, but as a time-process, an event, an “actual occasion”.²³ It was not casual that Whitehead widely inspired and influenced many organismic biologists.

However, if Phillips’ list of ideas is simplistic, what kind of ideas really characterised the organismic tradition overall? From a wide historical perspective, we will see that, since Kant, five other ‘core’ ideas were broadly assumed and commonly shared: a) denial of both vitalism and *naïve* mechanism which, especially during the early 20th century, was associated with the rejection of a naïve reductionism and mystical forms of holism; b) the acceptance of living organisation as a postulate: the organism had to be considered the unit of investigation and not a mere aggregate of physical, inorganic, entities; c) extensive use of teleological explanations. Because the organism was seen as a functional whole, in which the composing parts concurred for the welfare of the unity, the study of functions must always have priority over the study of structures; d) the essential and problematic recognition of the relation between the organism’s whole and its parts. Just as the whole was the cause of its components, the components were the cause of the whole. Causes and effects were essentially interconnected. During the first decades of the 20th century, such a position converged toward one general assumption: the organism must be seen as a Chinese box, an ordered hierarchically-layered system where each level of complexity (nuclei, cytoplasm, cells, tissues, organs, etc.) could be a result of both lower and upper levels. No fundamental substances, elements, structures or entities could be assumed as the starting point of a causal

²³ For an introduction to Whitehead’s philosophy see Emmett, 1932, Agar, 1936; R. Mesle, 2008, Simons, 1998. Books representative of Whitehead’s thought on the organism are: Whitehead, 1920; 1925; 1929.

chain of events. In sum, insofar as living processes exhibit a form of organisation in which causes and effects were strictly interdependent, the fundamental ‘event’ to investigate was the organism itself; e) the organism could be severed from its environment only abstractedly. A ‘living-event’ without the environment was a mere artefact. This position was transformed in the 20th century into the idea that organisms and environment had to be seen together as a unique dynamic system and not as two antagonistic elements. Therefore, in the study of life, both laboratory experiments and observations in the field were required.

What I aim to show in this dissertation is that this set of assumptions — ideas widely represented during the first half of the 20th century — derived essentially from Kant and his tradition. But the supposed neo-Kantian bio-philosophical tradition emerging in the 20th century did not exemplify a paradigm, a research program, a unified and coherent set of beliefs that all adherents to such a movement uncritically shared. Instead, it characterised a flexible and open tradition in which all these five assumptions were negotiated and interpreted in different ways. However, in order to assess the importance of this tradition, the routes through which it travelled, the institutions and individuals it affected, and the way it changed during the 20th century, we need to spend a few words on its original sources. We need to know what Kant himself believed.

1.4: Kant’s Doctrine of the Organism as a Whole.

It is well known that Kant himself speculated widely on the nature of organic beings in his 1790 work, *Kritik der Urteilskraft*.²⁴ To Kant, the organism was a particular entity which required the presupposition of its purposive whole in order to understand the organisation of its composing elements.²⁵ Kant indeed dubbed organisms, ‘natural products’ where: “...every part not only exists by means of other parts, but is

²⁴ For an introduction see Zammito, 1992.

²⁵ See in particular sections 65, 66, 78, 80, and 81 of Kant’s *Critique of Judgment*. On Kant’s bio-philosophy there is a large amount of literature. In particular see MacFarland, 1970, McLaughlin, 1990; Butts, 1990; Ginsborg, 2001; P. Guyer, 2001; Huneman, 2007. See also the excellent introductions to Kant’s philosophy of biology by T. Lenoir, 1982, and Richard, 2002.

thought as existing for the sake of the others and the whole, that is an (organic) instrument".²⁶ As a consequence, Kant felt that organisms could not be seen as mere machines. They exhibited properties which could not be reduced to a complex or simple mechanical device: "An organized being is then not a mere machine, for that has merely moving power, but it possesses in itself formative power of a self-propagating kind which is communicated to its materials though they have it not of themselves; it organizes them, in fact, and this cannot be explained by the mere mechanical faculty of motion."²⁷ However, Kant made things more complicated because, even though we need the notion of purpose to understand how organisms work, this did not imply the fact that organisms were, ontologically, purposive entities. In order to clarify this last point Kant distinguished between two different kinds of explanation: mechanical explanation (typical in physical sciences) and causal explanation (typical of natural sciences such as biology).

To him, mechanical explanations required a certain and definite chronological order between causes and effects:²⁸ for example, billiard ball 1 causes the movement of billiard ball 2, so that ball 2 moves as effect of the movement of ball 1. The cause-effect relation between the two balls is a linear and chronological one; we clearly know and distinguish which is cause and which effect. In the causal explanation this is impossible. As Kant argued, in an entity with a natural purpose (*Naturzwecke*), the relations between causes and effects are never linear and chronologically determined for the simple reason that: "An organized product of nature is one in which every part is reciprocally purpose and means",²⁹ therefore, reciprocally cause and effect. Kant, however, added that in the difference between mechanical and causal explanation lay something else: different kinds of explanations required different types of judgments: *determinant* and *reflective*. Now, to Kant, the notion of *determinant* judgment denoted, in general, an intellectual faculty which connects the particular empirical data with universal laws given by the *a priori* category of the intellect. Thus, whereas the "determinant judgment" could be employed in a mechanical explanation because, as he had argued in his first *Critique*, the objective

²⁶ Kant, 1914, p. 27, I am using the edition and translation of J. H. Bernard, see I. Kant, 1914, *Kritik of Judgment, Translated with Introduction and notes of J. H. Bernard*, 2nd Ed., Rev., MacMillan, London.

²⁷ Kant, 1914, p. 278.

²⁸ For a more complete discussion of the Kantian philosophy of biology see Lenoir, 1982, Richards, 2002 and Grene & Depew, 2004.

²⁹ Kant, 1914, p. 280.

knowledge about particular objects is *subsumed* under the *a priori* categories of the intellect (the linear and chronological relation between cause and effect for example), no such thing was possible when that particular object was an organism. In that case, insofar as the particular object of knowledge cannot be *subsumed* under the universal *a priori* categories; the intellect requires the *reflectierende Urteilskraft* (reflective judgment). In other words, in the case of reflective judgment, the intellect needs to find a proper regulative principle to make sense of the experiences made on a particular object or process when such an object or process, like an organism, implies reciprocity between causes and effects, parts and wholes. Yet, that regulative principle is neither in the empirical data nor an intellectual faculty; it is a heuristic principle and, as such, is purely subjective. Therefore, this heuristic principle was seen by Kant as subjective judgment about natural things; a judgment which attributes particular purposes and ends (hence functions) to natural entities. In sum, to Kant, we need teleology to make sense of life even though organisms can be the mere outcome of mechanical laws. As he clearly argues explaining the constitutive role of teleological judgment in the life's sciences:

According to the constitution of the human Understanding, no other than designedly working causes can be assumed for the possibility of organised beings in nature; and the mere mechanism of nature cannot be adequate to the explanation of these its products... This is only a maxim of the reflective, not of the determinant judgment; consequently only subjectively valid for us, not objectively for the possibility of things themselves of this kind.³⁰

It is because our intellect is limited by its universal *a priori* categories, Kant argued, that we need a subjective principle obviating our intellectual narrowness when we observe organisms. As Richards aptly puts it: "according to the Kantian system, we apply categories like causality and substance determinatively to create, as it were, the phenomenal realm of mechanistically interacting natural objects. But in considering biological creatures, we must initially analyze the anatomical parts in reflective search of that organizing idea that might illuminate their relationship."³¹ However, to Kant, this did not mean that mechanical explanations had no place in life sciences; on the contrary, he thought that the naturalist

³⁰ *Ibid.*, p. 331.

³¹ Richards, 2006, p. 146.

should push as far as he could mechanistic understandings of living beings: “The greatest possible effort, even audacity, in the attempt to explain them mechanically is not only permitted, but we are invited to it by Reason; notwithstanding that we know from the subjective grounds of the particular species and limitations of our Understanding that we can never attain thereto.”³²

But why define the organism in such a way? Why, in other words, Kant conceived organisms as entities in which causes and effects are reciprocally entwined? Indeed, as we have seen, from that definition he derived the fact that mechanical explanation (and therefore determinant judgment) was not applicable to organic entities. Yet, the core question is: from where did Kant get such a definition? This is a question less obvious that many Kantian interpreters would admit but it is a strategic one for my purposes here. Indeed, the way that Kant defined a being with natural ends – an organism – reveals which organic phenomena he deemed central and what characteristics had to be considered *conditio sine qua non* an organism *may be* catalogued as a *real* one (rather than a complex machine for example). Therefore, if we want to know how and where Kant developed his definition of organism we need to know the essential elements, abilities, and phenomena he thought typified what we recognise as a living being. First, to him, organisms were dynamic things insofar as they showed properties that no inert thing, however complex, could show. These properties were generally three: organisms reproduce, develop, and regenerate whereas machines do not. In sum, Kant believed that these three properties justified the gap between the use of a mechanical and a causal explanation; a careful reading of the sections dedicated to the philosophy of biology in his third *Critique* is the best evidence.³³

³² *Ibid.*, p. 352.

³³ As Kant pointed out in section 66: “...it may be that in an animal body many parts can be conceived as concretions according to mere mechanical laws (as the hide, the bones, and the hair). And yet the cause which brings together the required matter, modifies it, forms it, and puts it in appropriate place, must always be judged of teleologically: so that everything may be considered as organized, and everything again in a certain relation to the thing itself in an organ” (Kant, 1914, p. 282). As Kant is arguing: if we take the organism as it is, without asking how it has been formed and shaped, a mechanical knowledge is possible. However, when we start to investigate how the organism forms and builds itself, no mechanist explanation—an explanation based on the determinate judgment and therefore on a linear and chronological relation between causes and effects – could be satisfying. Still, at the end of section 82, Kant writes about formation of organisms and not merely understanding of the organism: “But in the solution given above of the Antinomy of the principles of the mechanical and teleological methods of production of organic beings of nature, we have seen that they are merely principles of the reflective judgment in respect of nature as it produces forms in accordance with particular laws. They do not determine the origin of these beings in themselves; but only say that we, by the constitution of our Understanding and our Reason, cannot conceive it in this kind of being except according to final causes” (Kant, 1914, p. 351). In sum, our reason can understand, mechanically, the organism statically conceived. However, our understanding cannot grasp *mechanically* its self-formation. Finally, the discussion Kant undertook in section 81 on the difference between the hypothesis of

To put it another way, the problem was not to make sense of the organisms and their constitutions once their process of development was terminated; the problem was to understand the laws ruling development itself. In principle, we could understand the organism mechanically; studying its anatomy, measuring its growth, observing its functions and so on; however, we cannot explain, from a mechanical viewpoint, how organism's body forms itself. In short, the mechanical explanation – and therefore, the determinate judgment – cannot be applied to organisms because organisms reproduce, develop, and regenerate: all dynamic processes requiring the reflective judgment. However, Kant probably did not observe these phenomena by himself since he did not perform experiments; in fact, for this, he was indebted to one of the greatest naturalists of the 18th century: J. F. Blumenbach.³⁴



BLUMENBACH.

Fig 1.1, J. F. Blumenbach (1752–1840)³⁵

Blumenbach was primarily a physiologist and anatomist (though he is also celebrated as anthropologist); he, like many naturalists with biological interests at that time, was involved in the debate between followers of the preformationist doctrine and advocates of the epigenesis hypothesis. A previously committed preformationist, Blumenbach turned his mind to epigenesis mainly because he felt that preformation could not explain the fact that mixed parents begot blended offspring. However, what

preformation and epigenesis is further evidence that what he considered central was not the organism abstractedly taken, but the laws of its formation.

³⁴ As Lenoir recognises: “Immanuel Kant regarded Blumenbach as one of the most profound biological theorists of the modern era” (Lenoir, 1982, p. 18).

³⁵ Source: Dr. Johan Friedr. Blumenbach J.W. Kobolt pinx. Casselis 1793. Laurens sc. Berolini 1804. See website <http://ihm.nlm.nih.gov>.

Blumenbach had in mind while writing his influential 1781 treatise on epigenesis – *Über den Bildungstrieb und das Zeugungsgeschäfte*³⁶ – were the staggering powers of a tiny creature that Linnaeus named Hydra. In 1739 an unknown Swiss tutor, Abram Trembley, discovered these organisms attached to plants growing in garden ditches. After a few days he discovered that when these organisms were cut, they regenerated missing parts. This discovery provoked a stir in the whole of learned Europe³⁷ and, before reaching Blumenbach’s attention, hydra was already a model organism supporting the epigenesist doctrine.³⁸

Blumenbach framed his notion of *bildungstrieb* (formative force) around the properties of this organism and, he – as other naturalists before him – not only adopted it as a model to support epigenesis, but also as example disproving mechanist explanations in biology. An organism in which any part can produce the whole and in which the whole drives and shapes its parts (as shown by the celebrated experiment of turning the hydra inside out) was hardly reducible to a mechanistic framework. As Kant wrote in his *Critique* mirroring hydra’s endowments:

If we consider a material whole, according to its form, as a product of the parts with their powers and faculties of combining with one another (as well as of bringing in foreign materials), we represent to ourselves a mechanical mode of producing it. But in this way no concept emerges of a whole as purpose, whose internal possibility presupposes throughout the idea of a whole on which depends the constitution and mode of action of the parts, as we must represent to ourselves an organised body.³⁹

Indeed, in the same way that hydra’s parts can reproduce a whole organism, so the whole can reproduce its missing parts, so that: “An organised product of nature is one in which every part is reciprocally purpose and means”.⁴⁰ A machine, Kant insisted, is never able to reproduce or re-form both its parts and its whole structure: “...it does not replace of itself parts of which it has been deprived”.⁴¹

³⁶ In English: The Formative Drive and its Relation to the Business of Procreation.

³⁷ On hydra’s impact in biology see Dawson, 1987.

³⁸ See also Roger, 1963; Gasking, 1968; Dinsmore 1991, and finally Moscoso, 1995.

³⁹ Kant, 1914, p. 324.

⁴⁰ *Ibid.*, p. 280.

⁴¹ *Ibid.*, p. 278.

Of course, for Blumenbach the hydra was a model-organism which typified the organic development in general and Kant probably agreed on that.⁴² Hydra,⁴³ with its analogical power, demonstrated that the theory of epigenesis had to be true for the entire organic realm; hydra's multiple reproductions mirrored a universal organic property of development which, given our limited intellect, could only be grasped through a subjective principle of reason. To Kant though, the first to establish epigenesis on firm ground was Blumenbach himself:

As regards this theory of Epigenesis, no one has contributed more either to its proof or to the establishment of the legitimate principles of its application than Herr Holfr. Blumenbach. In all physical explanation of these formations he starts from organised matter. That crude matter should have originally formed itself according to mechanical laws, that life should have sprung from the nature of what is lifeless, that matter should have been able to dispose itself into the form of a self-maintaining purposiveness—this he rightly declares to be contradictory to Reason. But at the same time he leaves to natural mechanism under this to us indispensable *principle* of an original *organisation*, and undeterminable but yet unmistakable element, in reference to which the faculty of matter in an organised body is called by him a *formative impulse*.⁴⁴

Hence, Kant's theoretical views of the organism reflected the observations and studies that Blumenbach had undertaken on reproduction, development, and regeneration.⁴⁵ His idea, according to which an organism need to be considered as an object in which the causes and effects of its formation are irreducibly entwined, reflected the phenomenon of animal regeneration, and, by analogy, all developmental phenomena. However, I think that the extraordinary influence and success of these ideas in the subsequent natural sciences (and their related philosophical discussions), did not rely so much on

⁴² Even though, as Richards shows, there could have been theoretical differences and *misunderstandings* between Blumenbach's and Kant's philosophical projects.

⁴³ Kant: "An organised being is the not a mere machine, for that has merely moving power, but it possesses in itself formative power of a self-propagating kind which it communicates to its materials though they have it not of themselves; it organises them, in fact, and this cannot be explained by the mere mechanical faculty of motion" (Kant, 1914, p. 278).

⁴⁴ Kant, 1914, p. 346.

⁴⁵ Richards: "...in the biological realm, say, in the epigenesis of the foetus as described by Blumenbach (whom Kant knew and read), the various early stages make sense only in relation to their final product: that is, we have to conceive the final stage of development, which is an effect of the earlier stages, as if it were also the cause of the earlier stages" (Richards, 1992, p. 23).

the conception of organism as an intricate web of causes and effects, but more on some interesting implications of this conception. In other words, Kant defined life in indicating which phenomena mattered for a possible definition; as a natural product, an organism is only comprehensible through a teleological approach because reproduction, development, and regeneration are understandable through a teleological approach. If development is the phenomenon which best characterises life, then the study of morphogenesis is the best way to make sense of an organism. It was an extraordinary though indirect advertisement for embryology for the coming centuries. Indeed, not surprisingly, both post-Kantian and neo-Kantian philosophies of biology, and therefore the diverse forms of organicism in the 20th century, deemed central, for any biological investigation, the dynamic phenomena related to development.

However, after Kant, and during the greater part of the 19th century, another element was added to the list of central phenomena in life sciences: heredity. But heredity, in the post-Kantian formulations, had little or nothing to do with the transmission of discrete stuff, but with forces, activities and dynamic mechanisms producing specific patterns: the forms typical of the race. Heredity became central because it had the potential to explain development whereas development (and its related phenomena) was seen as the manifestation of hereditary potentialities plus environment. Kant himself speculated on these things; though, of course, according to his own terms, notions and historical context. When, between 1775 and 1777, he developed the theory of *Keime* and *Anlage*, he assumed that variation among races was presumably due to some specific ‘structure’ and ‘potencies’ which could be ‘awakened’ or lie ‘dormant’ according to local environmental conditions.⁴⁶ To him, the so called ‘generative fluid’ contained a predefined set of potencies; a preformed type of structural organisation which, during development, blossomed according to external conditions. Of course, no evolutionary trends could be derived from such a scheme; in fact, neither ‘structures’ nor ‘potencies’ varied or changed, only their contextual ‘expression’ changed. Adaptations (and therefore new adaptive variations) were not conceived as new characteristics acquired due to the laborious and incessant activities of the organism, but as ‘capacity’ already included in the original stock, which was differently activated by the local ‘conditions of life’. In sum, organic form was due to both original and predetermined organisation (*Keime* and *Anlagen*), and its interaction

⁴⁶ On Kant’s theory of *Keime* and *Anlage*, see Lenoir, 1982, and Sloan, 2002. See also Zammito, 2006.

with the environment. Living organisation was due to this invisible transmission of irreducible structures that, in concert with the environment, produced all species variation visible on the earth.

In conclusion, Kant provided a third way between a mystical vitalism and a naïve mechanism (assumption a), he argued that living organisation had to be presumed (assumption b) because physical sciences, with their methods and principles, cannot explain it. He offered a heuristic model of biological explanation based on teleology (assumption c), he maintained that parts and whole are both effect and cause of themselves (assumption d), he stressed that living forms are strictly associated with their environment (assumption e). We will see that Kant, on Blumenbach's shoulders, provided a set of concepts and notions which, in the 19th century, were found extremely convincing by new generations of biologists.⁴⁷ Subsequently, in the 20th century, these concepts and notions, filtered through Romantic 'distortions' and interpretations, were used to solve new challenges and accommodate new discoveries.

⁴⁷ See Lenoir, 1982, Nyhart, 1995, Friedman & Nordmann, 2006, Richards, 2002. See also Huneman, 2006.

2.0: Kant's Multiple Lives

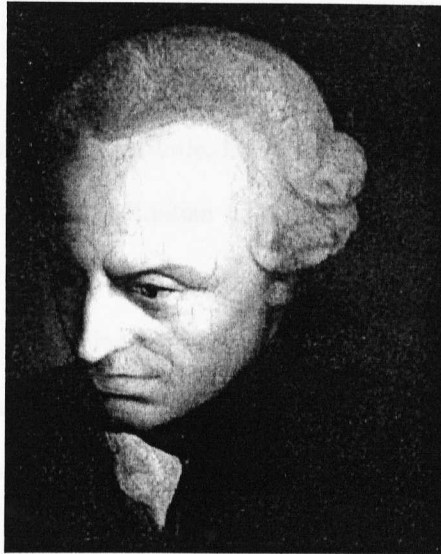


Fig 2.1, Immanuel Kant (1724-1804)

I reverence Immanuel Kant, with my whole heart and soul and believe him to be the only philosopher, for all men who have the power of thinking. I cannot conceive the liberal pursuit or profession, in which the service derived from a particular study of his works would not be incalculably great, both as cathartic, tonic and directly nutritious.

S. T. Coleridge¹

2.1: Introduction: Exporting Kant's Organicism

Kant's philosophy and epistemology had an enormous impact on 19th and 20th century sciences; as Friedman and Nordmann commented:

It is now a commonplace that the development of modern mathematics, mathematical logic, and the foundations of mathematics can be profitably seen as an evolution 'from Kant to Hilbert'. It is our conviction, in addition, that the development of modern scientific thought more generally – including the physical sciences, the life sciences, and the relationships between both of these and the

¹ Coleridge, quoted in Wellek, 1931, pp. 75-76.

mathematical sciences – can also be greatly illuminated when viewed as an evolution from Kant, through Poincaré, to Einstein and the logical empiricists and beyond.²

Yet Kant's philosophical and scientific influence on the budding life sciences in 19th century Germany has been particularly wide, deep, and enduring.³ Indeed, as we will see, Kant's bio-philosophy opened a wide intellectual space for new discussions and new interpretations of old dichotomies and issues affecting natural history since the time of Aristotle; however, he opened the way, rather than imposing a route. As Beiser wisely reminds us, post-Kantian history was essentially characterised by a constant attempt to transcend Kant's limits and problems, not to blindly or dogmatically disseminate his ideas.⁴ Kant's tradition, as many others, is studded with his disciples' treasons. Sometimes praised, exalted and incensed, then betrayed, condemned, and misunderstood; nonetheless, Kant's philosophy was almost always heeded, because his influence was too preponderant, the ramifications of his work too huge, its international dissemination too wide.⁵ In all its innumerable interpretations and receptions, many of the central tenets of Kant's philosophy persisted; even Kant's closer followers — the so called *Romantics* and *Naturphilosophen* — did not refuse it, but transcended, transformed and expanded its original core.

In Lenoir's controversial book, *The Strategy of Life*, the close relation between Kant's bio-philosophy and its immediate posterity is particularly highlighted. As he argues:

My principal thesis is that the development of biology in Germany during the first half of the nineteenth century was guided by a core of ideas and a program for research set forth initially during

² Friedman & Nordmann, 2006, p. 1.

³ See Gregory, 1989, Friedman and Nordmann, 2006, Sloan, 2007.

⁴ See Beiser, 2006.

⁵ On the significance of the first reactions to Kant's philosophy in England at the end of the 18th century, C. L. Reinhold, in his *Letter on the Philosophy of Kant (1790-92)* wrote that "The Critique of reason is cried up by dogmatists as the attempt of a sceptic to undermine the certainty of all knowledge – by sceptics as the vain presumption to erect a new universal dogmatism on the ruins of all other systems – by the supernaturalists as a cleverly contrived artifice to blow up the historical foundations of religion without the trouble of any specific attack against revelation – by the naturalists as a new support for the declining philosophy of faith – by the materialists as an idealist attack on the reality of matter – by the spiritualists as an unjustifiable limitation of all reality to the material world which is merely disguised under the name of experience – by the popular philosophers at least as a ludicrous enterprise to expel common sense in our enlightened and tasteful age by scholastic terminology and sophistry", Reinhold quoted in Wellek, 1931, pp. 4-5.

the 1790s. The clearest early formulation of those ideas is to be found in the writings of the philosopher Immanuel Kant.⁶

To Lenoir, indeed, a careful reading of the published works of some of the most important German naturalists active in 19th century shows how the Kantian world-view shaped and oriented a particular research program that diverse generations of young investigators would follow — a program Lenoir dubs “teleomechanism”. Relevant “teleomechanists”, — naturalists such as Gottfried Reinhold Treviranus (1776-1837), Carl Friedrich Kielmeyer (1765-1844), and Johann Friedrich Meckel (1781-1833) - were all followed by a new generation of celebrated “teleomechanists” such as Karl Ernst von Baer (1792-1876), Johannes Muller (1801-1858), Carl Bergmann (1814-1865) and Rudolph Leuckart (1822-1898). Kant, Lenoir argues, first set out the teleomechanist principles: living organization cannot be explained but always posited; life phenomena require a different kind of explanation from inorganic phenomena; the whole has a priority over its parts, function has a priority over structure and so forth. The story Lenoir tells is not about a vague chronological development of disembodied ideas within an abstract Kantian framework; it is instead a story about flesh and blood individuals in constant communication with one other; a lively community of naturalists deeply involved in debating philosophical and scientific issues of their time; biologists working in concrete institutions and setting feasible agendas for promising future students (and therefore future advocates of these agendas). In short, even though we do not need to accept the whole of Lenoir’s narrative, the so called ‘teleomechanist research-program’ is more than a fiction and it is vindicated from different and independent historical reconstructions.

Another historian of science, Robert J. Richards, in his book *The Romantic Conception of Life*,⁷ highlights the Kantian influence on the *Naturphilosophen* who, as Lynn K. Nyhart nicely illustrated, had a significant impact on the morphological research programs in German universities (and elsewhere too).⁸ In Richards’ words: “Those scientists to whom I refer as Romantic biologists generally accepted the metaphysical and epistemological propositions of *Naturphilosophie*. They took more to

⁶ Lenoir, 1982, p.2.

⁷ Richards: “Naturphilosophie derives from several sources, but its intellectual core grew from Kant’s critical philosophy, Schelling’s transcendental idealism, and Goethe’s developmental morphology”(1992, p. 21)

⁸ Nyhart, 1995.

heart, however, Kant's analysis of the logical similarity between teleological judgment and aesthetic judgment, which he developed in the *Kritik der Urteilskraft*"⁹. However, although Kant deeply inspired the *romantic* way of thinking about life, his doctrine underwent important revisions.¹⁰ Indeed, it is well known that his philosophy in general, including his bio-philosophical doctrine, was critically assessed and adulterated by philosophers and naturalists (conceived broadly) such as Johann Gottlieb Fichte (1762-1814), Friedrich Schlegel (1772-1829), Friedrich Wilhelm Schelling (1775-1854) and the polymath poet Johann Wolfgang von Goethe (1749-1832), who apparently coined the term "morphology". Lenoir himself stresses the difference between the Kantian teleological conception of organic phenomena and the *Naturphilosophie*'s approach to the emerging new science called 'biology'. In particular, Lenoir drew a sharp line between 'teleomechanists', who developed a successful empirical program based heavily on Kantian philosophy, and the Romantic *naturphilosophen*, who set out a speculative, vague, and abstract agenda that was far less successful. Of course, Lenoir had very good reasons (both historical and conceptual) to draw such a distinction; many figures he labelled 'teleomechanists' criticised the mystical excesses of *naturphilosophen* (for example, von Baer, Cuvier and Muller). However, the nature of such a distinction is not always easy to support because, as Nyhart nicely put it: "Most early nineteenth-century writers on form confound categorization schemes based on rigid philosophical distinctions, they appropriated the language of Kant, of Schelling, and of Cuvier in different places"¹¹. In fact, more recent historiography has stressed the continuity, the strong intellectual relations, the evident similarities between Kant's bio-philosophy and the Romantic conception of life¹². In other words, what seems to be emerging is a more variegated and sophisticated picture in which the Kantian tradition was shaped and

⁹ Richards, 2002, p. 12.

¹⁰ Richards: "...the third Critics furnished the starting point for the romantics' own theories of aesthetics and biological sciences" (Richards, 2002, p. 64). More recently Beiser argued: "...Kant was the father of *Naturphilosophie*. Kant's dynamic theory of matter in the *Metaphysical Foundations of Natural Science* was a formative influence upon the first generation of *Naturphilosophen*, more specifically upon Friedrich Schelling, Karl Adolf Echenmayer, Heinrich Link, and Alexander Scherer. These thinkers took Kant's dynamic theory a step further by applying it to the new chemistry and all the new discoveries in electricity and magnetism (Durner, 1994). Furthermore, Kant's methodological views – especially his demand for systematic unity and his insistence upon synthetic a priori principles – were also important for some *Naturphilosophen*. It is indeed somewhat ironic to find the Neo-Kantians criticising the *Naturphilosophen* for a priori speculation and system building when so much of their inspiration for these activities came from Kant himself! Even the method of analogy, for which *Naturphilosophen* had been so severely criticized, has its Kantian roots" (Beiser, 2006, p. 9).

¹¹ Nyhart, 1995, p. 8.

¹² See, for example, Jardine, 1996, Beiser 2002, Huneman, 2006. See also S. Schmitt, 'Succession of Functions and Classifications in Post-Kantian *Naturphilosophie* around 1800' and R. J. Richards, 2007.

interpreted in a quite elastic way. Post-Kantian morphologists, physiologists, embryologists or zoologists and naturalists *tout court*, absorbed Kant's teachings in their own ways and according their contextual needs.

Of course, one of the most important transformations was the distortion of Kant's reflective judgment. Kant had famously stated that: "...there will never be a Newton for a blade of grass", because no determinant judgment could never be consistently applied to the organic world; in doing that, Kant assumed that no life science could ever reach the status of physical science, which was considered the ideal model of reliable knowledge. To many of Kant's followers, the reflective judgment imposed too harsh a limit on the study of life because it could only provide inductive generalizations grouped together by the mere subjective heuristic of reason; in other words, there could never be a proper science of life. Post-Kantian naturalists, including transcendental morphologists and philosophers of nature, felt the need to extend or go beyond Kant's distinction; they conflated reflective and determinant judgment and "ontologized" or naturalised purpose in nature. By then, teleology was not a mere strategy of reason used as a tool to interpret organic phenomena, but as a constitutive or inherent property of organisms themselves (and often, of the whole of reality); in other words, the student of life requires a teleological approach not as epistemic heuristic justified by the limits of his intellect, but because life *is* intrinsically purposive. We will see that not only was the distinction between reflective and determinant judgment reframed or forgotten in the post-Kantian tradition, but it was simply ignored in 20th century organismic philosophies.

However, if we consider traditions not as monolithic and static sets of ideas, beliefs, or practices coming from a unique source,¹³ but as a result of a dynamic and complex sedimentation of elastic notions coming from different contexts, the distinction between teleomechanists and *naturphilosophen*, or between *proper* neo-Kantians and Romantics, does not need to be emphasised. What should be emphasised though is how such a tradition changed. Indeed, notwithstanding Lenoir's distinction, it seems quite difficult to question the influence, direct or indirect, of Kant's bio-philosophy

¹³ For example, the organicism defended by Goethe was probably inspired by Kant, also by Spinoza.

on disparate research agendas set out in Europe throughout the 19th century.¹⁴ After all, Lenoir's teleomechanist program, the morphological tradition that Nyhart portrays and links to German universities, the romantic conception of life that Richards depicts in his large volume, all exhibit a similar, recurring way of thinking. Yet, such a broad 'way of thinking' (that I have linked to the five points illustrated in the previous chapter), was not extinguished in the 19th century, neither did it remain confined to Germany. It was exported to other countries where it was critically assessed, slowly metabolised and, consequently, adapted to new contexts and needs.

Lenoir never contemplated the possibility that such a tradition, or way of thinking, would survive the 19th century and even be exported outside the German-speaking world. To him, the 'teleomechanist' research program died with von Baer, Bergmann, Bischoff, Virchow, and Leuckart. But, as I will show in the next sections, it was not so. Indeed, some forms of post-Kantian thinking filtered into England and thrived, during both the 19th and 20th centuries, informing some of the most interesting debates in biosciences during the first decades of the 20th century. Yet, towards the end of 19th century and the beginning of the 20th, we find important clusters of 'neo-Kantianism' in the U.S. too. In fact, the figure considered by Lenoir as the last 'teleomechanist' in Germany, Rudolf Leuckart, trained some of the most interesting 20th century American biologists: biologists who, once back in their own country, did not reject the teachings, approaches and ideas they had learned abroad.¹⁵

2.2: Kant Speaks English: Establishing Connections in the 19th Century

Towards the end of the thirties of the nineteenth century, the study of Kant seems to have become established as an organic element of English philosophical tradition. The year 1838, which marks the date of the publication of the first complete translation of the *Critique of Pure Reason*, is in a sense,

¹⁴ As Zammito rightly reminds us: "Many of the disciples Kant recruited in Germany simultaneously revered Lessing and Goethe, read Herder with attentiveness and appreciation, and found Spinoza and pantheism fascinating. Indeed, one of the crucial facts that must be retrieved from the context is the widespread conviction of the incompleteness of the Kantian system and of the agenda for philosophy which that created. Kant contributed substantially to this sense of the openness of his system and to the idea of its possible completion, and only very late, when it became apparent that what his disciples had made did not suit him, would he give public notice that his own works constituted and altogether complete system, and that his heirs had utterly misunderstood him" (Zammito, 1992, p.14).

¹⁵ See P.J. Pauly, 1984.

the end of a well-defined period. The careers of the first propagandists for Kant drew all to a close about that time. Coleridge died in 1834, Thomas Wirgman in 1840, John Richardson about 1839. A new era announces itself also in the study of Kant: the effect of Carlyle's important paper on German thought and literature, published around 1830, began to be felt, in 1836 Sir William Hamilton gave his inaugural address as Professor of Moral Philosophy at the University of Edinburgh. A new series of translators appeared. Wilhelm Gottlieb Tenneman's "Manual of the History of Philosophy" was published in English in 1832, translated by the Rev. Arthur Johnson. This book was written from an orthodox Kantian view and could have given a fairly accurate idea of Kant's doctrines and his historical position in the great tradition of philosophy.

R. Wellek¹⁶

In England, Kant's critical tradition thrived through complex ways. Though Wellek has reconstructed the different trajectories followed by Kant's critical philosophy in England from the late 18th century, the diffusion of Kant's bio-philosophy took other forms. In other words, although after the 1830s Kant's whole philosophy was widely discussed in England — especially thanks to the authority of William Whewell and his 1838 *History of the Inductive Sciences* — Kant's philosophy of biology was indirectly transmitted through the broad and deep influence of von Baer's embryology and Cuvier's comparative anatomy. The link between Kant and von Baer's embryology was first shown by E. S Russell in 1930 when he wrote that: "...von Baer's philosophical standpoint is definitely anti-materialistic. He is clearly influenced by Kant's teleology...".¹⁷ More recently, Lenoir extended the relation between Kantian philosophy of biology and von Baer in his article "Kant, von Baer, and the causal-Historical Thinking in Biology". Indeed, for Lenoir, von Baer improved the vitalo-materialist program first set out by Kant and Blumenbach — an agenda essentially organismal and anti-reductionist. As Lenoir put it: "I would urge that von Baer's work brings the conceptual framework enunciated by Kant and Blumenbach in their writings of the late 1780s and 1790s to its most robust formulation...not only was von Baer conversant with the works of these men; he built their leading concepts into his own theories of the developmental

¹⁶ Wellek, 1931, p. 245.

¹⁷ Russell, p. 37, 1930.

schema and primitive organs”.¹⁸ Von Baer’s biology was deeply Kantian insofar as its conception of the organism was essentially Kantian; as von Baer himself wrote in his celebrated monograph *Ueber Entwicklungsgeschichte der Thiere* in 1828, showing his clear debt to Kant and Blumenbach:

But all explanations of this [materialistic] kind the physiologist finds soon to be highly incomplete, since they touch only one single side of life; and he comes to see, above everything, that life cannot be explained from something else, but must be conceived and understood in itself. The time is approaching when even the physicist must admit that in his investigations he merely put together the isolated physical antecedents of the totality of life, and thereby fashions for himself an artificial beginning.¹⁹

If von Baer was one of the most successful propagandists of the Kantian bio-philosophical approach, he was not alone. Indeed, E. S. Russell, in his classic *Form and Function*, stressed the similarities between the von Baerian approach to biology and that of Cuvier; both endorsed a functional biology, both recognised the importance of embryology in order to establish homologies, but, especially, both were Kant’s pupils. Cuvier, Russell claims, was a “...teleologist after the fashion of Kant, and there can be no doubts that he was influenced, at least in the exposition of his ideas, by Kant’s *Kritik der Urtheilskraft*, which appeared ten years before the publication of the *Lésons d’Anatomie Comparée*. Teleology in Kant’s sense is and will always be a necessary postulate in biology”.²⁰ Lenoir too had no doubts: “Cuvier was responsible for deepening and extending the teleomechanist program of vital materialism”.²¹ Moreover, although not the only source, both empirical and theoretical tenets of Cuvierian biology – the principle of the conditions of existence and the principle of correlation – were well rooted in Kantian speculations on the nature of the organic beings.²²

Dorinda Outram considered too the influence of Kant on Cuvier, showing the tight intellectual connections. Indeed, between 1784 and 1788, Cuvier spent part of his training in Stuttgart.

¹⁸ Lenoir, 1982, p. 114.

¹⁹ Von Baer Quoted in Russell, 1930, p. 37.

²⁰ Russell, 1916, p. 49.

²¹ Lenoir, 1982 p. 54.

²² See Outram, 1986, and Taquet, 2006.

Bilingual in German and French he was a friend of Karl Kielmeyer (one of Lenoir's teleomechanist figures and follower of the Kantian philosophy) and Blumenbach; yet he was well aware of Kant's bio-philosophy, as the following quotation taken from his *Lésons d'Anatomie Comparée* demonstrates:

This general and common impulsion of all the elements [of a living body], is to such an extent the very essence of life, that parts which are separated from a living body quickly die, because they themselves do not possess their own impulsion, and only participate in the general movement which guarantees their union. In this way, as Kant has pointed out, each part of a living body is as it is, because of its work towards the whole; while in the case of inorganic bodies, each part exists for and by itself.²³

Furthermore, at the end of 18th century there were important connections between German and French science and these connections were fostered also from political reasons. Indeed, the Napoleonic politic of expansion eventually encouraged, indirectly, the diffusion of Kant's bio-philosophy in France. As Lenoir states:

In the 1790s all roads led to Gottingen, where the young men in Blumenbach's inner circle were envisioning a comprehensive approach to organic nature. Between 1800 and 1815, however, particularly after the German states had largely become satellites of France and many German universities were closed, those roads led to Paris, which for German zoologists meant they led to Georges Cuvier. During these years, when Alexander von Humboldt made Paris his home base for exploring the world, a small German colony sprang up around Cuvier. These young Germans had several features common in their backgrounds. They were either students of Blumenbach and Reil, or, through contact with their students, were about to become enthusiastic converts to the teleomechanist program".²⁴

²³ Quoted in Outram, 1986.

²⁴ Lenoir, 1982, p.55.

In sum, there are few doubts that the Kantian philosophy of biology — his stress on function rather than structure, the prominence of the whole over its parts, teleology as a necessary heuristic strategy to understand living beings — ran deep in the theoretical convictions of von Baer's embryology and Cuvier's functional biology. Furthermore, the influence of von Baer's and Cuvier's biological thought was not limited to Germany and France, but it spread, directly or indirectly, across all of 19th century continental Europe and, in a significant way, in England.²⁵

In England then, the first key figures to adopt the agenda of a functionalist and organismal philosophy of biology during the first half of the 19th century, included influential naturalists like Joseph Henry Green²⁶ and Martin Barry (both trained in Germany), the celebrated poet Samuel Taylor Coleridge and the controversial anatomist Richard Owen who, in 1831, went in Paris attending Cuvier's lectures²⁷. Yet, even though the sources on which those naturalists and thinkers drew could be heterogeneous, and although both von Baer and Cuvier certainly exerted their direct or indirect influence, there was another towering figure impacting British science during the first half of the 19th century; one of Lenoir's teleomechanist heroes: Johannes Muller. In 1833, Muller published an influential book: *Handbuch der*

²⁵ See also Ospavat, 1976.

²⁶ Green was a British surgeon and comparative anatomist. He studied in Germany as a medical student in Berlin and Hannover and, once back in England, he became a close friend with the poet and philosopher S. T. Coleridge (1772-1834), who, in turn, was an enthusiastic advocate of German romantic philosophy. As Sloan vividly describes Green's science: "Green's combination of medical expertise, his personal study of German philosophical and scientific tradition, and his professional appointments all made him an ideal vehicle by which a dynamic appropriation of German philosophical biology was realized...Green's philosophical synthesis of Kant, Schelling, Solger, and Blumenbach with endemic British philosophical, biological, and medical thought represents the most creative assimilation of the German tradition I have located among the British at this time" Sloan, 2007. About Coleridge, as Ritterbush describes: "In a number of lectures and essays, of which the most important was "On the Definitions of Life" (1830), Coleridge criticized empirical physiologists as pursuing too narrow an approach to the problems of life. They studied organisms as though they were simple physico-chemical assemblages, a piece at a time, while the most important phenomena of life resided at the level of the organism as a whole..." Ritterbush, 1968, p.16. Yet, like Green, Coleridge accepted all the tenets of the post-Kantian bio-philosophy: "...the origin of the whole precedes the differentiation of the parts. The whole is primary; the parts are derived...Second, the form manifests the process of growth by which it arose...The organic form proclaims itself as the end result of a progressive sequence of development. Third, as it grows the plant assimilates diverse elements into its own substance...Fourth, the achieved form of the plant is directed from within...The external aspect of living things is determined by internal processes, not, as in a human artefact, from without. Fifth, the parts of the living whole are interdependent". See Ritterbush, 1968, pp. 20-21. On Coleridge and the Kantian tradition, see also Ashton, 1980, Hamilton, 2007, Sheldrake 2005.

²⁷ Desmond mentions a very revealing letter that Owen sent to Whewell in 1840 : "how much we - i.e. the Cuvierian cultivators of comparative anatomy - are, and always must be, indebted to you for the clear statement of the scientific character of teleological thinking"(Desmond, 1992, p. 85), and yet, as he further reminds us: "...it is clear that German nature-philosophers (such as Oken and Carus) and "vital materialists" (such as Meckel and the transformationist Tiedemann) had a much broader influence in Britain on the philosophical anatomists and their allies (many - Knox, Shapey, Grant, Turner, Marshall Hall, Martin Barry - had attended courses in Germany)" (Desmond, 1992, p. 85).

Physiologie des Menschen, a book which was translated in England as *Elements of Physiology* in 1842 and, as Ospvat recounts, it was "...widely used as a textbook throughout Europe."²⁸ Now, Muller also was an enthusiastic follower of von Baer and Kantian philosophy and, as Adrian Desmond shows, *Elements of Physiology* influenced Owen deeply, as well as many British scholars fighting against the new materialist biology and morphology inspired by the French anatomist Geoffroy Saint-Hilaire. In fact, as Desmond puts forward in his *The Politics of Evolution*, such an anti-materialist and *functionalist* tradition, well characterised by von Baer, Cuvier and Muller, and then by Green, Barry and Owen, represented in England a bulwark not only against the 'subversive' biology of Geoffroy Saint-Hilaire, but also against the materialist doctrines of transformationism (evolution) led by various Lamarckians and radical reformers. In short, throughout the 19th century, functionalist, organismic and teleological biology represented the conservative orthodoxy in Britain; an orthodoxy, however, that was never really upset by various reformers who advocated for a materialist, structuralist, transformist, anti-teleological biology. For these reasons, Kant's bio-philosophy, filtering through the rhetoric of influential advocates belonging to the British 19th century establishment, left an important legacy to the next generations of biologists. However, between the late 19th and early 20th century, Kant's bio-philosophy stopped being an orthodox tradition; with the triumph of Darwin's biology on one hand, and other forms of Lamarckian materialism, Kant's bio-philosophy increasingly fell into the background; it became a philosophy of minorities and began to be associated with leftist biologists. We will see in the next section that the British neo-Kantian tradition advocated by figures such as E. S. Haldane, D'Arcy Thompson, E. S. Russell, and H. Woodger, although owing its general theoretical framework to the past, did not derive smoothly from the 19th century orthodoxy and its establishment; its route had been much more complicated and interesting.²⁹

2.3: Neo-Kantians in 20th - century Britain

In the previous section I have sketched the multiple possible routes through which Kant's philosophy travelled in England during the 19th century. However, if we expect a smooth and direct line between 19th

²⁸ Ospvat, 1976.

²⁹ On the first impact of German science on the British naturalist tradition in 19th century see A. Desmond., 1992 Secord, 1996 Richards, 1992, Ospvat, 1978.

- century British embryologists and anatomists and 20th century British biologists, we will soon be disappointed. Indeed, when we consider the new generation of ‘Kantian’ biologists born after the second half of the 19th century, and then well established in 20th century biology, we observe that they had few things in common with Owen, Coleridge, Green and Barry. Surprisingly, their direct sources were not their fellow old countrymen, but essentially the late 19th and 20th century German biologists. In other words, whereas the earlier 19th enthusiasts of Kant’s bio-philosophy certainly spread the myth of the superiority and quality of German biology in England, they did not influence, if not incidentally, the new generations which, as I will show in a moment, adopted Kant’s bio-philosophy either directly in Germany, or through German sources. What I think the previous British anatomists did achieve, though, was to convince the whole scientific establishment that German science generally mattered; therefore, during the late 19th century, if one wanted to be a good biologist, one had to study German!

Therefore, because there is not a unique and direct line drawing a map of reciprocal influences, if we want to get a general idea of how some leading British bio-scientists could be influenced by Kant’s bio-philosophy during the late 19th and 20th century, we need to look at individual biographies which will show a kaleidoscopic geography of intellectual and institutional connections. Take the Scottish physiologist J. S. Haldane (1860-1936) — according to Goodman,³⁰ two key figures influenced Haldane’s biological views: the English-German physiologist William Thierry Preyer (1841-1897) and the German botanist Eduard Strasburger (1844-1912).

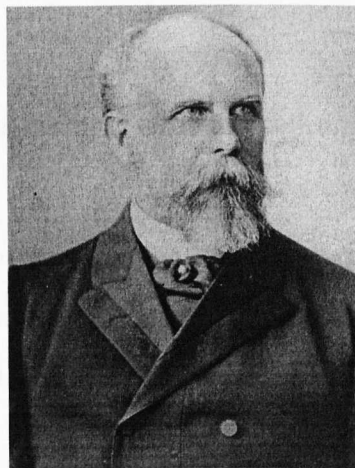


Fig. 2.2, W. T. Preyer³¹

³⁰ Goodman, 2007.

³¹ Source: <http://vlp.mpiwg-berlin.mpg.de/people/data?id=per299>

Although Preyer was born in Manchester, his training was mainly in German countries, attending university in Bonn, Berlin, Vienna and Heidelberg. Graduating in physiology at the University of Heidelberg, Preyer studied with Max Schultze (1825-1874) in Bonn³² and, later, with Claude Bernard in France.³³ Given the context in which Preyer undertook his training, it is not surprising that he, in his influential *Elemente der allgemeinen Physiologie* (1883), translated in French in 1884, endorsed a Kantian position about the study of life. In fact, Preyer's teacher at Bonn, Schultze – mainly remembered as one of the co-founders of the cell-theory — had been a pupil of Johannes Muller in Berlin. Furthermore, the post-Kantian 'discourse' that Preyer put forward was particularly evident when he discussed the relation between physiology and other sciences and also when he tried to shed light on the concept of life. Firstly, Preyer stressed the importance of physics and chemistry for the study of physiology — a science he defined as: "the pure science of the life's functions"³⁴ – but physiology remained an independent science nonetheless, because:

As explicative science, the theoretical physiology belongs to the exact sciences, such as physics. However, physiology is different insofar it is above all an applied science, a physics, a chemistry, an applied morphology, whose results are used for the study of the physiological phenomena. In the natural phenomena, the pure physics only regards the transformations of forces, pure chemistry the changing of the matter, pure morphology the modification of forms: the pure physiology study the natural phenomena that, as in the living bodies, presents all the three orders of changing.³⁵

Preyer's understanding of the concept of life is even more explicit in the following quotation:

The real nature of all the series of movements we call life is the result of facts of which physics and chemistry are not concerned because, without a transformation of their principles, they cannot explain life. Both sciences, physics and chemistry, are only concerned about the physical and chemical

³² J. Pagel *Biographical Encyclopedia of outstanding physicians of the nineteenth century*. Verlag Urban and Schwarzenberg / Vienna 1901, pp. 1550-1551.

³³ Obituary, William Thierry Preyer (1841-1897), *Nature*, No. 1448, Vol. 56, p. 296.

³⁴ Preyer, 1884, p. 4.

³⁵ *Ibid.*, pp.4-5.

properties of the bodies; now the psychical and the phenomena of evolution do not belong to such a domain...they are the object of physiology.³⁶

In sum, the methods used by physicists or chemists, though useful, cannot be considered sufficient for the study of life's functions. Haldane, as we will see, was deeply influenced by these ideas.

Strasburger held similar convictions to Preyer. Born in Warsaw in 1844, he studied both in France and Germany, obtaining his PhD at the University of Bonn in 1866. In 1894 he published the famous and still used *Lehrbuch der Botanik* (Textbook of Botany) which went through 35 editions and was translated into eight languages (the last edition was published in 2002).³⁷ In the first part of his monumental work he dedicated a section to the 'physical and vital attributes of plants'; a part in which he clearly exposed some 'Kantian' ideas informing botanical researches. Plants, Strasburger argues, are "...of the nature of solid bodies,"³⁸ therefore they have a weight and density; they have a conductivity of light, sound and electricity. However, he concluded, even though plants share many physical properties with inorganic matter, material and chemical substances are not enough to characterise life in itself. In Strasburger's own words:

No other substance exhibits a similar series of remarkable and varied phenomena, such as we may compare with the attributes of life. As both physics and chemistry have been restricted to the investigation of lifeless bodies, any attempt to explain vital phenomena solely by chemical and physical laws could only be induced by a false conception of their real significance, and must lead to fruitless results. The physical attributes of air, water, and of the glasses and metals made use of in physical apparatus, can never explain qualities like nutrition, respiration, growth, irritability and reproduction.³⁹

³⁶ Ibid., p. 97.

³⁷ Schwarz-Weig, 2002.

³⁸ Strasburger, 1898 p. 160.

³⁹ Ibid., p. 161.

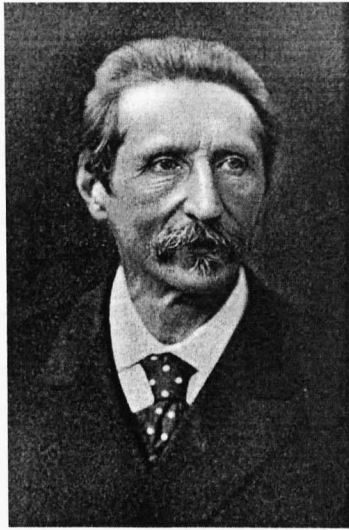


Fig. 2.3, E. A. Strasburger⁴⁰

The training Haldane received in Germany, as Goodman has emphasised, had been decisive for the development of his thought.⁴¹ However, once back, he also had occasion to discuss and deepen his theoretical convictions in his own country; indeed, Haldane had been a life-long friend of D'Arcy Thompson.⁴² Both were born on the same day of the same year, both were Scottish, and both Edinburgh students. In 1884, Haldane was hired as demonstrator in Physiology at the University College of Dundee, and there, he worked together with D'Arcy Thompson⁴³ in checking the quality of air breathed in slum houses, occupied by miners in nearby Dundee.⁴⁴ Although there were many similarities between Haldane and Thompson's training, Thompson was particularly influenced by the embryologist Francis Maitland Balfour (1851-1892) during his stay in Cambridge. Balfour started his career very early: in 1874 he was one of the first scientists working at the Naples zoological station and, in the same year, still as undergraduate student, he published with Michael Foster (an eminent Cambridge physiologist who spent part of his training in France and Germany)⁴⁵ an influential textbook *The Elements of Embryology* (1874),

⁴⁰ Source: <http://www.britannica.com/EBchecked/media/132838/Eduard-Adolf-Strasburger-1908>.

⁴¹ Haldane first went to Germany in 1879, to Jena, where he attended Haeckel's lectures and, secondly, to Fribourg where he aimed to improve his "microscope skills", attending Weismann's lectures (Goodman, 2007, p. 106). By that time he had already visited the country several times, for a variety of reasons.

⁴² See chapter 3.

⁴³ Talk: Daftie and Johnnie: D'Arcy Thompson's lifelong friend, J. S. Haldane, D'Arcy Thompson Zoological Museum, University of Dundee.

⁴⁴ I should mention that, in 1888, Geddes held the chair of Botany at the University College of Dundee. He, as we shall see, was highly influential on E. S. Russell's biological thought.

⁴⁵ See McDowall, 1936 and Geison, 1978.

a book in which, in the introduction, they praised von Baerian embryology: "...the advances made in Vertebrate Embryology, through the elaborate work of Remak, the labors of Rathke, Allen Thomson and others, the admirable lectures of Kolliker, and the researches of more recent inquirers, though many and varied, cannot be said to constitute any epochs in the history of the subjects, such as that which was marked by Von Baer..."⁴⁶



Fig. 2.4, M. Foster⁴⁷



Fig. 2.5, F. M. Balfour⁴⁸

Balfour was a central figure for British biological sciences; as director of the Cambridge Morphological Laboratory, he attracted students such as W. Bateson, W. Weldon, A. Sedgwick and, of course, D'Arcy Thompson.⁴⁹ It is probable that, through university textbooks such as that of Foster and Balfour (in 1880 Balfour also published a large two volumes treatise of Comparative Embryology), a new generation of investigators absorbed the continental embryological tradition. In fact, as Blackman comments: "the book [The *Elements of Embryology*] provided a standardised routine for students, taking them step by step through the laboratory work required for part of the course in elementary biology."⁵⁰

In the biography written by D'Arcy Thompson's daughter,⁵¹ Balfour's importance in the development of D'Arcy Thompson's conception of biology is stressed over and over again. As she wrote: "...the man who came to mean most to him, whom he loved and revered, who was his guide, philosopher,

⁴⁶ M. Foster, F. M. Balfour, 1874, p. 6.

⁴⁷ Source: <http://www.npg.org.uk/collections>.

⁴⁸ Source: <http://www.stanford.edu/group/auden/cgi-bin/auden/individual.php>.

⁴⁹ See Hall, 2003 and Richmond, 1997.

⁵⁰ H. Blackman, 2003.

⁵¹ D'Arcy Thompson, R., 1958,

and friend, was Frank Balfour.”⁵² Yet, as D’Arcy Thompson said during his inaugural lecture at the University of Dundee in 1885:

[as] a pupil under F. M. Balfour, I learned the power of a really great teacher, which is a rarer thing even than a great discoverer...under Balfour...one great branch of biology actually grew up in his end into science – the science of embryology. He gathered up all scattered knowledge that was hidden in books and floating in men’s brain, and he, for the first time, wove it together, and entwined with it the thread of his own originality and genius.”⁵³

In order to give a broader glimpse of the Cambridge Morphological Laboratory and its strong continental ties, we may consider another influential figure: Balfour’s pupil and former demonstrator, Adam Sedgwick (1854-1913). Sedgwick graduated from Cambridge in 1891, in Natural Sciences, and during his training he was deeply influenced, as Richmond recalls, by Michael Foster and Frank Balfour.⁵⁴ Sedgwick was an influential teacher and his views “...found a following among his students and future leading figures in British Zoology, including Gavin de Beer, C. Clifford Dobell, James Gray, E. W. MacBride, E. S. Russell, and D’Arcy Thompson.”⁵⁵ Looking at the introduction to Sedgwick’s *A Student’s Text-Book of Zoology* (1898), we find that Sedgwick clearly endorsed some central tenets of Kant’s bio-philosophy: although the student of life, the biologist, should never presuppose the existence of a vital force: “A vital element, i.e., an element peculiar to organisms no more exists than does a vital force working independently of natural and material processes,”⁵⁶ he could never explain life on the basis of physics alone: in fact, life could be never reduced to physico-chemical structures and compounds because, even though:

The properties and changes of living bodies are strictly dependant on the physico-chemical laws of matter...yet it must be admitted that we are entirely ignorant of the molecular arrangement of the material basis of a living organism, and it exists under conditions the nature of which is as yet unexplained. These

⁵² Ibid., p. 52.

⁵³ Quoted in R. D’Arcy Thompson, 1958, pp.70-71.

⁵⁴ Richmond, 2004, p. 365

⁵⁵ Ibid., p. 366.

⁵⁶ Sedgwick, 1898, p. 11.

conditions, which we may designate, as vital without thereby calling in question their dependence on material processes, distinguish organisms from all organized body.”⁵⁷

It is the peculiar organisation of structures which makes life, not a mere physico-chemical substrate. Finally, Sedgwick concluded, even though we are unable to find any substantial difference between inorganic and organic bodies, in observing even the most simple organisms, we cannot regard life as the result of the mere and simple movement of matter: the biologist, if he wants to explain living phenomena, must presuppose the existence of living organisation insofar as we are unable to get any further reduction. The existence of living bodies: “...presupposes, according to our experience, the existence of like or at least very similar beings from which they have originated.”⁵⁸ A pure Kantian could not explain the matter in a better way.

E. S. Russell belonged to a younger generation of scholars. He studied at the University of Glasgow in the early 20th century and, after his graduation, he went to work in Aberdeen with J. A. Thomson (1861-1933), a Scottish naturalist who, from 1899, was appointed as Regius Professor of Natural History.

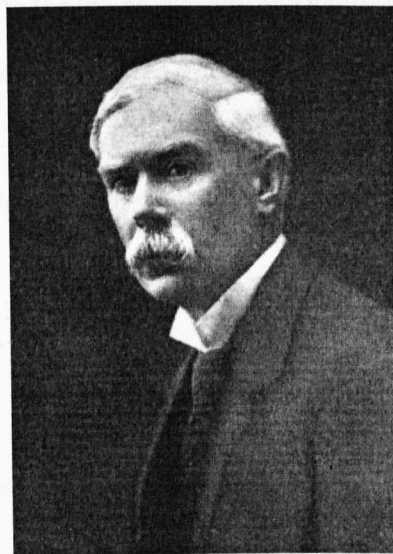


Fig. 2.7, J. A. Thomson⁵⁹

Thomson was a former student of Haeckel in Germany and a close friend and colleague of Patrick Geddes with who he published several books.⁶⁰ A prolific writer, Thomson endorsed an anti-mechanistic

⁵⁷ Ibid., p.10.

⁵⁸ Sedgwick, 1898, p.10.

⁵⁹ Source: *The days of a man* (1922) de D.S.Jordan.

conception of life, a conception elaborated through the study of Bergson and the direct influence of Geddes.⁶¹ He, with Sedgwick, accepted a form of organicism, according to which, though life depended on matter, it was irreducible to physico-chemical properties. In our possible experience of living organisms, he argued, life always comes from life and we have no evidence of how life has been built from inorganic matter: "...life probably began when the conditions of heat and solubility of substance were more favorable to the formation of peculiar and complex matter than at present. But such a statement is often thought to be unphilosophical in view of the fact that we have at present no experience of the formation of such substances, and that it has been conclusively proved that living creatures always proceed from preexisting life."⁶² Once again, the biologist should presuppose the existence of life rather than reduce it to simpler inorganic elements. As Thomson would state again during his Gifford lectures in 1915-16: "We considered the organism under the category of a material system — to see how that fitted, and we reached the conclusion that, while this is a legitimate and useful way of looking at a living creature, the formulae of physics and chemistry are inadequate for the re-description of the everyday bodily functions, or of behavior, or of development, or of evolution."⁶³

If Russell was indebted to the bio-philosophy of Thomson, he was also influenced by Geddes. Patrick Geddes (1854-1932) had been a student of Thomas Huxley at the London School of Mines and he spent part of his training in Europe. In 1878 he went to France, where he worked at the Marine station in Roscoff, and a year later in Italy, where he settled at the Naples zoological station.

⁶⁰ See Lightman, 2004, p. 1991.

⁶¹ See Bowler, 2001.

⁶² J. A. Thomson, 1901, p.141.

⁶³ Thomson, 1920.

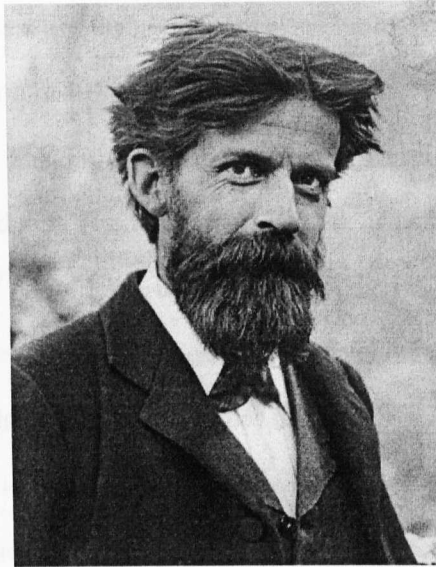


Fig. 2.8, P. Geddes⁶⁴

A prolific and polymath author, Geddes also endorsed an antireductionist approach to life sciences and, as the co-authored books with Thomson demonstrate,⁶⁵ (books like *Life: Outlines of General Biology*), Geddes argued against a mechanistic approach to biology.⁶⁶ After all, as Graham stresses in his short biographical sketch of E.S. Russell, it was Geddes who fostered Russell's interest in philosophical issues in biology. Indeed, all the philosophical books Russell published, Graham argues, are: "...corollaries of the main, essentially Geddesian, conclusion of *Form and Function*, that no appreciation of animals has been satisfactory that has rested content with analysis into parts, whether anatomical, physiological, or Pavlovian. The meaningful entity is the "frog", not its webbed feet, nor its reflex jumping, and studies will be fruitful when they end by considering the whole frog..."⁶⁷ Of course, Russell was a trained zoologist but also a skilled historian of science and, as we will see, he underpinned and justified his organismic approach with a learned and historical reconstruction of functional, organismal and antimechanist biology ever since Aristotle.⁶⁸ However, very probably, Thomson and Geddes were the first to convey such a philosophy to him.

⁶⁴ Source: <http://www.dundee.ac.uk/museum/exhibitions/naturesaccounts/nature1.htm>.

⁶⁵ See Kitchen, 1975.

⁶⁶ See Thomson and Geddes, 1904.

⁶⁷ Graham, 1954, p. 138.

⁶⁸ See chapter 4.

Woodger was the youngest of the group I am considering. He was born in Norfolk in 1894 and went to University College, London in 1911.⁶⁹ There he was trained by J. P. Hill (1873-1954), head of the zoology department at that time and Professor of Embryology. Hill⁷⁰ had been a student of J. Beard (1858-1923) in Edinburgh. Beard was Huxley's pupil and spent part of his training in Wurzburg and Freiburg studying embryology.⁷¹ After World War I, Woodger worked as assistant zoologist and comparative anatomist at University College London; however, the figure who most influenced and fostered Woodger's interests in the philosophical issues of biology was Hans Leo Przibram (1874-1944), during a term leave in 1926 in Vienna. Przibram had been a student of B. Hatschek (1854-1941) who, in turn, had been a pupil of R. Leuckart. After his graduation from the University of Vienna in 1899 and during his years of PhD study, Przibram bought the former Vienna Vivarium and converted it into a modern experimental laboratory – the Research Institute of Experimental Biology.⁷² A trained morphologist, Przibram started to work on animal regeneration and transplantation after his experiences in Naples and Roscoff. After 1903, with the help of Paul Kammerer (1880-1926) as assistant,⁷³ he organised his experimental laboratory as an international centre where students and scientists such as Woodger could spend time doing their researches:⁷⁴ a centre where the Kantian teachings were not forgotten because, as Cohen stresses: “Diverse as the Vivarium's scientists were in their experimental approaches and in their philosophical convictions, they converged in their search for a ‘third way’ between mechanical determinism and pure spontaneity, a framework that would do justice to the complex interactions between organism and environment.”⁷⁵ This was neither determinism nor vitalism, as Kant's bio-philosophy claimed, but a synthesis allowing a scientific study of life without reducing organisms to chemistry and physics. This was the environment in which Woodger worked and during his time in Vienna, he realised, as Floyd and Harris explain:

⁶⁹ See Gregg and Harris, 1964.

⁷⁰ See Watson, 1955, pp. 101-117.

⁷¹ See B. D. J. (1924) Dr. John Beard, *Nature*, NO. 2877, Vol. 114, p. 904.

⁷² See Cohen, 2006.

⁷³ See the classic Koestler, 1971.

⁷⁴ D'Arcy Thompson, Paul Weiss, Karl Frisch, Gregory Bateson and Eugen Steinach all worked there. The importance of this centre has been emphasised by Cohen, 2006.

⁷⁵ Cohen, 2006, p. 496.

...that there were fundamental unanalysed assumptions in the theories then in circulation amongst biologists and that his training had not equipped him, nor was likely to have equipped anyone else, to examine or identify these assumptions. On his return to England he threw himself into a study of philosophy, or those aspects of philosophy that were the necessary pre-requisite for an analysis of biological theory. Within two years he had completed the necessary spadework and had gone on to analyse the assumptions implicit in the biological antithesis between vitalism and mechanism, structure and function, preformation and epigenesis, for example, and the theory of explanation in biology.⁷⁶

Of course, all the figures I mention belonged to different generations and followed different trainings. However, as I shall show in the next chapters, they all shared a very similar conception of the organism and how the study of life should be carried out. They all had bequeathed, through diverse routes and ways, Kant's bio-philosophical tradition. However, they dealt with it in novel ways; they transformed and reshaped it in adapting Kantian and post-Kantian teachings to new contemporary needs, knowledge and discoveries. In fact, this Neo-Kantian tradition required a 'restyling', because problems and topics characterising the old traditions were slightly changed or restated under a different perceptive. If post-Kantian biologists had been deeply concerned with the problem of how a single cell can produce a complex multi-cellular whole, the new generation felt it more important to address the problems of heredity.

2.4: Kant in the New World

As a general rule, promising American zoologists in the last decades of the 19th century sought to spend some part of their overall training in Europe. Germany was certainly one of the most sought countries of the old continent; both for its celebrated figures and for its widely recognised scientific institutions. Germany in fact, was the country where many of the most exciting, advanced and innovative scientific

⁷⁶ See Gregg and Harris, 1964, p. 3.

discoveries were achieved.⁷⁷ It was the place where new research directions in biology were identified and pursued, and where new experimental methods and practices were established.⁷⁸ However, Germany was the country from which came some of the most controversial theories of the organism – its development, its functions, its morphology and its inheritance; some of the boldest views which raised deep discussions and created scientific divisions amongst the international learned community of the time. Darwinism and Lamarckism had easily triumphed, thanks to Haeckel's tireless campaign and the wide diffusion of his successful bestsellers evolutionary morphology thrived⁷⁹ and the *Entwicklungsmechanik's* program, first set by His and Roux in the second half of the 19th century, took form.⁸⁰ Finally, the mosaic theory of development advanced by Roux and Weismann, and Hans Driesch's hypothesis according to which the egg was a "harmonious equipotential system"⁸¹ reinforced the old debate between preformationists and epigenesists. In brief, at the end of the 19th century, German biology was full of debates, contrasting research programmes, diverse traditions and innovative ideas; all elements that made this country very attractive for young biologists trained elsewhere. Therefore, it is not surprising that American biologists, who had studied in the best institutions recently established in their country, regarded Europe, and in particular Germany, as the place to go if they wanted achieve great things. Indeed, it is not surprising that many leading American universities held very good relationships with German institutions: the American students had the opportunity, being also encouraged, to spend part of their formation abroad, gaining PhDs or doing particular researches in Germany or other German institutions such as the celebrated Naples Zoological Station in Italy.⁸²

However, over all of the widely recognised academic names and institutions, for some young promising American zoologists active in the second half of the 19th century, one figure clearly represented their hero in zoology; and this was neither Roux, His, Haeckel nor Gegenbaur or Weismann

⁷⁷ See Coleman, 1971.

⁷⁸ In the classic *Biology in the Nineteenth Century*, Coleman suggests: "The German universities were perhaps the most distinctive intellectual institutions of the nineteenth century. Their impact on all realms of learning was great and, on the sciences, not least among them medicine and biology, it was overwhelming. From Germany came new ideals and a legion of inventive, superbly trained men. By later decades of the century the German influence in biology was felt worldwide, from Russia to America, from Japan to Africa. German leadership in biology disappeared only after the double catastrophe of World War I and the Nazi purges of university and institute faculties and staff (Coleman, 1971, p. 4).

⁷⁹ See Kelly, 1981, and Nyhart, 1995.

⁸⁰ See Allen, 1975, Maienschein, 1991, 1994.

⁸¹ See Sander, 1991.

⁸² An institution directed by a student of Haeckel, Anton Dohrn. See Maienschein, 1985, Muller, 1996.

but a less familiar figure to us; the previously mentioned German zoologist Karl Georg Friedrich Rudolf Leuckart (1822-1898). Leuckart was a central figure in the academic German world — Nyhart ranks him as “The most important morphologist to work as a professor of zoology”, indeed “by the early 1860s, he had become one of zoology’s leading scientific lights; anyone who wanted a good introduction to state-of-the-art zoology went to Giessen to study with him”.⁸³ And yet:

Leuckart exerted a profound and yet underappreciated influence on zoology as it diversified into new sub-disciplines. Researches from around the world came to work to his lab. Together with his collaborators and more than 115 doctoral students he mentored in his long career, they assured that his research approach and his ideas continued to flourish well into the next century. All in all, Leuckart’s topics, interests, and functionalist approach to nature may be seen sprinkled through the works of his many students and co-workers.⁸⁴

Leuckart earned his degree in 1845 at Gottingen University working with the famous physiologist Rudolf Wagner.⁸⁵ In 1850 he was appointed associate professor at the University of Giessen and, from 1869 he moved to the University of Leipzig. In Leipzig, from 1880, he was able to organise a new zoological institute and establish a research program in which a sizable community of international students was involved; a community which eventually included figures such as the first future director of Woods Hole, and Chicago professor, Charles Otis Whitman (1842-1910), the future Harvard professor Edward Laurens Mark (1847-1946), the Harvard Medical School’s anatomist Charles Sedgwick Minot (1852-1914), and the Chicago physiologist Charles Manning Child (1869-1954).⁸⁶

⁸³ Nyhart, 1995, p. 96

⁸⁴ Nyhart & Lidgard, 2011, p. 7

⁸⁵ See unsigned “Rudolf Leuckart,” in *Nature*, 57 (1898), 542, and Blanchard, 1898.

⁸⁶ The Leuckart international community comprised, apart from Americans, students from England, France, Italy, Sweden, Russia, Switzerland, and Japan. See “Leuckart, Karl Georg Friedrich Rudolf” in [Encyclopedia.com](https://www.encyclopedia.com).



Fig. 2.9, K. G. F. R. Leuckart⁸⁷

Leuckart was a deep Kantian⁸⁸ and, although a converted evolutionist, he remained loyal to von Baer's teachings, with whom he remained on good terms until his death.⁸⁹ The attachment to von Baer is important because Leuckart, with Kant, von Baer and other embryologists in general, held that the unity of the organism was comprehensible only through the study of its development. Thus, as a prominent morphologist and, at the same time, physiologist and embryologist, Leuckart subscribed to all the Kantian tenets I have previously mentioned: to briefly recapitulate: 1) neither vitalism nor materialism would have been accepted, but a diverse form of 'mechanistic' (teleo-mechanist) explanation was required to comprehend organic phenomena. 2) Living organisation must be supposed and not reduced, 3) organic functions have priority over their structures, 4) the importance of the multiple relations of parts to the whole, and the whole to the parts, 5) the essential role of the environment for the organism's behaviour and form.

Leuckart first established his Kantian organicism in a monumental work written with the anatomist and physiologist Karl Bergmann and published in 1852: *Die anatomisch-physiologische Übersicht des Tierreichs*. In this work the authors adopted a physiological approach to the study of the

⁸⁷ Source: <http://clendening.kumc.edu/dc/pc/l.html>.

⁸⁸ Apart from Lenoir 1982, see in particular L. K. Nyhart & S. Lidgard, 2011.

⁸⁹ As the letters Leuckart exchanged with von Baer and that Lenoir quotes attest.

animal form.⁹⁰ Indeed, drawing directly on the works of the philosopher Hermann Lotze and the chemist Justus von Liebig, as well as on Kantian teleology, they forged a synthesis in which mechanical and teleological explanations in the life sciences could find a profitable relationship. Organisms had to be conceived as material entities though their understanding required, at the end of their investigation, a teleological framework. The functional morphology Leuckart set out was quite successful. Ever since the publication of his *Über die Morphologie und Verwandtschaftsverhältnisse der wirbellosen* (On the morphology and conditions of relationship of the invertebrates) in 1848, he had defined morphology as the science that would find a middle way between the embryological approach of von Baer and the teleological and functional approach of Cuvier.⁹¹ And this definition certainly did not die with Leuckart.

Although interested in theoretical and philosophical issues surrounding life science, Leuckart spent the last years of his career studying parasitic worms. He is indeed nowadays mostly celebrated as parasitologist rather than zoologist or physiologist. However, his intellectual legacy cannot be overlooked; especially regarding his influence on the students he trained. As Nyhart rightly reports “Leuckart continued to defend the language of purpose as useful heuristic, and his students did the same”⁹², in fact, as we will see in the next sections and chapters, some of his American students remembered Leuckart’s lessons well. Indeed, we can easily track the conceptual chain through which Leuckart’s biology was directly or indirectly diffused in USA. Firstly, Whitman went to Leipzig in 1875, to study for his PhD with Leuckart.⁹³ After a brief experience in Japan, Whitman returned home and became one of the relevant defenders of organismic biology in the US (as we shall see later on). In 1892 he was appointed professor at the Zoological Museum of the University of Chicago and there he mentored Frank R. Lillie and hired Charles M. Child.

Frank Lillie became a staunch collaborator of Whitman both at the University of Chicago and at the newly founded Woods Hole. Starting as assistant director there, from 1908 Lillie replaced Whitman as director at Woods Hole. As I will show in chapter 5, Lillie acquired Leuckart’s lessons through Whitman’s important influence. Charles Manning Child instead, went directly to Leipzig in 1892. In

⁹⁰ For a detailed discussion of functional morphology in Germany, see Lenoir, 1982, pp. 157-194.

⁹¹ See Lenoir, p. 217, 1982.

⁹² Nyhart, 1995, p. 340.

⁹³ Morse, 1912.

1894, after concluding his PhD, he spent a semester at the Naples Zoological Station (another German Institution) and, in 1895, he was hired by Whitman as Zoological assistant at the Zoological Museum of Chicago. Hence, not only had Child directly absorbed Leuckart's teaching in Leipzig, he also was in contact with someone who had studied with Leuckart and disseminated his agenda in the US. The zoologist Edward Laurens Mark (1847-1946) had been a pupil of Leuckart in Leipzig and in 1877 he was hired by Agassiz at Harvard's Museum of Natural History. As Winsor remarks: "Mark, with his new PhD from the University of Leipzig under his arm, was determined to bring back home the latest techniques in cytology and the high standards he had learned in Rudolf Leuckart's laboratory."⁹⁴ William Emerson Ritter (1856-1944), a central figure in my story⁹⁵, was a pupil of Mark at Harvard. After concluding his PhD in 1894, he sailed to Europe where he worked at the Naples Zoological Station and then at Berlin University. In Naples Ritter befriended Child, with whom he remained in contact for the rest of his life. In short, Ritter, as the all other figures I mention, worked with someone who was directly acquainted with Leuckart's biology.

Ernest Everett Just was a younger American organicist who I will consider in my work. He was awarded his PhD at the University of Chicago in 1916 under Lillie. During his stay in Chicago he also attended Child's lectures in physiology. However, in 1928, Just went to Europe, to work at the Naples Zoological Station, at Kaiser-Wilhelm-Institut für Biologie of Berlin (today Max Planck institute, relocated to Tübingen in 1945) and finally, at the French Marine Laboratory in Roscoff (a Delage's feud). His experience in Europe was a determining factor in his bio-philosophical formation; as both Manning's excellent biography and Just's 1939 book attest.⁹⁶ Thus, thanks to Leuckart and his international laboratory in Leipzig, the Kant's bio-philosophical tradition thrived in the US. It was never forgotten, as Lenoir argues, but rather transformed and adapted to another context. This American group of neo-Kantians, people such as Child, Ritter, Lillie and Just, aimed for an organismic version of biology characterised by a strong anti-reductionist approach; an approach that clashed with the newly emerging theories of heredity.

⁹⁴ Winsor, 1991p. 174.

⁹⁵ See Chapter 6.

⁹⁶ See Chapter 5.

2.5: Conclusion: New Wine in Old Bottles

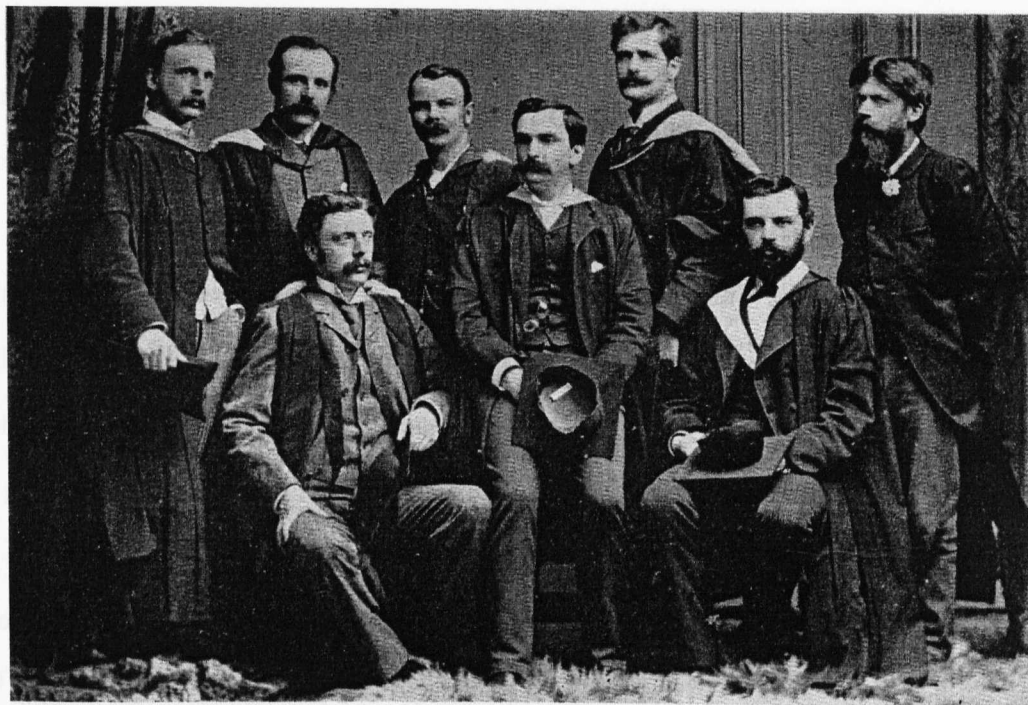
In this chapter I have shown that Kant's bio-philosophy neither died with the German Romantic naturalists and philosophers, nor was it extinguished with Leuckart in Leipzig, but that it thrived through different routes and ways both in the UK and the US. Of course, Kant's tradition as understood or accepted by Muller and Leuckart in the 19th century was not the same as that of Ritter or Russell, Just or Woodger in the 20th. New challenges, discoveries and issues would necessarily impact upon such an old theoretical framework. However, the general questions remained; my five points continued to be discussed and considered as controversial themes. Therefore, although after the *Naturphilosophen* and the Romantics, Kant's strategy of reason was transformed into an ontological stance, although the issue of heredity acquired an increasingly importance, and although the relation of parts to the whole was then reframed as relations in a complex system-hierarchy, the way of thinking about biological problems remained profoundly Kantian; it characterised what, in the 20th century Morton Beckner dubbed "The Biological Way of Thought."⁹⁷ In the next chapters I will consider some 20th century figures who shared that way of thinking; however, even though I have defined this group of thinkers as "neo-Kantian biologists", with the term "neo-Kantian bio-philosophical tradition" I intend neither a well-defined generation of scientists nor a circle of individuals sharing the same training, coming from the same universities or laboratories, or heirs of one unique school of thought.⁹⁸ Instead, with such a label, I embrace all those individuals discussing the mentioned five points, sharing a similar theoretical universe, engaging with each other's work, and proposing an alternative view on heredity based in their organismic convictions. In fact, I am totally conscious that between Russell and Woodger or between Child and Just there was a quite extended generational gap; however, I will show that, although they belonged to different academic worlds and contexts, they all shared methods, approaches to science and, especially, a way of thinking particular issues: to them for example, as I emphasised in the previous chapter, biology had to be thought of as an independent science with its own rules, goals, and objects. Yet, they not only

⁹⁷ See Beckner, 1959.

⁹⁸ Although the majority of the figures I'm considering shared part of their career in the same universities: Haldane, D'Arcy Thompson and Geddes worked at University College of Dundee, Thomson and Russell at the University of Aberdeen, Woodger at University College London. Finally, Whitman, Child, Lillie, and Just were at the University of Chicago. Almost all had received a direct training in Germany or in German institutions.

shared the five points, they also understood the notion of heredity is a very particular way. In fact, for all of these ‘neo-Kantians’, heredity — to use an analogy — was the term replacing Wolff’s *vis essentialis*, Blumenbach’s *Bildungstrieb*, von Baer’s *Trieb* or Muller’s vital force, or any un-analysable and irreducible cause supposed to lie behind living organisation. In other words, heredity came to be represented as the material *quid* explaining for the origin of living organisation, as well as its persistence and its continuity through generations. It is for precisely this reason that, to them, the central question to pose for any science of heredity based on organismic principles was not about the ratio-distribution of visible characters transmitted generation over generation but about the fact that individuals persist and insist on forming the same complex functional structures. As Just clearly and ironically said, the mystery of heredity was not solved by counting the bristles on *Drosophila*’s back, or the transmission of its eye pigment, but by understanding how the embryo forms its back and its eyes. This is what I consider a neo-Kantian or organismic conception of heredity; a forgotten conception I am here trying to reconstruct.

3.0: Neo-Kantian Bio-Philosophical Tradition in UK: Haldane's and D'Arcy Thompson's Debates



IV. The staff of University College, Dundee, 1887

Fig. 3.1, Haldane and D'Arcy Thompson in the first and second row on the left, P. Geddes on the extreme right¹.

3.1: J. S. Haldane and D'Arcy Thompson's Lifelong Critical Debate

John (Haldane) is an extraordinary man. He has a knack of approaching every subject in the spirit of the consulting physician, that whatever the other fellow thinks or says may be presumed to be wrong. This has grown on him, till nowadays he seems to have convinced himself that neither physicists nor physiologists know anything about their subject: — and who am I that I should think otherwise...whatever faults or eccentricities he may have, John is a very good fellow indeed, who wouldn't do an ill turn to anybody; on the contrary, he is almost quixotically anxious to do good to all mankind, — and to teach them all a thing or two.²

D'Arcy Thompson

¹ Source Thompson, 1958, p. 56.

²D'Arcy Thompson, draft of a letter from Thompson to his brother, 11/12/1928, quoted in Goodman, 2007, p. 363.

As we have seen in the first chapter, when J. S. Haldane delivered his paper at the History of Science Congress in 1931, he was recognised as one of the leading physiologists in England and the whole Western world. Born in Edinburgh in 1860, exactly one day after D'Arcy Thompson's birth, like him, Haldane studied medicine at the University of Edinburgh and, like many biologists of his generation, spent part of his training in Germany; in particular in Jena, where he attended the lectures of J. W. Dobereiner, J. Loder, E. Haeckel, and the famous botanist E. Strasburger.³ Throughout his life, he was a staunch supporter of German biology and philosophy as well as being very critical of the British university system. He loved and praised Goethe's philosophy and science, and acquired a deep knowledge of Kant's critical philosophy.⁴ In his first publication, an article written together with his brother Robert,⁵ Kant's bio-philosophy dominated. One of the venerable conclusions of this early work is striking and demonstrates the overwhelming pervasiveness of Kantian philosophy and its wide diffusion:

For Kant then, the relation of reciprocity, as the most concrete of the categories, is the highest relation of reality... The fact is that every part of the organism must be conceived as actually or potentially acting on and being acted on by the other parts of the environment, so as to form with them a self-conserving system. There is nothing short of this implied in saying that the parts of the organism can adapt themselves to one another and to the surroundings.⁶

Philosophical speculations would always be an essential part of Haldane's scientific career; even in the most technical and specialist books and papers. Indeed, as we will see later, the organismic approach he supported informed all of his physiological results and experiments.

³ As Goodman reports, Haldane was highly enthusiastic about his German training. As he wrote in a letter to his Edinburgh professors: "These German universities are infinitely ahead of us...a student there has, as a rule, the chance, if he likes to use it, of coming into real contact with men who are making the scientific history of their time" see M. Goodman, 2007, p. 67.

⁴ As Goodman pointed out: "A century had passed, but Haldane now found himself in both the intellectual and physical space of Goethe". See p. 65.

⁵ Robert Haldane was mainly a philosopher. He too was trained in Germany and became the first translator of, and expert in, Schopenhauer's philosophy in Britain. See Richard and Andrew Seth, 1883.

⁶ See Haldane and Haldane, 1883 pp. 45 and 55. As they continue: "It would thus appear that parts of an organism cannot be considered simply as so many independent units, which happen to be aggregated in a system in which each determines the other. It is on the contrary the essential feature of each part that it is a member of an ideal whole, which can only be defined by saying that it realizes itself in its parts, and that the parts are only what they are in so far as they realize it", Haldane and Haldane, p. 56.

In 1884, invited by D'Arcy Thompson, Haldane moved to the University of Dundee. They had been close friends from a young age, when they founded a naturalist club called 'Eureka'; a club including amongst its twelve members, not only Haldane and Thompson, but also William Abbot Herdman (1858-1924), who would become a reputed marine zoologist and oceanographer at the University of Liverpool.⁷ As Thompson's daughter recalls, all together, they used to spend every Saturday in: "...botanising through the countryside, howking fossils in quarry and railway-cutting, grubbing in the rock-pools at Wardie, or searching the jetsam of Newhaven fishing boats."⁸ When Haldane arrived in Dundee, Thompson held a chair as Professor of Biology there and was actively involved in research regarding hygienic and material conditions affecting the local population. Indeed, together with Haldane, Thompson organised a small laboratory to study the pathological living conditions in Dundee's slums; by then, Haldane and Thompson, with a policeman as guide, wandered in the night through local slums gathering information and experimental data in order to assess the quality of air breathed in the overcrowded and undersized houses occupied by poor people.⁹ These experiences shaped Haldane's future interest and expertise in the physiology of respiration as well as his lifelong concern for working class conditions.¹⁰ Haldane tried to always match his philosophical and theoretical interests with concrete and practical science; a science aimed at improving both the life and working conditions of the most disadvantaged people.

Even though Haldane quite soon moved to Oxford — after spending a few months at the University of Berlin's Pathological Institute, attending the lectures of Bois-Raymond — his friendship with Thompson continued. In fact, although interested in very different topics and having diverse opinions about life sciences and methods of investigation, they shared common views on what biology

⁷ In 1893, Herdman would welcome in his Liverpool department a young American biologist, William Emerson Ritter, during his first trip in Europe. See B. R. N. Rudmose 'Sir William Abbott Herdman' (1858-1924) in *Dictionary of National Biography* 1922-1930, pp. 415-6. See also Chapter 5 of this thesis.

⁸ Thompson, 1958, p. 25.

⁹ Haldane built a device through which external air passed and deposited microscopic germs in a jelly substance that worked as substrate for the growth of microbial colonies so that, once back in the lab, he could study and see the level of pollution and air contamination breathed by dwellers. See R. D'Arcy Thompson, 1958, As Goodman also points out: "Haldane walked the slums with Wentworth Thomson and the new Professor of Chemistry, Thomas Carnelley. It was easy to feel pity and disgust for the living conditions of the slums. The new breed of scientists looked around and saw beyond that. These slums were a laboratory in which to investigate the human conditions and instigate improvements in public health". In M. Goodman, 2007, p. 83.

¹⁰ As J. B. S. recalls of his father: "His experience of the Dundee slums may not have made him a radical but it kept him one. He was a strong supporter of national insurance, old age pensions, and the like, and had little patience with statements by the rich that the poor were really well off, or could be if they tried", quoted in Goodman, 2007, p. 85.

should be. After all, Thompson had been a pupil of Balfour in Cambridge and therefore had had an embryological formation. During his Cambridge years he had become a friend of both Whitehead and Sherrington¹¹ and, once in Dundee, he worked together with Geddes. Yet, like Haldane, he was a deep admirer of General Smuts' work¹² and, also like Haldane, he loved German biology¹³ as well as philosophical speculations. For example, in 1884, Thompson published a short article in *Mind*, discussing Haldane's philosophical interpretation of animal regenerative phenomena.¹⁴ Haldane, Thompson observed:

...makes use of the phenomena of regeneration of lost parts in contending that we must sublimate our view of the nature of life from a mechanical or cause-and-effect category to a category of reciprocity, and from that further to one in which the parts must be regarded as determined in relation to an idea of the whole; in other words that organic processes cannot be reduced to series of causes and effects, or to what is the same thing, matter acting as a vehicle of energy.¹⁵

After a list of regenerative phenomena (beginning with Trembley's Hydra), Thompson concluded that, even though, in the process of animal regeneration, the cells seemed to follow a specific "custom" or "habit" acquired during the organism's phylogeny, and even though some mechanistic explanations were possible, Haldane was right in arguing that the whole played an essential role in shaping the parts during regeneration:

For though we bring in with some show of proof the hypothesis of old habit to account for the cells dividing in such a manner as to reproduce the newt's lost limb, yet something further is needed to

¹¹ The first, as is well known, a philosopher who would eventually be a determining figure in the development of organismal biology, not only in England, but elsewhere too. The second would become a famous neurophysiologist and pathologist, sympathetic to organismal biology too. Sherrington was awarded the Nobel Prize in 1932 for his work in physiology (see F. C. Rose, 2002, *Twentieth Century Neurology: The British Contribution*, Imperial College Press, London).

¹² As his daughter recalls. See R. D'Arcy Thompson, 1958, p. 194-195.

¹³ At a very early age, D'Arcy Thompson translated into English Hermann Muller's *Fertilization of Flowers*, with an introduction by Charles Darwin. See H. Muller, 1883, *The Fertilization of Flowers*, translated and edited by D'Arcy W. Thompson, with a preface of Charles Darwin, MacMillan, London.

¹⁴ In this piece, Thompson was answering an article that Haldane had published a few months earlier in *Mind*. See J. S. Haldane, 1884.

¹⁵ D'Arcy Thompson, 1884, p. 419.

account for its accurate regeneration when the line of section is oblique or irregular. We cannot but see that the procedure of each cell is regulated and conditioned by the needs of all the rest. Whatever histological or protoplasmic continuity there may be between cell and cell, we may dimly fancy some system of forces interconnecting them, which dynamical system may be again reciprocally influenced by the conditions of the outer world.¹⁶

In sum, even though some hereditary tendencies could mechanically explain the re-formation of lost parts (as Weismann had argued), there were phenomena where the influence of the whole organism was required to explain particular cellular arrangements and behaviours.

Many years later, in 1918, both friends participated in a symposium held at the Aristotelian Society in London; the theme was very philosophical: 'Are Physical, Biological and Psychological Categories Irreducible?'¹⁷ The debate was introduced by Haldane himself, who quickly dismissed the hypothesis according to which biological categories could be reduced to physical ones; indeed, as he argued:

...it is only through the central working hypothesis or category of life that we can bring unity and intelligibility into the group of phenomena with which biology deals; and it is because the biological working hypothesis is for the present absent in our ordinary conceptions of physical and chemical phenomena that we must treat physical and biological categories as radically different. The popular and completely natural distinction between the living and non-living is thus wholly justified on the ground that biological observations cannot be expressed or described in terms of ordinary physical working hypotheses.¹⁸

For Haldane, just as biological categories (or working hypotheses as he called them) could not be reduced to physical categories, so psychological categories could never be reduced to biological ones: all three sciences required different theoretical frameworks insofar as they dealt with different phenomena. As

¹⁶ Ibid., p. 420.

¹⁷ See also W. H. Sheldon's review of the meeting in *The Journal of Philosophy, Psychology and Scientific Methods*, Vol. 16, No. 19, pp. 523-529.

¹⁸ Symposium: Are Physical, Biological and Psychological Categories Irreducible?, Authors: J. S. Haldane, D'Arcy W. Thompson, P. C. Mitchell, L. T. Hobhouse, *Proceeding of the Aristotelian Society: Supplementary Volumes*, Vol. 1, Life and Finite Individuality (1918), p. 22.

Haldane would eventually argue several years later, at the 1931 History of Science Congress in London, life exhibits a unity of diverse irreducible characteristics; organic composition, structure, environment and process, all pointing towards one individual entity we call the 'living organism'. Any kind of mechanist or physical analogy fails, concluded Haldane, in grasping such a dynamic unity. Furthermore, the psychological world is a subjective world; it is the world of consciousness and, as such, it requires its own categories. Indeed, conscious perception of an object was always determined or shaped by other objects of consciousness in the past and potential future: "A psychological object is thus in dynamic relation with other objects surrounding it, not merely in space, but also in time. It has therefore an element of timelessness, inasmuch as it is in direct relation not only with present, but also with future and past objects."¹⁹ In sum, any physiological reaction of a conscious organism in its environment was not solely determined by physical and biological objects; there were also subjective elements affecting possible response-reactions.

In D'Arcy Thompson's reply, there were some apparent points of disagreement. Firstly, Thompson carefully reported and synthesised Haldane's position, then he declared that psychology should be kept outside the discussion because: "that matter and mind are incommensurables seems to my judgment so obvious that it needs no argument and risks no serious denial...I must leave it at that, and be content to state rather than to defend my dualistic attitude."²⁰ However, things were different concerning physics and biology. Indeed, Thompson argued, there was not a necessary incommensurability between the two; both the physicist's concepts and methods were of fundamental importance for biologists; organisms, after all, were plainly part of the physical world and subject to physical and material forces: "I know that change and form in a concrete material body involves the movements of matter, and the movements of matter are to be symbolically ascribed to the action of force, and actually to the transference of energy. The body consists of matter; it is set in a material world; it has its store of energy within, it has its share in the great store of energy without."²¹ However, Thompson did not support physical reductionism; what he was arguing was that, even though organisms were mechanisms and could be described or understood in mechanical terms, they were nonetheless mechanisms of a very special

¹⁹ Haldane, 1918, p. 23.

²⁰ D'Arcy Thompson, 1918, p.30.

²¹ Ibid, p. 48.

kind.²² Biological categories could include mechanical analogies, but not in the ordinary sense as, for instance, Cartesian tradition intended. In fact, the meaning of ‘mechanism’ itself was in constant change.²³ In addition, Thompson regarded the whole of nature as a ‘glorious’ living mechanism and dismissed the idea that a neat and definite separation between inorganic and organic world subsisted. As he put it, quite poetically:

The earth itself and the sea, the earth with her slowly changing face, and the sea multitudinous with all its tides and currents and great and little waves, constitutes a mechanism; the heavens themselves, the sun and the moon and all little stars, are a glorious mechanism. The whole material aspect of the universe is a mechanism; we know not how it has its being, but we know that it lives and moves obedient to everlasting laws.²⁴

In sum, Thompson defined himself a mechanist without being a mere materialist and convinced reductionist.²⁵

Haldane replied to Thompson and totally agreed with him: “I fully accept Professor Thompson’s suggestion that it is only the ‘ordinary’ working hypothesis of physics and chemistry that seem to me inadequate in biology. Recent developments of experimental physics and chemistry are profoundly changing these conceptions, and, as it seems to me, tending to bring physics and chemistry not only much closer to one another, but also much closer to biology. Here, then, our differences seem to disappear.”²⁶ In sum, at the end of the debate Haldane synthesized all interventions and concluded that biological

²² As he would say in his *Growth and Form*: “even the warm-blooded animal is not in reality a heat-engine; working as it does at almost constant temperatures its output of energy is bound, by the principle of Carnot, to be small. Nor is it an electrostatic machine, nor yet an electrodynamic one. It is a mechanism in which chemical energy turns into surface-energy, and working hand in hand, the two are transformed into mechanical energy, by steps which are for the most part unknown” (Thompson, 1942, p. 464).

²³ As Thompson explained: “For mechanism is not a stationary concept but a growing one, what it meant to Aristotle is not what it means to us. Chemistry has opened our eyes, and electricity (for instance) has strained them to keep the nature and significance of a ‘mechanism’ in view”, Thompson, 1918, p. 46.

²⁴ Thompson, 1918, p. 52.

²⁵ As he added: “the physicist is, *ipso facto*, a mechanist, but he is not by implication a materialist; nor is the biologist of necessity a materialist, even though he may study nothing but mechanism in the material fabric and the bodily activities of the organism” Thompson, 1918, p. 54. Moreover, Thompson’s stance had striking similarities to, and connections with, Whitehead’s philosophy of the organism; See Emmet, 1932.

²⁶ Haldane, 1918, p. 73.

categories were not becoming closer to physical ones, but, contrarily, physical categories were getting more and more biological.

The discussion between Haldane and Thompson about the nature of life phenomena continued; in fact, Thompson read and commented on Haldane's work, eventually writing critical and accurate reviews of his books. For example, in 1919, Thompson wrote a review in *Mind* about the controversial, new work Haldane had just published: *The New Physiology*. Thompson acknowledged the radical potential of the book: "...Dr. Haldane is in revolt with much more than the tenets and the methods of the modern biology; it is a larger philosophy that he has mind, and his challenge is to the world".²⁷ Although he accepted Haldane's teleological approach to medicine and biology, and his practical recommendations to physiological practices (in fact, in medicine, as much as in all phenomena of life, the Aristotelian Τέλος — the final cause — seems sometimes to be an inescapable principle to which any investigator must succumb) Thompson felt that Haldane's position was too strong; rejecting all physico-chemical approaches purely because they could not give a comprehensive understanding of all living phenomena betrayed, Thompson complained, Haldane's impatience. Even though Thompson felt himself heretic regarding some biological theories, such as cell-theory, he maintained that the quest for mechanical causation remained still open, even though it could not be universally applicable.²⁸

The discussion on mechanism and other possible alternatives in biology continued, in England and elsewhere. Ten years later, in 1929, both men, now old, participated at the British Association conference in South Africa. Haldane participated as lead speaker in a session titled "The Nature of Life."²⁹ Both Haldane and Thompson, together with other speakers and many participants, discussed with the notorious Cape Town host, Jan Christiaan Smuts, who, three years later, published a rather controversial and provocative book: *Holism and Evolution*.

²⁷ Thompson, 1919, p. 361.

²⁸ As Thompson argued: "In some things biological I also am inclined to be heretic, and certain of my doubts might alarm and horrify Dr. Haldane himself. He seems to me to have no doubts whatever as to (for instance) the 'cell-theory', or the main principles thereof; it is, indeed, the very fact the cell-theory renders a 'mechanical explanation' of the whole organism so superlatively complex that seems to me to form one of Dr. Haldane's chief arguments for rejecting the mechanical concept" (Thompson, 1919, p. 362).

²⁹ See British Association for the Advancement of Science, Report of the Ninety-Seventh Meeting, South Africa, 1929, July 22- August 3. Office of the British Association, Burlington House, London, 1930. As Thompson's daughter, Ruth, reports: "This meeting was packed to the doors and many people were turned away." (Thompson, 1958, p. 194).

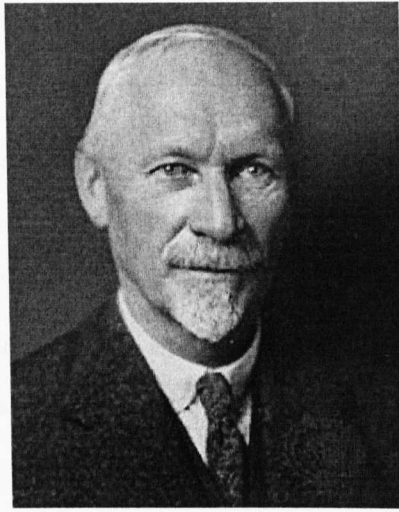


Fig. 3.2, J. C. Smuts (1870-1950)³⁰

The meeting was, in fact, a joint session of physiology, botany and zoology³¹; Smuts opened the debate with his new, holist hypothesis of life and evolution as opposed to mechanist approaches in biology.³² L. Hogben played the devil's advocate, strongly arguing for reductionism and mechanism in biology.³³ Unfortunately, we have no clue about Thompson's contributions to the South African session; we only know that organismal or holist interpretations of living phenomena were always at the centre of his interests.

³⁰ Source: Library of Congress, Prints and Photographs Division, Bain Collection - Reproduction number: LC-DIG-ggbain-21150 (digital file from original negative).

³¹ As Goodman describes the relationship between Smuts and Haldane: "Haldane met many times with Jan Smuts and his wife Isie, getting along famously. When Smuts visited Oxford later that year for a series of sell-out lectures at the Sheldonian, Haldane gave him guidance as to how to handle English audiences. Such was Smuts's charm that he managed to bring Kathleen into his and Haldane's holistic way of thinking", Goodman, 2007, p. 365. Yet, D'Arcy Thompson's daughter, Ruth, records that his father met Smuts in South Africa the first time but, she adds, Smuts was a scholar: "...he had always greatly admired". R. W. Thompson, 1958, p. 194.

³² See Goodman, 2007, p. 366. A few years later Haldane recalls that: "In his Presidential Address to the British Association (1931) he gave (Smuts) a summary of his reasoning, and particularly of its relations to the interpretation of evolution, which he regards as the unfolding of holistic reality in what had commonly been regarded as purely mechanic universe"(Haldane, 1935, pp. 40-41).

³³ As Haldane remarked two year later in reviewing one of Hogben's books: *The Nature of Living Matter* (1930). See Haldane, 1931, p. 133.

3.2: J. S. Haldane: A Post-Kantian Physiologist and Philosopher

...whether Dr. Haldane would countenance the word ‘design’ or not, he certainly maintains, not as mere working hypothesis but as an essential criterion of biology, a teleological principle in physiology, by virtue of which ‘regulation’ is effected, a ‘normal state’ is maintained — and all goes well...in short, the Aristotelian Τέλος dominates the situation. A certain result, not only the maintenance of ‘life’, but the maintenance of a ‘normal’ condition, has got to be attained; it is the Τέλος, the ‘final cause’, and attained it is”.³⁴

D’Arcy Thompson



Fig. 3.3, J. S. Haldane (ca. 1900)³⁵

As the introduction to his 1935 *Philosophy of a Biologist* demonstrates, Haldane had always seen himself as a pupil of Kant and a well acquainted interpret of the British post-Kantian philosophical tradition. Yet, as we have seen, Haldane returned to study in Germany several times, and he had an enthusiastic and expert Germanophile in his own family. His older brother, Richard Haldane, had studied in Gottingen with R. L. Lotze and, years later, would publish the first British translation of a book by one of the most

³⁴ D’Arcy Thompson, 1919, p. 360.

³⁵ Source: <http://www.coheadquarters.com/figjhaldane.htm>.

controversial of Kant's scholars: Schopenhauer's *World as Will and Representation*³⁶. In sum, it would be no exaggeration to say that the young John Haldane 'breathed' German science and philosophy within his family and in the intellectual context in which he lived; therefore, it is not surprising that his science would be influenced accordingly.

In fact, one year after he had published the article with his brother, Haldane, now 24 years old, published a new paper in which he denounced the general tendency of physiology to reduce all organic processes to a well-defined series of causes and effects.³⁷ Such an approach, Haldane argued, rested on the false analogy of the organism seen as a machine like, for example, a steam-engine. However, even the simplest organism, such as the common earthworm, showed 'purposive' behaviour which could never be reduced to a machine behaviour; Darwin, Haldane continued, had clearly showed that earthworms act in an intelligent and unexpected ways because they are able to adapt their actions to unusual circumstances.³⁸ Not only do earthworms exhibit purpose but the regeneration of tissues and limbs in many animals, especially lower forms, demonstrates an elastic and purposive action of the whole organism on its parts so that: "purposive behaviour displayed in the attainment by organisms of such ends as the reproduction of a newt's limb, or the stopping up of an earthworm's burrow, cannot be due to the mere action of neuromuscular or intracellular mechanism."³⁹ In sum, the young Haldane added, both the behaviour of the organism and other phenomena related to reproduction, development and regeneration, show that the category of cause and effect, as an instance of a misplaced mechanical analogy, could never be applied to the study of life phenomena, because, as Kant had taught and Haldane followed, organisms must be seen as systems in which the parts: "...are determined , not only as regards their

³⁶ A. Schopenhauer, *The World As Will and Idea*, 3 vols. transl. R. B. Haldane and J. Kemp, London: Routledge & Kegan Paul, 1883-1886.

³⁷ J. S. Haldane, 1884, pp. 27-47.

³⁸ Darwin in *The formation of vegetable mold, through the action of worms* (1881), had studied, among other things, the behavior of earthworms. In particular, he had observed that earthworms usually close their burrows with leaves and other appropriate materials they find in their environment. According to Darwin, the fact that earthworms possessed the ability to drag the appropriate materials as the means to close their burrows, even in different and unexpected circumstances, demonstrated a degree of intelligence: "To sum up, as chance does not determine the manner in which objects are drawn in to the burrows, and as the existence of specialized instincts for each particular case cannot be admitted, the first and most natural supposition is that the worms try all methods until they at least succeed; but many appearances are opposed to such a supposition. One alternative alone is left, namely that worms, although standing low in the scale of organization, possess some degree of intelligence" (Darwin, 1881, p. 98). Haldane interpreted these observations as 'purposive' behavior that, as such, could never be reduced to the behavior of a machine.

³⁹ Haldane, 1884, p. 31.

reciprocal action on one another, but, also as regards what is inherent in the part themselves of a system whose parts reciprocally determine one another.”⁴⁰ The right category for studying organisms — as Haldane had argued with his brother one year before, drawing on Kant — is that of ‘reciprocity’, in which the organism is built and works not through a web of consequential causes and effects, but through a system of “reciprocal determinations”.⁴¹ Haldane concluded with an example taken from one of his favourite disciplines — a discipline that would occupy him for the rest of his life: physiology. In fact, the well-known physiological phenomenon of reflex action,⁴² and the hypertrophy of muscular organs (and other kinds) when corresponding organs are disrupted by injury or inflammation, all show that a mechanistic approach fails in explaining these phenomena, and physiologists, like biologists, require an ‘organismic’ approach to life phenomena.⁴³

In the following years, Haldane’s commitment to these points is striking; even before the successes of mechanist and reductionist explanations, he would state, over and over again, that the analogy of the machine is fundamentally wrong as applied to the organism. In fact, his program becomes more and more Kantian, although acquiring a more original and personal direction; from a well-circumscribed critique of mechanist and reductionist biology, Haldane began to conceive a broad ‘organismic’ agenda which included not only biology and physiology, but medicine, psychology and even politics. When, in 1913, Haldane was a well-established international physiologist working in Oxford, he

⁴⁰ *Ibid.*, p. 35.

⁴¹ “There is, then, not merely a reciprocal determination of one another by the parts as subordinate independent wholes; but this reciprocal determination extends right through the parts. That is to say, what appeared to belong to the parts independently of their relation to the whole, for instance their size, shape, and structure, is really only the manifestation in the parts of the influence of the whole”. Haldane, 1884, p. 37.

⁴² Haldane reports an experiment in which a frog’s spinal cord had been severed from the brain. When an irritating substance was applied to the skin of the frog’s limb, the limb tried to get rid of such a substance. If the leg was blocked, the other leg tried to get rid of the irritating substance on the first leg. This demonstrated, Haldane argued, that there was not a direct relation between the stimulus and response happening between brain, spinal cord and skin receptors and that a mechanist viewpoint as applied to that problem was too simplistic in approaching a far more complex phenomenon.

⁴³ For Haldane, this biological viewpoint had particular importance for medicine too. Indeed, for him, curing a disease meant restoring a natural equilibrium in the body-system, as Hippocrates had taught; in other words, the drugs and therapies that the physician prescribes to the patient should have no “action” but therapeutical “function”, they should merely help the organism to restore its previous state. In his own words: “...it is clearly impossible to replace artificially the exquisitely delicate tissues which are destroyed or injured by disease. But experience shows that remedies actually do most materially assist in the process of restoration of the function of a part of the body that has been injured or destroyed. For instance, when a valve of the heart has been injured by inflammation, and the circulation thus becomes inefficient, digitalis can be given, not merely in order to palliate the disease, but with the hope that a relative cure may follow. The digitalis causes the heart to contract powerfully, so as to overcome the obstruction to the circulation and this keeps the patient in health”. Haldane, 1884, p. 43. This position would be essential for Haldane in developing the appropriate treatments for soldiers affected by poisonous gases during the First World War.

published one of his first great syntheses: *Mechanism, Life and Personality*. The book was a result of four lectures delivered at the Physiological Laboratory of Guy's Hospital in London, in May of the same year. In these lectures Haldane developed all the tenets characterising Kant's bio-philosophical tradition: denial of both vitalism and mechanism, the acceptance of living organisation as a postulate, the use of teleological explanations, the prominence of function upon structure, the essential organic relationship between parts and whole, and the fundamental interrelation between organism and environment. In particular, regarding physiology, Haldane drew on J. Muller and his "famous" old text-book; indeed, Muller was considered by him one of the great heroes of physiology and developmental biology.⁴⁴ Also, he introduced one of his most recurrent themes characterising his holist view of life: physiology of respiration. Respiration in fact, demonstrated the intricacy and interconnection of many different factors involved at the same time (I will discuss this in the next section). Then, once he had established his general organismic framework, Haldane criticised Weismann's theory of heredity and development, considered: "...little more than empty words".⁴⁵ Finally, he concluded with a fairly long discussion of Kant and his transcendental theory of experience, and started framing his own, original Schopenhauerian philosophy of the individual and personality.⁴⁶ He argued, among other things, that our world of experience is, first and foremost, a world of personality; namely, a world where man is considered primarily as a person: "...in conscious relation through perception and volition to his environment."⁴⁷ For

⁴⁴ As Haldane wrote: "Muller had himself taken a prominent part in disproving by his microscopical observations on glands the mechanistic theories previously prevailing with regard to secretion, and his numerous observations on growth and development had led him in the same direction." Haldane, 1913, p. 42. Yet, as he stated in the preface of the first edition of his large 1935 monograph *Respiration*, in relation to the work of Muller and other old physiologists: "My treatment of the subject may possibly be looked on askance in some quarters as reactionary; for I have been largely influenced by the ideas and work of older physiologists. If, however, I have gone backwards, it is only to pick up clues which had been temporarily lost; and all these clues lead forward – forward to a new physiology which embodies what was really implicit in the old". Haldane, 1935, p. x.

⁴⁵ Haldane went on for few pages in criticising Weismann: "The mechanistic theory of heredity is not merely unproven, it is impossible, it involves such absurdities that no intelligent person who has thoroughly realized its meaning and implications can continue to hold", Haldane, 1913, pp. 54-58.

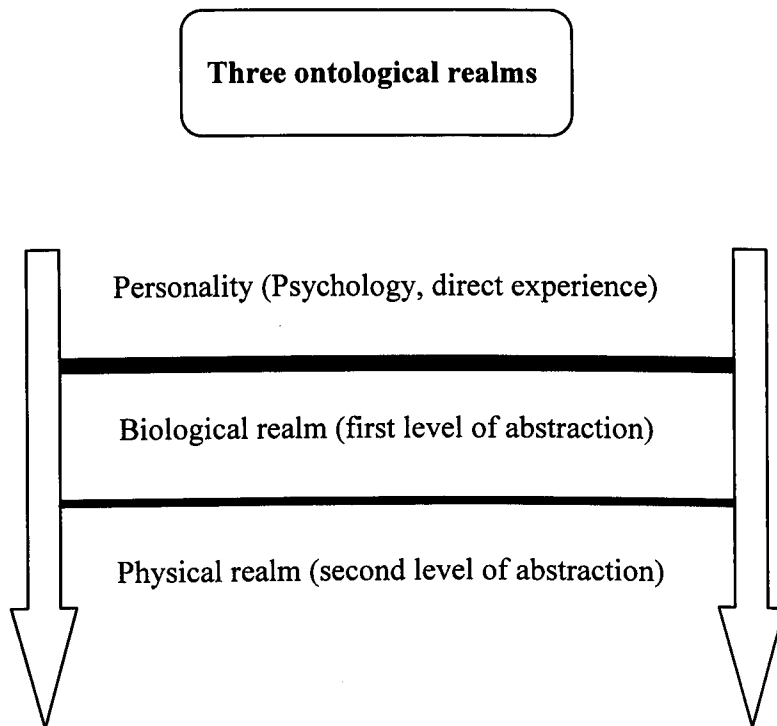
⁴⁶ As many years later, in one of the last and most philosophical of his books, Haldane would eventually specify: "Just as a living organism is regarded as an active manifestation of life, and the same active manifestation is present in the biological environment which cannot in thought to be separated from it, so a person and all his perceived world, thoughts, motives, and acts, are active manifestations of personality. As Schopenhauer in particular pointed out in his book *Die Welt als Wille und Vorstellung*, we cannot separate thought from will; and it seems to me, one of the great defects of much other post-Kantian German philosophy, and particularly the Hegelian philosophy, was just this artificial separation of thought from will, or subordination of will to thought. All our perceptions have a motive aspect as entering into our willed behaviour. What we will is also perceived or imagined, and what we perceive embodies the interest expressed on our behaviour. Thus we cannot separate perception and will, any more than we can in biological interpretation separate stimulus from response..." (Haldane, 1935, pp. 98-99).

⁴⁷ Haldane, 1913, p. 124.

Haldane, in effect, both physical and biological realities were mere abstractions of the world of personality; a world scientifically open to the psychologist's investigations. Psychology itself was a science dealing with a different and irreducible realm of experience than physics and biology, which, in turn, had their own irreducible realms:

Just as biology is a more concrete science, nearer to reality, than physics and chemistry, so psychology is a more concrete science than biology. We can abstract from the psychological aspect of a man or animal, and regard him only from the biological aspect... Perception, voluntary response, and conscious activity of every kind belong to personality, and therefore cannot as such be dealt with scientifically from the merely biological or physiological standpoint.⁴⁸

We could schematise Haldane's philosophy in the following way:



Of course, as we have already seen, the conclusion was that each level is irreducible to the other, therefore, each level required its own science and language. This grandiose philosophical scheme allowed

⁴⁸ Ibid., p. 118.

Haldane to justify and reinforce the presumed independence of life sciences from physical sciences. Furthermore, it allowed Haldane to open the way for a general discussion about epistemology in life-sciences; namely, the way we perceive life and gain knowledge of it.

3.3: Haldane's Organismic 'Concrete' Physiology

Those who in their innocence cling, on theoretical grounds, to a mechanistic conception of the passage inwards of oxygen are straining at a gnat while swallowing a camel.⁴⁹

J. S. Haldane

Although, in his later years, Haldane continued to philosophise, he had a very active life. His science, far from being a quest for disinterested and abstract topics, was a search for applied knowledge: he invented technological devices like gas masks; he introduced safety measures and apparatus for miners, inventing the famous "Haldane box",⁵⁰ and made fundamental contributions to diving techniques, formulating the pioneer "Haldane's diving decompression tables".⁵¹ All his great contributions to science and technology were mainly related to his studies on the physiology of respiration and this became the prototype of his organismic physiology that, in turn, brought him to criticise Weismannian and Mendelian sciences of heredity as well as British individualist society. Indeed, between 1917 and 1921 he published three important books all dealing, mainly, with the physiology of respiration: *Organism and Environment as Illustrated by Breathing* (1917), *The New Physiology* (1919), and *Respiration* (1921). By the time the first of these books was published, he had acquired an outstanding knowledge out in the field: he had worked in the sewers of Dundee and London, studying the so-called "sewer gas"; he had explored working conditions in the deep caves of coal-mines (and tried to develop measures to avoid mine disasters); he had

⁴⁹ Haldane, 1932, p. 38.

⁵⁰ It consisted of a cage with a canary or mouse inside; it was a device used to warn miners about the presence of carbon monoxide or other poisonous gases.

⁵¹ In 1905 Haldane was appointed by the Royal Navy, and in particular by the Deep Sea Diving Committee, in order to perform research on deep diving technical problems. In fact, the main aim was to understand how to avoid the so-called "caisson disease" or, as we would say nowadays, decompression disease. In 1907 he published his decompression tables which were widely used until the late 1950s.

performed expeditions on the highest available peaks in order to study the processes of physiological acclimatisation (in particular, Ben Nevis in Scotland and Pikes Peak in Colorado, in 1911); he had directly experienced trench warfare in the First World War, in order to find measures against German poisonous gases; he had worked and was a member of the “Deep Sea Diving Committee” in order to improve deep-sea diving techniques and, finally, he had made experiments on himself in his lab in Oxford. In sum, as Goodman writes, Haldane brought his lab into the field, and, I would add, applied his theoretical conceptions to concrete inventions. After all these experiences, Haldane was even more convinced that breathing was essentially a phenomenon of organic self-regulation, entailing many different interrelated elements.

Throughout the 19th century, as Allen observes, there were two main hypotheses about respiration: on the one hand, it was thought that breathing depended principally on the activity of the nervous system, which worked as the main stimulus for respiration. On the other, it was assumed that respiration was stimulated by some specific chemical substances dissolved into the blood through tissues.⁵² Both hypotheses presumed that breathing represented a delimited or circumscribed phenomenon caused by a well-defined underlying mechanism. Haldane totally challenged such an assumption; in the phenomenon of respiration many other causal elements were involved (including metabolism). Indeed, even though the mere act of breathing could be seen as a series of muscular movements of the chest following a well-defined rhythm, and even though the rhythmic exchanges of oxygen and carbon dioxide could be understood in physico-chemical terms, respiration seen as a whole process implied the ordered functioning of other organs, tissues and bodily fluids, such as blood.

Oxygen indeed, once absorbed in the lungs, passes into the blood and is carried and distributed throughout the body by capillary vessels. Afterwards, the unoxygenated blood is carried back, through the veins, to the heart and lungs in order to acquire new oxygen and repeat the cycle. However, muscular rhythmic movements related to respiration are regulated by nerve stimuli produced in a central area within the *medulla oblongata*; such an area is in turn influenced by chemical states of the blood coming from the heart to that central area. Chemical states depend on the rate of carbon dioxide previously dissolved in the blood, which causes a weak alkalinity of arterial blood so that the central area

⁵² See Allen, 1967.

reacts to small differences of alkalinity. The weak alkalinity in the blood depends, in turn, on the presence of other substances in the blood; for instance, the presence of salts which is regulated by a balance between absorption in the intestines and excretion by the kidneys. The kidneys have therefore a fundamental importance in regulating respiration because they control the rate of some essential substances which, in turn, influence the central area in the medulla oblongata. Of course, even though salt excretion by the kidneys depends on alimentation and other external factors, the organism is able to regulate its internal environment despite changes in the external environment; therefore, Haldane added, internal organic balance is not necessarily due to external constancy of the environment. In sum, the result is that, as Haldane argued, we play: "...an aimless game of battledore and shuttlecock".⁵³ Respiration, as many other related organic processes, shows that:

The phenomena represented by a living organism cannot possibly be grasped and interpreted one by one, in the manner in which we grasp and interpret what present themselves to us as physical or chemical phenomena occurring in space and time. We must grasp them as a whole, simply because, whether we will or not, they present themselves to us as an organically determined whole.⁵⁴

To Haldane, respiration did not represent a discrete physiological process among others; it represented an instance of the general organic self-maintenance processes of the organism as a whole.

As I have already mentioned, the holist interpretation of physiology was applied as well as reinforced by Haldane's direct experiences and observations on the field; from the extraordinary abilities of miners to work in unimaginable conditions of stress and heat, to divers' remarkable powers of adaptation to different pressures and ever-changing circumstances of a hostile environment. When, in 1911, Haldane reached the peak of Colorado's pikes, he could experience, in his own body, the capacity of the organism of self-adjust and self-regulate as whole to the decreasing amount of oxygen in the air.⁵⁵

⁵³ Haldane, 1919, p. 40.

⁵⁴ *Ibid.*, p. 40.

⁵⁵ As he recounted in a lecture delivered at the South-Eastern Union of Scientific Societies in June 1915: "When we first went up we were, like other newcomers, slightly blue in the lips and face, and after a few hours began to suffer from the very unpleasant symptoms of mountain sickness. In the course of the next two or three days these symptoms of oxygen-want passed off, and though we were still unusually short of breath after muscular exertion, we

The well-known phenomenon of acclimatisation, which he had discussed extensively in his *Organism and Environment*, proved that many of living phenomena and abilities had a purposive tendency; in fact, in higher altitudes, the lungs' epithelium tends to absorb more oxygen and the rhythm of breathing, together with haemoglobin's concentration, increase. Then: "...the last raises the oxygen pressure in the capillaries of the body, the second diminishes the fall in alveolar oxygen pressure, and the first raises the arterial oxygen pressure much above the alveolar oxygen pressure, whereas at the sea level the arterial oxygen pressure is no higher, as a rule, than the alveolar oxygen pressure. *The teleological significance of these changes seems clear.*"⁵⁶ In sum, a wide range of phenomena (acclimatisation, breathing, as well as other phenomena of physiological regulation), the extensive capacities of organisms to recover function and organic balance (as Haldane had directly observed in men recovering after gas intoxication or infected wounds), and the unexpected vicarious functions of organs and developmental phenomena, all spoke in favour of organismic biology and physiology.⁵⁷

3.4: Organism as Metaphor: Haldane's Ideas on Medicine, Heredity and Society

Had I been content with mechanistic interpretation I should not have suspected the presence of various defects in existing knowledge, nor known in what direction to look for them.⁵⁸

J. S. Haldane

Neither biologists nor physiologists accepting the organismal approach to biology could fail to see the relevance of it for medicine. In fact, when in January 1918 Haldane read a paper at the Edinburgh Pathological Club, he made clear that there was a very close connection between physiology and

remained extremely well, and of perfectly normal colour, like the other persons living on the summit". Haldane, 1919, p. 25.

⁵⁶ Haldane, 1917, p. 59.

⁵⁷ As Haldane explained about vicarious functions: "When structural elements are destroyed or actually removed, the process of reproduction is limited in the higher organisms. We then observe the phenomenon of other parts with similar functions taking on the special functions of the lost part. Gradual recovery owing to other parts performing missing functions is a matter of everyday experience in Medicine and Surgery; and though the evidence is to a large extent still indirect, we cannot doubt that in all such cases structural changes are associated with the functional adaptation.", Haldane, 1917, p. 97.

⁵⁸ Haldane talking about physiology of respiration in Haldane, 1932, p. 36.

medicine. He first recalled the therapeutical measures he used for curing soldiers exposed to lung-irritant gases. These gases caused poor oxygenation in the affected lungs which, if prolonged, damaged the nervous system causing haemorrhages in the brain as well as injuring other vital organs. However, if oxygen was administered, all the damages following want of oxygen could be easily avoided: "What we do by giving oxygen is to keep the patient alive, by preventing secondary injury, until time has been given for the natural processes of recovery of the lung".⁵⁹ After all, Haldane continued, surgeons and physicians of different specialities worked in the same way and pursued the same scope: in treating wounds antiseptically or aseptically, they prevent infections and allow these injuries to heal themselves; the use of drugs or anaesthetics was intended to break a vicious and dangerous circle and permit the body to regain the balance lost in disease; in administering digitalis and *strophanthus* physicians helped the diseased heart to regain its natural equilibrium. There are many other examples, but what Haldane was essentially arguing was that: "We cannot repair the living body as we repair a table or a clock, the surgeon is not a carpenter, nor the physician a mechanician or chemist"⁶⁰, indeed, he continued, "...in practical medicine the assumption of the existence of organic regulation of both structure and function is absolutely fundamental. Disease is the breakdown of this regulation at one point or another; and practical medicine is simply assistance to Nature in restoring and maintaining effective organic regulation".⁶¹ In medical as well as physiological disciplines, in anatomy, pathology or pharmacology, the fundamental phenomenon of organic regulation should never be forgotten and belittled because it not only stands, as evident data, before the eyes of every scholar of living phenomena; it should also guide the doctor's diagnosis and prognosis.

Haldane noticed that physicians did not consider physiology a central discipline because it was taught in physico-chemical terms, whereas practical medicine was clearly based on a teleological conception of the organism. However, in the very last years of his life, when in 1932 he published an essay denouncing, once again, the artificial gap between physiology and medical practice, he insisted that

⁵⁹ Haldane, 1919, p. 86.

⁶⁰ Ibid., p. 87.

⁶¹ Ibid., p. 89.

Institutes of Medicine had to be based on a new physiology: organismic physiology.⁶² In fact, doctors, like biologists, always deal with an “actively persistent relationship” which requires a deep physiological knowledge of what is considered “normal regulation”; namely, the normal, not pathological, functional state of the organism as a whole.⁶³ In sum, the new physiology, as conceived by Haldane, had to become to the keystone of medical sciences because it was the only discipline giving the appropriate foundational knowledge for dealing with self-regulated systems; in fact, as Hippocrates had taught centuries before, curing means re-establishing a balance in a disrupted body; as Haldane concluded his discourse: “The nature of life in the ‘nature’ which Hippocrates seems to have first seen clearly and made the basis of his teaching and practice; the ‘nature’ of which the etymology of the word ‘physiology’ ought always to remind us; the ‘nature’ of which the conception had run like a golden thread through the history of scientific medicine”.⁶⁴

However, the organismic view of life that Haldane professed not only supported his new conception of physiology in relation with medicine, as it had done with biology before, but it guided his ideas about heredity and his critiques against Weismann’s germ plasm and Mendelian genetics. In 1890 Haldane went in Fribourg and attended Weismann’s lectures; however, as he recalled many years later in one of his Donnellan lectures delivered at the University of Dublin in 1930, he remained rather intellectually disappointed: “Attracted by his vigour and genial personality, I went to work under Weismann when I was a young man; but I soon realised that, since it is actively maintained structure that we are dealing with, we cannot hope to interpret living structure, whether in the embryonic or adult stage, apart from its environment, although, since we are also dealing with actively maintained life, neither can we disregard heredity”.⁶⁵ Haldane regarded Weismann’s theory of germ-plasm as an instantiation of the mechanistic approach to biology, which was for him misleading, in principle at least. It was so because such an approach tended to separate the phenomena of life into well-defined compartments: heredity, as

⁶² The essay entitled ‘The Institutes of Medicine and Surgery’ was based on a paper he delivered at the Middlesex Medical Society and published in his 1932 book, *Materialism*.

⁶³ “The more we understand of the biological relations of both function and structure, the more easy does it become to detect and understand deviations from the normal, and to suggest methods of meeting the deviations and promoting recovery. Without this understanding we are simply groping in the dark, unable, except by rule of thumb, to diagnose the condition of a patient, or to see how he can be helped” (Haldane, 1932, p. 42).

⁶⁴ Haldane, 1932, p. 46.

⁶⁵ Haldane, 1931, pp.27-28.

conceived by Weismann, was a phenomenon limited to the cell nucleus and its substances: elements that determined all the complex changes happening during development. In other words, Weismann's germ plasm, with all its sets of supposed determinants, not only pretended to explain the organism's reproduction, but also living organisation. As a consequence, all manifestations of life had one specific and well delimited material and efficient cause; the germ-plasm — a relatively simple nuclear substance able to form or produce a complex epiphenomenon: the organism. However, as Haldane contended, such a view ran against the most basic conception of life as regarded from an organismic viewpoint. In fact, as we have seen, Haldane's organicism maintained that causes and effects, as well as stimuli and responses, all constituted an interrelated system forming a unique organised whole. Instead, as C. M. Child was arguing from Chicago (see chapter 5), all phenomena of life (including heredity) were based on metabolic changes and Haldane was of the same opinion:

Biology deals at every point with phenomena which, when we examine them, can be resolved into metabolic phenomena – exchange of material and energy, as exemplified in growth, development, maintenance, secretion and absorption, respiration, gross movements in response to stimuli, and other excitatory processes. Now metabolism is itself a constant process of breaking down and reproduction of what is living. There is no reason for separating the reproduction of a whole organism from the constant reproduction of parts of it in ordinary metabolic process. *Hence our conception of heredity involves every part of biology.*⁶⁶

Because it was impossible to separate such a specific substance from the whole organisation and, at the same time, insofar as it was impossible to imagine that such a substance was responsible for the organisation of the whole, Weismann's theory was rejected. Haldane never changed his mind. In 1932 he returned to this topic in a paper delivered at the British Institute of Philosophical Studies; after harshly criticising Weismann and his advocates, he advanced his own suggestions of how research on heredity should be carried out. The student of heredity should never try to identify one substance, one single stuff, one unique cause explaining transmission and development, because during reproduction all living

⁶⁶ Haldane, 1913, p. 60.

activities are involved: “We can everywhere observe the breaking-down processes, with the formation of various end-products, in the ever-present metabolism of living tissues; but along with these go characteristic processes of reproduction. What is reproduced is living structure and activity with all their delicacy of detail”.⁶⁷ All particulate theories of heredity, along with mechanistic approaches to biology, necessarily bring back vitalism and mysticism because, ultimately, these theories always assume what they intended to explain. Heredity, like respiration, was just one instance, one manifestation, one characteristic of a unique interconnected system; therefore heredity was a *systemic* phenomenon, not a transmission of material stuff.

Weismann was not alone on Haldane’s black list. In a 1917 lecture delivered at the Birmingham and Midland Institute, he also attacked both Mendel and Bateson. First of all, insofar as both organism and environment are one unique dynamic thing, and insofar as, in any living entity: “...each part and each activity of the body is intimately dependent on the other parts and activities”⁶⁸, then environmental changes in adult organisms can be fixed and transmitted in the germ cells so that: “...acquired characters must be capable of hereditary transmission”.⁶⁹ Indeed, Weismann’s hypothesis, according to which there was a physiological separation between germ and soma cells, left the origins of variation unexplained. In order to overcome this difficulty, Haldane argued, Mendelian heredity was invoked. Because Mendel had argued that characters or factors were transmitted and distributed generation over generation without being blended, variations could be explained as statistical “re-shuffling” of factors during the reproductive process. Variations were never acquired directly through the environment, but were a consequence of intracellular processes. Now, Haldane continued, Bateson was the champion of such a hypothesis which, if analysed properly, entailed absurd consequences; it implied that all possible factors giving rise to all variations during evolution had to be contained in the first unicellular organism that appeared on earth: “in presence of such hypotheses — concluded Haldane — “one feels that it is high time to return to sanity”.⁷⁰ To Haldane, even to suppose, for the sake of the argument, that there were some

⁶⁷ Haldane, 1932, p. 62.

⁶⁸ Haldane, 1919, p. 122.

⁶⁹ Ibid., p. 122.

⁷⁰ Ibid., p. 124.

“atomic” particles of life hidden in cell nuclei was absurd because even the simplest organic units were still highly complex and worked in a universe of irreducible dynamic relations.

One year before his death in 1936, when his famous son J.B.S., together with other biologists, was involved in a movement that aimed to synthesise Mendelian genetics, Darwinian evolution and other biological disciplines, Haldane the father left his last reflections on heredity in one of his most Kantian works;⁷¹ *The Philosophy of a Biologist*. Here, once again, Haldane supported the possibility of acquired characters as the origin of novelty in evolution; the passage is worth quoting in full:

In the acquisition of a new character the organism is just as much active as the environment, and were it not so new characters would not be transmitted to descendants. It is only in the light of the distinctively biological conception of a life which embraces environment that evolution can be interpreted. Every new character is an active adaptation of pre-existing life, and its transmission to descendants is a sign that in the adaptation the life itself of the organism is expressing itself. Acquisition of a new character is always a distinctively biological phenomenon, just as life itself is. The controversy as to how far acquired characters can be inherited seems to me to turn largely on a misunderstanding of what the acquisition of a new character implies. If we attempt to attribute the acquisition to the mere influence of environment we can always also show that a hereditary factor is involved. In biological interpretation we can never separate organism from environment.

⁷¹ In this book, Haldane developed one of his most extensive critiques and discussions of Kant's philosophy. He started with a quite detailed discussion of Kant's *Critique of Pure Reason*, and then discussed post-Kantian philosophies (Hegel, Fichte, Schopenhauer etc.). Finally, he introduced a long discussion about Kant's *Critique of Judgment*. In fact, Haldane was not satisfied with Kant's treatment of the organism as entity perceived as a mere manifestation of aesthetic judgment. Life phenomena, he maintained, could be subject to a proper scientific investigation insofar as they were treated as phenomena belonging to a different ontological realm; in other words, experiencing life was irreducibly different from experiencing physical objects because the two consisted in two different abstractions of one unique reality. Of course, Kant was right in saying that the category of cause and effect, as applied to physical objects or the inorganic world, could never be totally applied to the study of organisms; however, as we have seen, Kant maintained that treating organic beings as teleological entities was not a substantial epistemic strategy, but an heuristic strategy of reason. Now, for Haldane, looking at the organism as purposive entity was not a heuristic epistemic strategy because, ontologically, organisms were *de facto* purposive entities. As Haldane explained: "As regards life, therefore, Kant was mistaken in separating a phenomenal world of perception from an unperceivable world of aesthetic judgment. He was misled by the rigid character of his interpretation of perception, and his mistake is constantly being repeated in present day science and literature. Life is just as much an object of ordinary perception as is mechanism, and belongs just as much to our 'common-sense' world, inconsistent with itself as that world is. We have just as good a right to consider the biologically interpreted world to be a directly perceived world of common sense as we have to consider the physically interpreted world in this manner, and biologists, albeit unconsciously, are constantly making use of biological common sense" (Haldane, 1935, p. 65). In further support of his stance, Haldane cited Whitehead's philosophy of physics and Smuts' *Holism and Evolution*.

In the same way the attribution in individual development of all adult characters to the physical and chemical structure of its germinal material assumes that we can describe life as appertaining to physical and chemical structure apart from the environment. This we certainly cannot do. *The chromosomes and chromomeres of a living germ-cell are an expression of its whole life, and its further life in essential connexion with embryonic and adult environment furnishes the only key to an understanding of their real nature*⁷².

What is really striking is that Haldane never mentioned Lamarck; however, his view on evolution was entirely Lamarckian. Organisms constantly adapt themselves to the environment and, in so doing, they improve. In transmitting their “ameliorations” to descendants, organisms constantly become more complex. In short, evolution, in the eyes of Haldane, was characterised by constant progress and human society was not excluded from such a scheme. In fact, his vision of biology, shaped by organicism (that, in part, he took from Delage) and Lamarckian evolution, was applied to his views on society and its endless conflicts.⁷³ As his son J.B.S. recalled, although Haldane had never been a radical, he was really concerned about social conflicts due to the iniquitous distribution of wealth. When, in 1883, Haldane published the previously mentioned article with his brother Robert, he attacked what he considered: “...the idea of the state as mere aggregate of isolated individuals”. Indeed, they continued, “A less abstract category would prove more adequate to the facts in embracing, in the conception of the individual, his determination by the social organism of which he is a member.”⁷⁴ In the following years, Haldane expressed his political convictions and ideas of society during his numerous public lectures he addressed to societies and institutions. For example, in 1924, in a period of social unrest and communist threats, Haldane was elected president of the Institution of Mining Engineers. In the presidential address entitled “Values in Industry” he exposed his ideas and convictions about the aims and scope of that Institution, in regard to British economy and society. First of all, engineers should always have a special care about safety and health in the working conditions of miners and employees. In other words, the mining management should give the highest value to human comradeship, and, in so doing, it had to

⁷² Haldane, 1935, p. 74.

⁷³ In the Silliman Lectures delivered at Yale University in 1915, Haldane clearly made the connection between his stance and Delage’s organicism as expressed in his book *L’Hérédité*. See Haldane, 1917, p. 2.

⁷⁴ Haldane, quoted in S. Sturdy, 1988, p. 322.

promote education and housing for all miners and their families. Miners must be considered precious fellows and not mere unskilled workers:

It is not with scientific abstractions called 'labour' or 'capital' that British mining engineers have to work, but with their own fellow countrymen, their own flesh and blood. These fellow-countrymen will give loyal and efficient service, will face any danger, will forgive imagined or real mistakes, and will take the rough with the smooth, the bad times with the good; but what they will not tolerate is being treated as if they were mere tools, to be cast aside without compunction.⁷⁵

In sum, miners must be considered people and not gears in a capitalist machine. A colliery, like society, had to be seen as an organism with all his different parts unified in a superior, unique, whole. Indeed, if a company — an industrial enterprise — was deemed a mere economic machine, where its employees represented selfish units or independent individuals, then: "...it has no soul to hurt, though it has body to kick"⁷⁶. However, Haldane added, if we consider society and industry as mere aggregates of selfish individuals pursuing their own interests, we should not be surprised by social unrests and uprisings. The struggle between classes, between employers and employees, between capitalists and the working classes, was not only due to a mere unequal distribution of goods, but as "...human rebellion against what are regarded as inhuman relations".⁷⁷ In a colliery, for example, if positive relations could be established, a natural cooperation and comradeship would follow. The real problem, indeed, the main cause behind strikes and revolts, lay in a materialist and mechanist conception of economy which ran against the natural predisposition of men to cooperate for a unique goal. The concrete human being, as seen in his working and social context and in his daily life was not, as depicted by economists, a selfish individual, but a person naturally endowed with sympathies towards his fellows: human communities worked as whole organisms and when solidarity among parts was disrupted, the social organism (community) died.

Haldane had no sympathies for communism, he was rather a liberal socialist, thinking that societies could progress and thrive as long as the relations among their members were "human" relations.

⁷⁵ Haldane, 1932, p. 195.

⁷⁶ *Ibid.*, p. 197.

⁷⁷ *Ibid.*, p. 198.

Societies, like living organisms, were purposeful entities where parts and whole were in constant, irreducible, relation.⁷⁸ From his neo-Kantian organismic conception of life, a conception based on his physiological findings as well as his philosophical convictions, Haldane not only criticised medical sciences and current conceptions of heredity, he also applied organismal notions to British capitalism. As Sturdy well puts it: “Haldane saw the demonstration of biological teleology as a way of vindicating his metaphysical world view, with all the implications he believed that held for social theory”⁷⁹; with Haldane, the Kantian bio-philosophical tradition acquired a leftist taint.

3.5: D’Arcy Thompson’s Bio-Philosophy

...D’Arcy Thompson did not merely unite a series of truths generally known in their isolated state; he combined truths long forgotten by his colleagues.⁸⁰

S. J. Gould



Fig . 3.4, D’Arcy W. Thompson⁸¹

⁷⁸ As he concluded his talk: “My own work in pure science can be summed up in the conclusion that the mechanical conceptions of physical science break down irretrievably when we endeavour to apply them to life and conscious behaviour, both of which are just a part of what we call Nature; and I have just tried to point out that mere economic conception of industrial life breaks down equally hopelessly when we try to apply it to such an industrial undertaking as a British coal-mine” Haldane, 1932, p. 204.

⁷⁹ Sturdy, 1988, p. 334.

⁸⁰ S. J. Gould, 1971, p. 257.

⁸¹ Source: <http://martingoodman.com/soyouwanttobeawriter/2007/01/darcy-wentworth-thompson.html>.

D'Arcy Thompson began his *magnum opus*, *On Growth and Form*, with Kant: "Of the chemistry of his day and generation, Kant declared that it was a science, but not a science – *eine Wissenschaft, aber nicht Wissenschaft* – for that the criterion of true science lay in its relations to mathematics."⁸² Of course, the Kant approached by Thompson in these first lines was not the Kant of *Critique of Judgment*, but the very different Kant of the *Critique of Pure Reason*; namely a Kant enamoured of Newton's physics, Euclid's geometry and Laplace's mathematics. However, even though a modern reader might interpret Thompson's emphasis on the importance of mathematics in the study of living things – and the weight he gave to physics and mechanism to explain organic forms, the importance he attributed to geometrical symmetries in morphology — as a merely reductionist and Cartesian approach, it was not so intended by Thompson. Indeed, the use and application of mathematics to biological problems was considered a very promising strategy for many 'holist' theorists; the existence of some simple geometrical forms and quantifiable physico-chemical processes was not in contradiction with organismal biology, and the mathematisation of morphology was not inconsistent with teleological approaches or stances.⁸³

There is one fundamental distinction we should draw before I introduce Thompson's philosophy of the organism and biology; it is one thing to argue that living bodies are totally explainable and completely reducible to physico-chemical properties, another to say that organisms never contravene physical laws or disprove chemical knowledge. Thompson readily accepted this second alternative; he believed that organisms did not break any physical law, they did not require any vital principle or transcendent energy in order to work, apart from physics and chemistry; however, he felt that organisms exhibit some peculiarities that, as George Kimball nicely explained, made living entities special: "Thompson tries as often as possible to show the identity, or at least the analogy, between ordinary particles and organic creatures...and yet he considers that there is a unity of the living body which the non-living does not have. The unity is sometimes conceived as subservience of organic part to the whole, sometimes as an absence of dividing line between head and body – i.e. a physical continuity of

⁸² Thompson, 1942, p. 1.

⁸³ In Germany and Austria for instance, influential scholars such as Adolf Meyer Abich (1893-1971) and von Bertalanffy (1901-1972), highlighted the use of mathematics to solve or describe biological phenomena. See K. S. Amidon, 2008, Adolf Meyer-Abich, Holism, and the Negotiation of Theoretical Biology, in *Biological Theory, Integrating Development, Cognition and Evolution*, MIT Press, pp. 357-370. See also A. Meyer -Abich, 1934, *Ideen und Ideale der biologischen Erkenntnis: Beitrage zur Theorie und Geschichte der biologischen Ideologien*, J. A. Barth, Leipzig, L. von Bertalanffy, 1933.

material”.⁸⁴ Although the difference between organic and inorganic matter was not seen by Thompson as fundamental, nonetheless living bodies manifested different mechanical properties due to specific chemical changes.⁸⁵ Of course, he disagreed with Haldane’s philosophy, according to which biology and physics represented two different levels of reality; for Thompson, the organisms and the way we get information and knowledge about them were, in effect, part of one single reality that could be investigated with one method of inquiry. Nevertheless, as I mentioned, Thompson had never been a reductionist. As Medawar specified, he tried to integrate different approaches and not merely to reduce life to physico-chemical laws:

We are mistaking the direction of the flow of thought when we speak of ‘analysing’ or ‘reducing’ a biological phenomenon to physics and chemistry. What we endeavour to do is very opposite: to assemble, integrate, or piece together our conception of the phenomenon from our particular knowledge of its constituent parts. It was D’Arcy’s belief, as it is also the belief of almost every reputable modern biologist, that this act of integration is in fact possible.⁸⁶

Yet, although Thompson apparently criticised the overuse of teleological thinking in biology, he was too Aristotelian to deny purpose in nature.⁸⁷ What he mainly denied, in fact, was Darwinian teleology or, to put it differently, the adaptationist thinking according to which an organ, a conformation or an organic part was there because useful for the survival of the organism during its phylogenetic past; like many biologists of his generation, Thompson felt that this adaptationist thinking introduced into biology a speculative approach: an approach very hard to disprove because it supposed what it pretended to explain. Organisms were nicely adapted because they had been selected for, and, as Medawar complained, explaining Thompson’s position: “...the formula would accommodate all comers”.⁸⁸ In addition, to Thompson and many of his contemporaries, the hypothesis that adaptation was explainable through the mechanism of natural selection could not be accepted because natural selection was considered, at most, a

⁸⁴ Kimball, 1953, p. 143.

⁸⁵ Ibid., p. 141.

⁸⁶ Medawar, 1958, p. 227.

⁸⁷ He admired Aristotle. He had translated *Historia Animalium*, and a Glossary of Greek Fishes and Birds.

⁸⁸ Medawar, 1958, p. 222.

negative factor in evolution.⁸⁹ It destroyed but never created new organic forms, and therefore, new adaptations.⁹⁰ In brief, not only could natural selection be considered, at most, a very secondary mechanism of evolutionary diversification; but it also introduced a bad form of teleology.⁹¹

Probably, there is no better chapter than that which Thompson dedicated to form and mechanical efficiency to illustrate the tension between bad and good uses of teleology in biological thinking; whereas explanation based on adaptation through natural selection mirrored an empty theological reasoning (not very far from Paley's style),⁹² the perfect adaptations that organisms manifested could be explained with the use of analogies taken from architecture or human artefacts; in these, both efficient and final causes (to use Aristotelian terms) are evident: efficient causes subsist for the sake of final causes, though the former are comprehensible only assuming the latter. In other words, the good use of teleology must be always associated with efficient causes — one explains the other, and vice-versa:

...of very different order from all such "adaptations" as these are those very perfect adaptations of form which, for instance, fit a fish for swimming or a bird for flight. Here we are far above the region of mere hypothesis, for we have to deal with questions of mechanical efficiency where statical and dynamical considerations can be applied and established in detail. The naval architect learns a great

⁸⁹ See Bonner's editor's introduction to the abridged edition of Thompson's *Growth and Form*, first published in 1961, Cambridge University Press.

⁹⁰ As Thompson beautifully puts it: "...we are entitled to use the customary metaphor, and to see in natural selection an inexorable force whose function is not to create but destroy – to weed, to prune, to cut down and to cast into the fire" (Thompson, 1942, p. 270). Accordingly, he quoted Delage, who had expressed a similar point: "la sélection naturelle est un principe admirable et parfaitement juste. Tout le monde est d'accord sur ce point. Mais où l'on est pas d'accord, c'est sur la limite de sa puissance et sur la question de savoir si elle peut engendrer des formes spécifiques nouvelles. Il semble bien démontré aujourd'hui qu'elle ne le peut pas. (Thompson, 1942, p. 270).

⁹¹ In Thompson's words: "It is hard indeed (to my mind) to see in such a case as this where Natural Selection necessarily enters in, or to admit that it has had any share whatsoever in the production of these varied conformations. Useless indeed we use the term Natural Selection in a sense so wide as to deprive it of any purely biological significance; and so recognise as a sort of natural selection whatsoever nexus of causes suffices to differentiate between the likely and unlikely, the scarce and the frequent, the easy and the hard; and leads accordingly, under the peculiar conditions, limitations and restraints which we call "ordinary circumstances", one type of crystal, one form of cloud, one chemical compound, to be of frequent occurrence and another to be rare" (D'Arcy Thompson, 1943, p. 849)

⁹² As Thompson explained: "To buttress the theory of natural selection the same instances of 'adaptation' (and many more) are used, as in earlier but not distant age testified to the wisdom of the Creator and revealed to simple piety the immediate finger of God. In the words of a certain learned theologian, "the free use of final causes to explain what seems obscure was temptingly easy...when you failed to explain a thing by the ordinary process of causality, you could 'explain' it by reference to some purpose of nature or of its Creator". *Mutatis mutandis*, the passage carries its plain message to the naturalist. (Thompson, 1942, p. 960).

part of his lesson from the stream-lining of a fish; the yachtsman learns that his sails are nothing more than a great bird's wing, causing the slender hull to *fly* along; and the mathematical study of the stream-lines of a bird, and of the principles underlying the areas and curvatures of its wings and tail, has helped to lay the very foundations of the modern science of aeronautics".⁹³

Human artefacts are intrinsically purposive, as organisms and their parts; both are made to work under precise circumstances and operate according specific to physical constraints. Just as bridges built by engineers are designed to resist certain specific loads and stresses, the architecture of vertebrate skeleton is made accordingly. The skeleton of a bison, horse or ox works like a suspension bridge; both are made according to a well-planned distribution of lines of force and tensions: "...if we try to look, as an engineer would look, at the actual design of the animal skeleton and the actual distributions of its loads, we find that the one is most admirably adapted to the other, according to the strict principles of engineering construction".⁹⁴ Now, for Thompson, the efficient causes lying behind the skeleton's adaptations were the phenomena of growth; bones grew under specific strains, stresses and tensions: all factors guiding and shaping the skeleton's architecture as a whole:

Each animal – Thompson argued – is fitted with a backbone adapted to his own individual needs, or (in other words) corresponding to the mean resultant of the many stresses to which as a mechanical system it is exposed", [therefore] "...skeletal form, as brought about by growth, is to a very large extent determined by mechanical considerations, and tends to manifest itself as a diagram, or reflected image, of mechanical stress."⁹⁵

However, mechanical stresses — as efficient cause of bone morphology and skeleton structures — were comprehensible only in the light of assumed functions; efficient and final causes had to be considered as two faces of the same coin. The same discourse was readily applicable to other cases; the forms of *Spicule* or *Foramifera*, leaf arrangements or cellular aggregates. Nature was filled with instances

⁹³ Thompson, 1942, p. 961.

⁹⁴ *Ibid.*, p. 992.

⁹⁵ *Ibid.*, pp. 1110-1117.

showing the close interdependence of efficient and final causes. So, after this brief digression, we can better understand some opening words of Thompson's *Growth and Form*:

...like warp and woof, mechanism and teleology are interwoven together, and we must not cleave to the one nor despise the other; for their union is rooted in the very nature of totality. We may grow shy or weary of looking to a final cause for an explanation of our phenomena; but after we have accounted for these on the plainest principles of mechanical causation it may be useful and appropriate to see how the final cause would tally with the other, and lead towards the same conclusion".⁹⁶

As we have seen, although Thompson was not a reductionist and he never accepted a pure structuralist biology, he believed that physical and chemical sciences offered the best tools for studying and understanding organic form: "As soon as we adventure on the paths of the physicist", Thompson admitted, "we learn to *weigh* and to *measure*, to deal with time and space and mass and their related concepts and, to find more and more our knowledge expressed and our needs satisfied through the concept of *number*."⁹⁷ Cell, tissues, organs, then flowers, leaf, trees, all obeyed physical laws; they were neither more nor less complex than inorganic phenomena: "...the physicist proclaims aloud that the physical phenomena which meet us by the way have their forms not less beautiful and scarce less varied than those which move us to admiration among living things".⁹⁸ In brief, the morphologist, Thompson concluded, is, at the end: "...a student of physical sciences".⁹⁹

Once again, if we take these statements out of context, we risk interpreting Thompson's agenda as essentially alien to the group of biologists I am considering and the tradition they endorsed. But, as long as we adhere to the whole discourse that Thompson was developing, and understand the kind of theoretical agenda to which he was committed, we realise that he was well within the Kantian tradition I am reconstructing. First of all, as he himself admitted, even though, as a hypothesis, he considered the

⁹⁶ Ibid., p. 7.

⁹⁷ Ibid., p. 2.

⁹⁸ As Thompson continues: "the waves of the sea, the little ripples on the shore, the sweeping curve of the sandy bay between the headlands, the outline of the hills, the shape of the clouds, all these are so many riddles of form, so many problems of morphology, and all of them the physicist can more or less easily read and adequately solve; solving them by reference to their antecedent phenomena, and to which we interpret them as being due. (Thompson, 1942, p. 10).

⁹⁹ Ibid., p. 10.

organism as material and mechanical entity of a certain kind,¹⁰⁰ he was well aware that physico-chemical properties were often not enough to explain life phenomena: "...I would not for the world be thought to believe that this is the only story which life and her Children have to tell. One does not come by studying living things for a lifetime to suppose that physics and chemistry can account for them all."¹⁰¹ Mechanical and physical representations (what we would call models today), were deemed by Thompson to be useful simplifications, heuristic tools and promising conceptual vehicles in understanding the simplest manifestations of life. After all, E. S. Russell used to say that Thompson was involved in understanding: "...the negative conditions of functional activity, or the direct action of environment".¹⁰² Studying organisms' material condition of life, as Russell dubbed such an agenda, was well within the aims of Russell's functional and organismal biology. Furthermore, although Thompson was focused on those phenomena that could be explained through simple mechanical representations, he did not pretend to apply them to all living phenomena; he had never been involved in the kind of materialist and monist philosophy as expressed, for instance, by Haeckel in Germany or Loeb in the US.

In addition, he did not betray Kant's bio-philosophy insofar as Kant himself, in his third *Critique*, had clearly stated that the student of living things, should stretch, as far as he could, mechanical explanations to life; though the natural philosopher should be aware that those explanations cannot go very far where life is concerned. It is not surprising that Thompson's biology was essentially focused on the lower organisms and the simplest of life's manifestations.

Finally, Thompson was well within the tradition I am considering not only because Haldane, Russell or Woodger considered him part of their community, but also because his texts demonstrate admiration for Kant's philosophy, deep knowledge of Goethe and Cuvier, and full adherence to the doctrine of the organism as a whole. Furthermore, as I will show in the next section, his philosophical convictions and ideas about morphology rendered him critical about particulate theories of heredity – from Weismann to Mendel and beyond. Finally, Thompson's theory of transformation was, as we will see, a formidable example of holistic evolution; an unconventional synthesis of Lamarck's transformism

¹⁰⁰ And we have seen that "mechanism" for Thompson did not refer to a mechanical engine such as a steam-engine or an automaton, but to a biological mechanism. In fact, with this term, he meant an entity that did not defy physical and chemical laws.

¹⁰¹ Thompson, 1942, p. 14.

¹⁰² See Russell, 1924, p. 101.

and Cuvier's theory of organic correlation, all within a context which reminds one of the aesthetical and poetic world of Goethe and the German romantic naturalists, who regarded nature as a source of creative and lawful forms. In summary, we will see that Thompson was much more than an anachronistic Victorian enamoured with old-fashioned books and a keen interpreter of Greek or medieval science; we will look at Thompson's biological thought under a new and unexpected light.

3.6: D'Arcy Thompson Revisited: Growth and Form as Manifestations of Physical Forces

...if the cells acts, after this fashion, as a whole, each part interacting of necessity with the rest, the same is certainly true of the entire multicellular organism...as Goethe said long ago, "Das lebendige ist zwar in Elemente zerlegt, aber man kann es aus diesen nicht wieder zusammenstellen und beleben."¹⁰³

D'Arcy Thompson

We cannot comprehend Thompson's *Growth and Form* without a general understanding of the context in which the book was written. In 1917, when the first edition appeared, some comparative anatomists, embryologists and morphologists (including Thompson) began to react against the idea that, to use Medawar's expression: "...zoological learning consisted of so many glosses on the evolutionary text".¹⁰⁴ In other words, anatomists, embryologists and morphologists tended to interpret organic forms as a sign or clue of evolutionary relations and not as manifestations of direct causal factors. As Foster clearly demonstrated in writing to Thompson in 1894: "If the form is constant in a group – it does not matter how the form is brought about",¹⁰⁵ the main interest of naturalists – apart from the pioneering 19th century works of Roux and followers of the *Entwicklungsmechanik* tradition — was in how forms (related or not) change over time, and not what forces or elements operated behind the constitution of individual organisms. After all, as a student of Balfour in Cambridge, Thompson was very familiar with the Darwinian style of reasoning; he had been trained to think of embryology as evidence for, or indication of

¹⁰³ "When a living organism is broken down into its elements, you cannot put these elements together and expect that the organism would return to life again." (my translation), Thompson, 1942, p. 344.

¹⁰⁴ Medawar, 1958, p. 221.

¹⁰⁵ Foster quoted in R. Thompson, 1958, p. 90.

evolutionary relations. However, when he published *Growth and Form*, the most unorthodox argument he defended – partially unorthodox even to Roux's and His's advocates – was that certain physical or material forces (either internal or external) shaping organic forms were more relevant than evolutionary relations and hereditary ties.¹⁰⁶ In other words, various kinds of forces, acting in diverse ways and diverse magnitudes constituted organisms' structures, conformations and adaptations; no history was necessarily required to explain organic forms.¹⁰⁷ As Thompson explained:

The form, then, of any portion of matter, whether it be living or dead, and the changes of form which are apparent in its movements and in its growth, may in all cases alike be described as due to the action of force...In an organism, great or small, it is not merely the nature of the motions of the living substance which we must interpret in terms of force (according to kinetics), but also the conformation of the organism itself, whose permanence or equilibrium is explained by the interaction or balance of forces, as described in statics.¹⁰⁸

Although the external conformation of a single cell, in virtue of its small size, was essentially due to surface-tension forces; within cells, Thompson argued, other relevant factors were involved: chemical, electrical and thermal forces that, interacting each other, cause the phenomenon of growth. Growth itself was seen by Thompson as having two related meanings: growth as *process* or as *force* itself. For him, organic or inorganic *forces* were, in turn, manifestations of specific forms of energy. It is precisely for this reason that Thompson considered all phenomena related to development and inheritance as manifestations of energy expressed through an equilibrium of forces, and not as expressions of transmission of material particles: "...we must carefully realise that the spermatozoon, the nucleus, the

¹⁰⁶ As Bonner has explained well: "Phylogeny, the study of animal ancestry and relationships, which was the central concern of the comparative anatomists at the turn of the century, is pushed aside and replaced by the idea that functional aspect of form is far more important than blood relationships and family trees" (Bonner, 1966, p. XVIII).

¹⁰⁷ Thompson made a difference between physical explanations and biological explanations: "The physicist explains in terms of properties of matter and classifies according to a mathematical analysis, all the drops and forms of drops and associations of drops, all the kinds of froth and foam, which we may discover among inanimate things; and his task ends there. but when such forms, such conformations and configurations, occur among living things, then at once the biologist introduces his concepts of heredity, of historical evolution, of succession of time, of recapitulation of remote ancestry in individual growth, of common origin (unless contradicted by direct evidence) of similar forms remotely separated by geographic space or geologic time, of fitness for a function, of adaptation to an environment, of higher and lower, of "better and "worse". This is the fundamental difference between the "explanations" of the physicist and those of the biologist." (Thompson, 1942, p. 872).

¹⁰⁸ Thompson, 1942, p. 16.

chromosomes or the germ-plasma can never *act* as matter alone, but only as seats of energy and as centres of forces.”¹⁰⁹ Mere matter was, for Thompson, merely inert substance; his universe was a cosmos of *active* energy interacting with lifeless stuff.

Organic growth, as an expression of dynamic forces caused by the action of energy on matter, was essentially related to organic form or conformation. Indeed, all those physical forces acted in relation to the size of forms: “I have called this book a study of *Growth and Form*, because in the most familiar illustrations of organic form, as in our own bodies for example, these two factors are inseparably associated...”¹¹⁰ Because physical forces act as constraints on organic growth, Thompson’s book was essentially a long list of cases showing how forces ‘compenetrate’ organic matter in directing (or constraining) growth according to specific trends, and therefore producing diverse configurations. From the smallest organisms (for instance: minute bacteria, human blood corpuscles and protozoa) to middle-sized creatures (for example: minute insects, jellyfish or tiny fish), to the largest life forms (for example, mammals or birds), all were influenced by diverse forces: surface-tension in the first, surface tension and gravity in the second, and gravity in the last case.¹¹¹ Of course, growth was not only constrained by direct physical forces; it was a dynamic process entailing differential rates among various organic parts. Rates depending on osmotic, catalytic and physiological secretions that, interacting with extant temperatures, retarded or accelerated the growth of organisms. For Thompson, as long as growth rates changed, the overall configuration of the organism changed accordingly.

Knowledge about differential growth rates was deemed useful by Thompson; not only because it could give the morphologist predictive power, but also because stock-breeders would find it helpful in their practices. In fact, breeders usually ‘select’ desirable general characters, such as fertility, constitution, quality of milk or wool, but, Thompson maintained, growth rate was the most important property to work on: “In size and rate of growth, as in other qualities, our farm animals differ vastly from their wild progenitors, or from the ‘un-improved’ stocks in days before Bakewell and the other great breeders began. The improvement has been brought about by ‘selection’ but what lies behind? Endocrine

¹⁰⁹ Thompson, 1942, p. 20.

¹¹⁰ *Ibid.*, p. 57.

¹¹¹ See also Gould’s introduction to Thompson in his large monograph *The Structure of Evolutionary Theory*, Belknap Press, Harvard University Press, pp. 1179-1208.

secretions, especially pituitary, are doubtless at work; and already the stock-raiser and the biochemist may be found hand in hand.”¹¹² Here Thompson was drawing on Lillie’s papers about the physiology of development of feathers; in particular the relation between growth rates and feather patterns (see chapter 4).

In 1942, when Thompson published the second extended edition of *Growth and Form*, he upgraded the new version with a reference to Lillie’s works; indeed, he admired Lillie’s biology. This is quite clear if we consider that, in the same year, Thompson sent Lillie an early copy of the new edition of *Growth and Form*’s and wrote: “It is a loss to me that we have never met, and a matter of great regret that we are little likely to do so — unless the present plight of the world mends very soon. Pray accept the new edition of my book on *Growth and Form*, of which I am sending you an early copy today, under separate cover. I am sending it you for what it may be worth, to bridge the gulf between us.”¹¹³ Lillie replied with enthusiasm, betraying his admiration for Thompson’s undertakings: “Your kind letter tempers a little the regret I have long felt at not having met you in the flesh. Your beautiful translation of Aristotle’s *Historia Animalium* has long been one of my joys; and the speaking acquaintance that I have had with your *Growth and Form* renders your gift of the new edition, now on the way, an appreciated honour.”¹¹⁴ The gulf was indeed bridged, and in the following months of 1942, they started a correspondence discussing feather development as well as other more mundane topics.¹¹⁵

Of course, Lillie was not the only resource on whom Thompson relied. Another important American figure represented for him a privileged source of inspiration; this was the physiologist C. M. Child (see chapter 5). In fact, the phenomena related to animal regeneration represented for Thompson relevant instances of the phenomena of growth.¹¹⁶ In particular, he was fascinated by Child’s experiments on planarian regeneration, which demonstrated the existence of gradients following the body-axis of the

¹¹² Thompson, 1942, p. 268.

¹¹³ Thompson to Lillie, 8th June, 1942, Box IIA, Folder 84, Lillie correspondence, MBL archives.

¹¹⁴ Lillie to Thompson, 15th July, 1942, Box IIA, Folder 84, Lillie correspondence, MBL archives.

¹¹⁵ Lillie read the new edition of *Growth and Form*’s when he received it in Woods Hole; indeed, on the 12th October of 1942 he wrote: “I immediately dipped into it, and wish to congratulate you on the completion of such a monumental task of scholarship. Who else but you could span the gap from Aristotle to the present with apposite citations spread along the way!” (Lillie to Thompson, 12th October, 1942, Box IIA, Folder 84, Lillie correspondence, MBL archives).

¹¹⁶ As he specified: “...the more we consider the phenomenon of regeneration, the more plainly does it shew itself to us but a particular case of the general phenomenon of growth, following the same lines, obeying the same laws, and merely started into activity the special stimulus, direct or indirect, caused by the infliction of a wound.” (Thompson, 1942, p. 274).

organism: gradients operating between two poles, one dominant and the other subordinate.¹¹⁷ With Child, Thompson felt that the configuration of an organism was a function of its differential growth and, as such, it characterised a space-time event and not a mere spatial entity.¹¹⁸ Also with Child, Thompson assumed that differential growth rates depended on several factors: in particular age and external temperature. Finally, and most important, with Child, Thompson concluded that differential growth rates are behind all morphological characters, peculiar or shared, of all organisms, and therefore specified individual or species qualities and conformations.¹¹⁹ In sum, like Child, Thompson was saying that morphological variations were due to growth variations rather than genes or any other posited nuclear particle.

After discussing growth-rates and regeneration, Thompson passed to cell theory. This chapter, together with the chapters on form and mechanical efficiency and on the theory of transformations, represent the best evidence to show that Thompson was irremediably part of the organismal tradition. First of all, he underscored De Bary and Whitman's critique of cell theory;¹²⁰ the cells were not the individual building blocks of the organism because the organism itself coordinated and drove their distribution. Famous naturalists, botanists, zoologists and embryologists of different periods were enlisted by Thompson to support this stance: as well as De Bary and Whitman he also mentioned Goethe, Sachs, Rauber, E. B. Wilson, A. Sedgwick and others. All together they strongly reminded that in cellular differentiation:

...we deal not with material continuity, not with little bridges of connecting protoplasm, but with a continuity of forces, a comprehensive field of forces, which runs through the entire organism and is by no means restricted in its passage to a protoplasmic continuum. And such a continuous field of forces,

¹¹⁷ See Thompson, 1942, p. 282.

¹¹⁸ This was another staple theme in Whitehead's philosophy of organism, a philosophy that both Thompson and Child, as many Neo-Kantian biologists, shared. See also Chapter 5.

¹¹⁹ As Thompson clearly explained: "The differences of form, and changes of form, which are brought about by varying rates (or laws) of growth, are essentially the same phenomenon whether they be episodes in the life-history of the individual, or manifest themselves as the distinctive characteristics of what we call separate species of the race." (Thompson, 1942, p. 284).

¹²⁰ De Bary's famous remark towered at the end of the chapter: "Die Pflanze bildet Zellen, nicht Zelle bildet Pflanzen". Thompson, 1942, p. 345, Whitman's oft-quoted passage concluded: "...the fact that physiological unity is not broken by cell-boundaries is confirmed in so many ways that it must be accepted as one of the fundamental truths in biology". Whitman quoted in Thompson, 1942, p. 345.

somehow shaping the whole organism, independently of the number, magnitude and form of the individual cells, which enter like a froth into its fabric, seems to me certainly and obvious to exist.¹²¹

In sum, the entire organism was conceived as more than its composing parts; however, what about individual cells? The position Thompson defended was once again similar to the stance supported by organismal biologists; the cell was metaphorically conceived as a *sphere of action*, where an unstable equilibrium of forces dwelled. Surface-tension, of course, but also chemical and electrical forces were involved too. Yet, the cell is inseparably connected with its environment:

A living cell is a little fluid (or semi-fluid) system, in which work is being done, physical forces are in operation and chemical changes are going on. It is in such intimate relation with the world outside – its own *milieu interne* with the great *milieu externe* – that substances are continually entering the cell, some to remain there and contribute to its growth, some to pass out again with loss of energy and metabolic change.¹²²

A dynamical conception of the cell, Thomson maintained, must entail that the whole system work as an integrated individuality; there were neither active or passive regions nor relevant or irrelevant parts: “for the manifestations of force can only be due to the *interaction* of the various parts...certain properties may be manifested, certain functions may be carried on, by the protoplasm apart from the nucleus; but the interaction of the two is necessary, that other and more important properties or functions may be manifested.”¹²³ In fact, for Thompson, as for Just (see chapter 5) and many others upholding the importance of the cell surface and cytoplasm for reproduction and inheritance, the cortical regions of the cell played a fundamental role in all cellular activities.¹²⁴ Thompson’s holist conception of the cell is

¹²¹ Thompson, 1942, p. 345.

¹²² *Ibid.*, p. 333.

¹²³ *Ibid.*, p. 342.

¹²⁴ See J. Sapp, 1987. According to Thompson: “It is far from correct to say, as is often done, that the cell-wall, or membrane-cell, belongs to ‘the passive products of protoplasm rather than to the living cells itself’; or to say that in the animal cell, cell-wall, because it is ‘slightly developed’, is relatively unimportant compared with the important role which it assumes in plants. On the contrary, it is quite certain that, whether visibly differentiated into a semi-permeable membrane or merely constituted by a liquid film, the surface of the cell is the seat of important forces, capillary and electrical, which play essential part in the dynamics of the cell (Thompson, 1942, p. 343). He

particularly important when we consider his critique of Weismann's germ-plasm and Mendelian genetics; even though he was not directly opposed to the latter, it certainly did not fit his general framework.¹²⁵ And the reasons for that derived not only from Thompson's views on the cell, but also from his understating of morphology. Firstly, Thompson believed that investigations about cell functions were more important than knowledge about cell structure. In fact, studying cell structure did not necessarily advanced our knowledge about cellular activities: "The *things* which we see in the cell are less important than the *actions* which we recognise in the cell; and these latter we must especially scrutinise, in the hope of discovering how far they may be attributed to the simple and well-known physical forces, and how far they be relevant or irrelevant to the phenomena which we associate with, and deem essential to, the manifestation of *life*."¹²⁶

As we have already seen, matter was conceived by Thompson as inert substance, unable to move or act for itself. Therefore, cellular structure alone, as inert matter, could not explain or illuminate cellular function insofar as structure could only exhibit or manifest movements and actions in parallel with specific forms of energy. In other words, to Thompson, identifying specific structure – for instance, the germinal spot, chromatin or chromosomes – did not explain, *de facto*, cellular functions. All hypotheses that correlated special properties to material stuff contained in the cells – hypotheses such as Darwin's pangenesis or Weismann's germ-plasm – confused the action of energy with supposed physical particles: "if we speak, as Weismann and others speak, of an 'hereditary substance'...we can only justify our mode of speech by the assumption that a particular portion of matter is the essential vehicle of a particular charge or distribution of energy, in which is involved the capability of producing motion, or of doing work."¹²⁷ All particulate theories of inheritance committed the sin of attributing to matter what was a manifestation of cellular forces; inheritance was not only a property of the whole cell, but it was also a manifestation of energy that, for its own nature, could not be identified or circumscribed to specific cell

concluded elsewhere: "...we begin to look on a surface-layer or membrane, visible or invisible, as vastly important thing, a place of delicate operations, and a field of peculiar and potent activity." (Thompson, 1942, p. 464)

¹²⁵ As Bonner argued: "Heredity and activity of geneses in development are wholly missing in the book except for few passing references which seems to imply that they do not fit into his scheme of things." Bonner, 1966, p. XVIII.

¹²⁶ Thompson, 1942, p. 289.

¹²⁷ *Ibid.*, p. 288.

areas.¹²⁸ Although all this ran against Darwin's and Weismann's hypotheses of heredity and development, it could not be easily fitted with the new paradigm developed by Morgan and his students at the Columbia Lab because, as we will see clearly in the next section, for Thompson, heredity was not based on the transmission of 'factors' or 'genes' but on the transmission of systems or equilibriums of forces.

Even though Thompson mentioned heredity rarely and never developed a personal, coherent, and articulate view on the field, his ideas on how organisms transmit and maintain their form, generation over generation, were clearly expressed when he dealt with evolution. Indeed, to him, evolution was not only Lamarckian in principle (although a adulterated form of Lamarckism) but it was based on a holist perspective of evolutionary transformations and novelties; transformations entailing whole and dynamic systems of energy which could never be reduced to some physical properties of the cell nucleus alone.

3.7: The Organism as a Whole and its Inherited Transformations

The agreement of so many species of animals in particular common schema, which appears to be grounded not only in their skeletal structure but also in the organization of other parts, whereby a multiplicity of species may be generated by an amazing simplicity of a fundamental plan, through the suppressed development of one part and the greater articulation of another, the lengthening of now this part accompanied by the shortening of another, gives at least a glimmer of hope that the principle of mechanism, without which no science of nature is possible, may be in a position to accomplish here.¹²⁹

I. Kant

The biologist, as well as the philosopher, learns to recognise that the whole is not merely the sum of its parts. It is this, and much more than this. For it is not a bundle of parts but an organization of parts, of parts in their mutual arrangement, fitting one with another in what Aristotle calls 'a single and indivisible principle of unity'; and this is not merely metaphysical conception, but is in biology the fundamental truth which lies at the basis of Geoffroy's or Goethe's law of 'compensation' or 'balancement of growth'.¹³⁰

D'Arcy Thompson

It is revealing that Thompson directly quoted Johannes Muller in rejecting what he called the doctrine of single characters i.e. the idea that the adult organism represents, in truth, a set of discrete hereditary

¹²⁸ Thompson: "...in all the theories which attribute specific properties to micellae, chromosomes, idioplasts, ids, or other constituent particles of protoplasm or of the cell, we are apt to fall into the error of attributing to matter what is due to energy and is manifested in force: or, more strictly speaking, of attributing to material particles individually what is due to the energy of their collocation." (Thompson, 1942, p. 288)

¹²⁹ Kant, 1914, pp. 267-268.

¹³⁰ Thompson, 1942, p. 1019.

factors. “Die Ursache der Art der Existenz bei jedem Theile eines Lebenden Körpers ist im Ganzen enthalten”¹³¹ was indeed a statement that Muller, in his celebrated *Handbuch der Physiologie des Menschen* (Textbook of Physiology), attributed directly to Kant.¹³² It conveyed the idea that not only was the organic whole explicatively more important than its parts, but also that organic parts could only be separated through a process of abstraction — biologists’ distinctions — so that organs, tissues, cells, bones etc., were mere theoretical tools that could be helpful only if the scholar was fully aware that they were, in truth, abstractions. Organisms, from an ontological viewpoint, were irreducible and composite wholes. As Thompson explained metaphorically:

we divide the body into its organs, the skeleton into its bones, as in very much the same fashion as we make a subjective analysis of the mind, according to the teachings of psychology, into component factors: but we know very well that judgment and knowledge, courage and gentleness, love or fear, have no separate existence, but are somehow mere manifestations, or imaginary coefficients, of a most complex integral.”¹³³

Now, for Thompson, one of the most evident instances of organic integration was the animal skeleton and its efficiency; it showed that the old morphological and anatomical observations — observations based on the structural analysis of parts as abstracted from the whole — were necessarily misleading.¹³⁴ In fact, mirroring Kant’s saying, he argued that the same principles were at work both in the architecture of the whole skeleton and in the constitution of a single bone; yet, as Haldane had shown in the case of breathing physiology, both skeleton and bones were in turn “moulded” with muscles and other tissues so that a complete understanding of the skeletal structure and function was possible only if the whole was taken into account. In fact, as the majority of organismal and neo-Kantian biologists argued (see chapter 4

¹³¹ “The cause lying behind the existence of every part of the living body is included into its whole.” (My translation)

¹³² See Muller, 1837, p. 18. See also Thompson, 1942, p.1020.

¹³³ Thompson, 1942, p. 1018.

¹³⁴ Thompson: “the skeleton begins as a continuum, and a continuum it remains all life long. The things that link bone with bone, cartilage, ligaments, membranes, are fashioned out of the same primordial tissue, and come into being *pari passu* with the bones themselves. The entire fabric has its soft parts and its hard, its rigid and its flexible parts, but until we disrupt and dismember its bony, gristly and fibrous parts one from another, it exists as a ‘skeleton’, as one integral and individual whole.” (Thompson, 1942, p. 1018)

and 5), biological investigation entailed a double process of investigation: analysis, whereby parts were abstracted from the whole and described in their own specificity, and synthesis, whereby the parts were understood as interconnected elements of the whole. Thompson subscribed to this principle and applied it to his morphological investigations; however, even though he believed that organisms could be seen as teleologically directed wholes, he preferred to focus on the idea that living beings were a product of well-defined physical causes acting on the whole organic system of forces.¹³⁵ This is the central idea behind his hypothesis of transformation. In the same way as the skeleton was a result of pressures, stresses and forces acting on growing heterogenous matter, so the forms of organism were the product of forces acting on the whole plant or animal structure. If forces explained form, then heredity and evolution (as conceived by Thompson's contemporaries) lost its privileged explicative power: "To look on the hereditary or evolutionary factor as *the guiding principle* in morphology is to give to that science a one-sided and fallacious simplicity."¹³⁶

Indeed, for Thompson, though affinities among organisms (and morphological similarities among their parts) could indicate phylogenetical relations, they could also be (and often were) the product of similar forces acting on the system as a whole. After all, organisms can be similar to each other, or maintain their invariable morphology for many generations, because they live in similar environments and, therefore, are subjected to similar stresses, pressures and forces. If form were strictly related to growth rates (what Thompson dubbed morphological heredity), and if growth rates be related to environmental stresses and forces, organisms' morphology may change if environmental forces change. In other words, the systems of forces constraining or influencing growth rates can be disrupted by external forces or new habits, which, in turn, may lead to a new equilibrium or system of forces. As a

¹³⁵ A viewpoint that, as we have seen in the case of form and mechanical efficiency, required nevertheless a heuristic use of teleology.

¹³⁶ Thompson, 1942, p. 1022. And yet: "...though I have tried throughout this book to lay emphasis on the direct action of causes other than heredity, in short to circumscribe the employment of the latter as a working hypothesis in morphology, there can still be no question whatsoever but that heredity is a vastly important as well as mysterious thing; it is one of the great factor in biology, however we may attempt to figure to ourselves, or howsoever we may fail even to imagine, its underlying physical explanation. But I maintain that it is no less an exaggeration if we tend to neglect these direct physical and mechanical modes of causation altogether, and to see in the characters of a bone merely the results of variation and of heredity, and to trust, in consequence, to those characters as a sure and certain and unquestioned guide to affinity and phylogeny." Thompson, 1942, p. 1023.

consequence, in evolution, organisms were neither transformed through acquired characters nor through stochastic gene mutations, but they changed through new ‘acquired’ systems of forces:

The deep-seated rhythms of growth which, as I venture to think, are the chief basis of morphological heredity, bring about similarities of form which endure in the absence of conflicting forces; but a new system of forces, introduced by altered environment and habits, impinging on those particular parts of the fabric which lie within this particular field of force, will assuredly not be long of manifesting itself in notable and inevitable modifications of form.¹³⁷

The system of forces Thompson had assumed was represented in the last celebrated chapter of his book; they were pictured as Cartesian deforming grids outlining the *bauplans* of organisms:¹³⁸

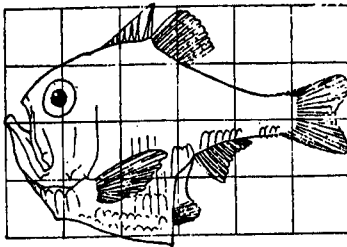


Fig. 517. *Argyropelecus Olfersi*.

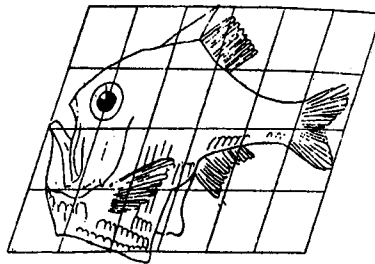


Fig. 518. *Sternoptyx diaphana*.

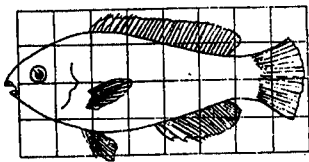


Fig. 519. *Scarus* sp.

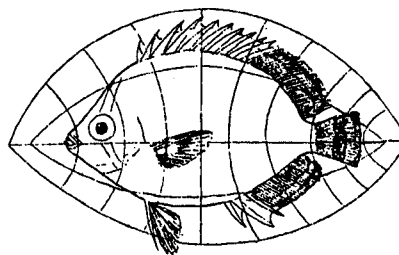


Fig. 520. *Pomacanthus*.

¹³⁷ Thompson, 1942, p. 1025.

¹³⁸ This is not a term used by Thompson himself. Apparently, the first to use it was Woodger in 1945, while commenting Thompson's theory of transformation. See Clark and Medawar, 1945, p. 115. See also Hall, 1999, p. 93.

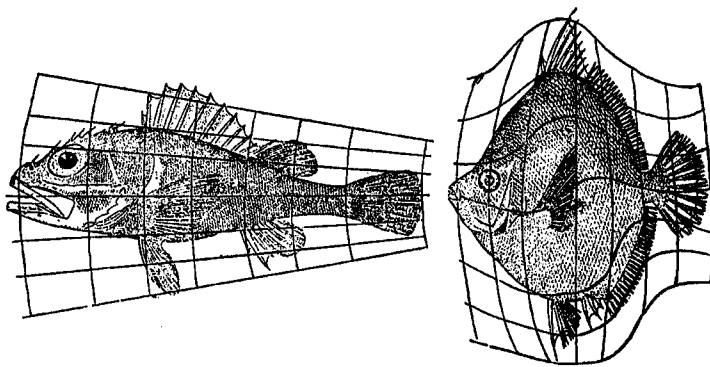


Fig. 523. *Scorpaena* sp.

Fig. 524. *Antigonia capros*.

Fig. 3.5, Thompson's grid transformations¹³⁹

Similar and related forms were compared and described through these geometrical grids. Thompson thought that similar forms varied in correspondence with various deformations of these coordinates-representing lines of force acting on the organism's whole body and on its parts:

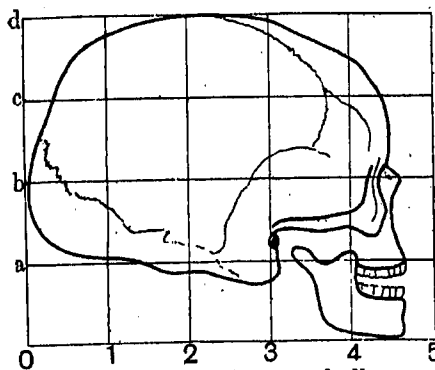


Fig. 548. Human skull.

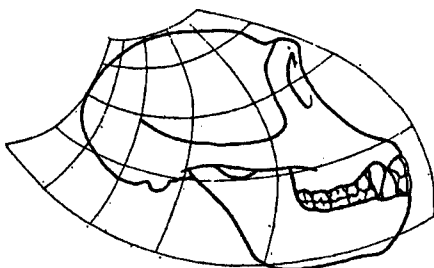


Fig. 550. Skull of chimpanzee.

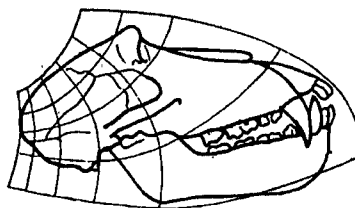


Fig. 551. Skull of baboon.

Fig. 3.6, Skull's transformations¹⁴⁰

¹³⁹ Source, Thompson, 1942, p. 793

¹⁴⁰ Source, Thompson, 1942, p. 890.

As Gould points out, Thompson's coordinate (or grid) transformations held an ontological status; they represented a real and concrete process of morphological change and not a fictitious or symbolic description.¹⁴¹

...we tend to interpret these Thompsonian transformed coordinates as a crude, and ultimately failed, attempt to operationalize (by pictorialization) a good intuition about the multivariate nature of evolutionary change before the development of appropriate statistical techniques, and the invention of computers, permitted us to apply genuine multivariate mathematics to problems of form. Most of us, I think, envisage the deformed coordinate grid as mere residuum of a qualitative analysis focused on the transformed bodies themselves – just a set of guidelines needed to make a crude map of the organisms under consideration.

In so doing, we misunderstand D'Arcy Thompson's intention in a precisely backwards manner. His interest lay primarily in the lines of the stretched and deformed grids, for he had remained true to his theory that physical forces shape organisms directly.¹⁴²

In addition, Thompson grid's transformations illustrated how organisms change as a whole. In fact, unlike the old morphological tradition, which tended to analyse and compare single morphological parts,

¹⁴¹ Although, I think, Gould was not totally correct in his interpretation. Indeed, though the diagrams of transformation represented real processes of transformation, they did not represent real adult *bauplans* changing in that way. If so, Thompson would have been exposed to the easy and devastating criticism that both Woodger and Medawar describe: "The Thompsonian transformations are transformations in the sense that they can be depicted or described by the help of mathematical transformations, but they are not transformations in the sense that they belong to the beginnings and ends of actual natural processes, and this point may possibly be partly responsible for the fact that D'Arcy Thompson's method of treating them has not been developed to a greater extent. For no one supposes that an adult crocodile's skull has ever been transformed into another adult crocodile's skull, or that an adult fish of a certain shape have ever been transformed into another adult fish of a different shape" (J. H. Woodger, 1945, 'On Biological Transformations', in *Essays on Growth and Form presented to D'Arcy Wentworth Thompson*, Edited by W. E. L. Clark and P. B. Medawar, Clarendon Press, Oxford, p. 115). Thompsonian grids had to be interpreted, Woodger argued, as "typical taxonomic transformations". However, Thompson maintained that his transformations 'depicted', somehow, *real* organic transformations. In my own interpretation, what Thompson's diagrams represented were descriptive line of forces shaping organisms in general and operating during all ontogenic stages; in other words, they were maps describing how definite and quantifiable lines of force, working during both embryonic stages and adult forms, may change or transform related adult *bauplans*. To use an analogy, Thompson diagrams can be seen as underground maps. These are neither accurate geographical descriptions nor precise representations of distances between stations, they only inform customers, through a quite functional, simplified and schematic model, about possible connections and spatial and temporal sequences of stations. Likewise, Thompson's diagrams are not faithful representations of organic transformations as happening in the adult organisms, they rather sketch how presumed lines of forces, which underline individual development, can bring ordered, predictive and quantifiable morphological modifications in adult stages. So, Thompson's diagrams may 'depict' real processes like underground maps represent the real transport lines.

¹⁴² Gould, 2002, p. 1198.

Thompson's diagrams illustrated not variations or comparisons of single characters, but an overall reshaping of the entire *bauplan*. After all, he remained loyal to Cuvier who had argued that 'correlation' among characters was a distinctive feature of the organism.¹⁴³ Specific morphological characters were indeed considered by Thompson, once again, as a mere abstraction, only conceived in the mind of the investigator because, as he claimed:

...the living body [is] one integral and indivisible whole, in which we cannot find, when we come to look for it, any strict dividing line even between the head and the body, the muscle and the tendon, the sinew and the bone. Characters which we have differentiated insist on integrating themselves again...The coordinate diagram throws into relief the integral solidarity of the organism, and enables us to see how simple a certain kind of *correlation* is which had been apt to seem a subtle and complex thing.¹⁴⁴

Therefore, coordinates illustrated organic 'holist' transformations as represented in closely-related *bauplans*. Indeed, Thompson's grids were not appropriate to deal with transformations of unrelated or barely related *bauplans* because, just as in geometry it is impossible to conceive a transformation of very different figures (Thompson used the example the incommensurability of helicoid and ellipsoid figures): "We cannot transform an invertebrate into a vertebrate, nor a coelenterate into a worm."¹⁴⁵ Incommensurability among forms, therefore among certain grids, reflected incommensurability among 'types' in nature, as Cuvier had taught and used as criticism against evolutionists in his own time. However, unlike Cuvier, Thompson believed in evolution and, unlike Darwin, he maintained that organic transformation entailed big leaps: "Our geometrical analogies weigh heavily against Darwin's conception of endless small continuous variations; they help to show that discontinuous variations are a natural thing,

¹⁴³ As he explained: "for the morphologist, when comparing one organism with another, describes the differences between them point by point, and 'character' by 'character'. If he is from time to time constrained to admit the 'correlation' between characters (as hundreds of years ago Cuvier first showed the way), yet all the while he recognises this fact of correlation somewhat vaguely, as a phenomenon due to causes which, except in rare instances, he can hardly hope to trace." (Thompson, 1942, p. 1036).

¹⁴⁴ Thompson, 1942, p. 1037.

¹⁴⁵ *Ibid.*, p. 1094.

that ‘mutations’ – or sudden changes, greater or less – are bound to have taken place, and new ‘types to have arisen, now and then.’¹⁴⁶

Like Lamarck, Thompson felt that organic forms change over time and evolve as a function of the environment and new acquired habits, however, with Aristotle, Kant, Goethe, and Cuvier (and all neo-Kantian and organismal biologists), he held that organisms are correlated and integrated individualities. He synthesised all these positions and conceived organic evolution as a process entailing ‘holist’ transformations among related “types”: transformations due to inherited and plastic systems of forces.¹⁴⁷ Just as Child had argued that hereditary transmission entailed systems of reaction and not genes, so Thompson believed that evolution required the transmission of systems of forces and not factors. Thompson’s biology was a result of a venerable, and still vital tradition that, from Aristotle to Kant, shaped many British naturalists’ minds.

3.8: Conclusion

We have seen how highly relevant the intellectual connections were between Haldane, German science and post-Kantian bio-philosophy. During his studies in Edinburgh, J. Muller was probably the first Kantian figure that Haldane approached; his training in Germany had to reinforce his fascination for such a tradition; his intellectual context – enriched from the discussions with his brother Robert and lifelong friend D’Arcy Thompson facilitated his acquaintance with classics in philosophy and science. His direct experiences in the field (and in his own body) strengthened his faith in the Kantian idea that organisms were entities in which: “...every part is reciprocally purpose and means.”¹⁴⁸ His important inventions, hypotheses and contributions in physiology were essentially shaped, as he explicitly claimed, by his professed organicism.

¹⁴⁶ Ibid., p. 1095.

¹⁴⁷ R. Richards, in reconstructing the intellectual context behind Haeckel’s famous work on *Radiolaria*, recalls that: “The idea that descent relationship might operate according to various mathematical deformations of the basic sphere was quite in the older Goethean tradition of morphology, comparable to Carus’s derivation of the form of the vertebra from geometrical arrangements of the basic sphere”, Richards, 2008, p. 94. See also his brief History of Morphology in appendix one of the same book. Indeed, Richards linked D’Arcy Thompson’s mathematical analysis to the German morphological tradition. See Richards, 2008, p. 474.

¹⁴⁸ Kant, 1914, p. 280.

Thompson's connections with neo-Kantian tradition were, though less direct, highly explicit. He grew up and worked in a very similar intellectual context; he admired German biology and, as a polymath, he had a deep knowledge of both its history and its contemporary progress. As a scholar of Aristotle, he never abandoned teleology, even though he attempted to explore possible alternatives. In addition, Thompson's fascination with numbers and geometrical ideals and forms, his quest for simple laws, symmetries, and patterns regulating both inorganic and organic worlds (with the help of analogies such as soap bubbles, snow crystals or clouds), his whole conception of Nature, as a creative, mysterious, active, and feminine entity able to shape and produce beautiful and admirable things,¹⁴⁹ his wonder and mystical respect for all he observed and investigated, and finally, his obsession with organic form: all point the reader — even more than Hellenic philosophy and Hellenistic mathematics and science — to a personal and original Romantic conception of life.¹⁵⁰ As Ritterbush pointed out: “The concept of organic form originated as literary aesthetic principle but became a primary guiding idea in biology, where it was attended with numerous consequences.¹⁵¹ During the second half of the 19th century, Ritterbush continued, this aesthetic principle of form was translated by scientists into a concept open to rigorous scientific investigation. Thomas Huxley was one of those who supported this shift: “In his writings on comparative anatomy, Huxley betrays an aesthetic sensibility, a fondness for the common ideal plan, of which he thought there were only five for the animal kingdom...The beauty of birds, the radial symmetry of the sea urchin, or diverse elegance of Foraminifera are not of any use to the animals, nor is the harmonious appearance of a few ideal types for all animals.”¹⁵² As Huxley wrote, proffering words that D'Arcy Thompson could easily have written himself:

¹⁴⁹ There are few examples of how Thompson conceptualised Nature as active entity: “...and Nature, as in all her handiwork, is quick to ring the changes of the theme”(p. 709), “That Nature keeps some of her secrets longer than others – that she tells the secret of the rainbow and hides that of the northern lights – is a lesson taught me when I was a boy”(p. 733); “There is never a discovery made in the theory of aerodynamics but we find it adopted already by Nature, and exemplified in the construction of the wing”(p. 964); “Nature seems content...if the strength of the fibre be ensured up to the elastic limit”(p. 973); “...precisely those stresses-lines has Nature kept in the building of the bone, down to the minute arrangement of its trabeculae”(p. 995); “...in each case the problem has been solved by Nature herself, very much as she solves the difficult problems of minimal areas in a system of soap-bubbles”(p. 1010); “Nature's engineering is marvellous in our eyes, and our finest work is narrow in scope and clumsy in execution compared to her construction and design”(p. 1016).

¹⁵⁰ See R. Richards, 2002.

¹⁵¹ Ritterbush, 1968, p. 25.

¹⁵² *Ibid.*, p. 59.

In travelling from one end to the other of the scale of life, we are taught one lesson, that living nature is not a mechanism but a poem; not a mere rough engine-house for the due keeping of pleasure and pain machines, *but a place whose foundations, indeed, are laid on the strictest and safest mechanical principles, but whose superstructure is a manifestation of the highest and noblest art.*¹⁵³

Both Haldane and Thompson were parts of a venerable tradition; a tradition that, beginning with Kant himself, ran through post-Kantian philosophies and romantic interpretations; interpretations that afterwards affected and inspired important naturalists in France and England and that, in the hands of younger investigators, changed according to the contexts (intellectual or institutional) into which they were transplanted. However, Haldane and Thompson had different ideas; they did not share a unique and monolithic set of beliefs. Haldane was a physiologist keen to formulate grandiose philosophical schemes affecting his scientific practices and results, while Thompson was instead a morphologist trying to apply new mathematical and physical tools to problems that, since Aristotle, had never been solved.¹⁵⁴ What they really shared though, was Kant's idea that organisms were organised and material wholes, in problematic interaction with their environment, and acting in purposive and creative ways. In sum, from diverse perspectives, they represented two extraordinary examples of neo-Kantian biology as practiced in the UK during the first decades of the 20th century.

However, followers of both Haldane's and Thompson's physiology and biology did not proliferate; they did not lay the foundations for a school; they did not indoctrinate students. Nevertheless,

¹⁵³ T. Huxley, 1856, quoted in Ritterbush, 1968, p. 60.

¹⁵⁴ However, in the 20th century, Thompson was not alone in applying mathematics to morphology. Before him, as Drack, Apfalter and Pouvreau write, Przibram in Vienna: "...committedly discusses the possibility of applying mathematics to biology in general and to morphogenesis in particular. He also considers laws of higher order in cases where the detailed underlying single processes are not known. "Anyway, the influence of the 'whole' on the 'part' turns out to be accessible to mathematical processing, grounded on our ideas from exact natural history [*Naturlehre*]". Thus, he proposes a "mathematical morphology" by which the parameters of the developing forms (e.g., proportions) should be described, also in relation to physical measures such as surface tension. The investigation should reveal "constants" that explain similar forms in various species... the fundamental idea here is to unite morphology and physiology, an improvement compared to D'Arcy W Thompson's approach of mathematical morphology" in Drack, Apfalter, Pouvreau, 2007, p. 354. Thompson knew Przibram's work, indeed, as we will see in the next chapter, he sent students to him in Vienna. However, it seems that they were rather reciprocally critical about their scientific approaches. As Drack, Apfalter and Pouvreau report again, in 1924, Przibram criticised Thompson's approach to mathematical morphology, considering it of little predictive value and too inductive. On his part, Thompson felt that Przibram's experiments and results were not reliable (see next chapter).

they were at the tip of a small crowd that, in the UK, expanded and updated their insights; E. S. Russell and H. Woodger were part of this crowd.

4.0: A New Generation: E. S. Russell and J. H. Woodger's Biological Agendas

Lines to a Biochemist by a living specimen

A word or two in your ear, my friend!
Before you tear me apart - unbend!
If you want to measure me, body and soul,
Don't forget to measure me whole!
If you don't think I own all my water, you oughter.
A fat-free mass is not me, you ass,
And I'll thank you to leave my bone alone.
My bits and pieces are kept in action
By that which lies in the packing fraction.
All of them make up the living me;
Take them apart and I'll vanish. See?¹

D. Worrall

4.1: Introduction: Haldane's Blessing

In 1931, Haldane published a book representing his Donnellan Lectures delivered at the University of Dublin in the previous year.² The book addressed some philosophical issues as related to practices and theories in biology; in fact, not coincidentally, it was titled *The Philosophical Basis of Biology*. Haldane, now 71 years old, not only reported and synthesised all the convictions about philosophy, biology, physiology, and psychology he had developed and promoted throughout his intense life; he also felt the need to conclude the book with a brief supplement, a supplement in which he discussed three recent and promising books: Hogben's *Nature of Living Matter*, Woodger's *Biological Principles*, and Russell's *Interpretation of Development and Heredity*. All these books were published between 1929 and 1930.

¹ Worrall to Woodger, ca. 1940, Box C 1/3 Misc, p. 1, UCL Archive, London.

² 1931 was also the year of the 2nd London Congress for the History of Science. As we have seen in the previous chapter, Haldane participated in a session chaired by Ritter and attended by Russell and Woodger, who both contributed.

Haldane was rather critical of Hogben's mechanistic interpretation of life phenomena: in his reductionist approach (an approach extended to animal behaviour) he overlooked – Haldane complained – the organic coordination and integratedness exhibited by any organism. Furthermore, his mechanist interpretation of hereditary phenomena - an interpretation drawing heavily on the latest advances promoted by the Mendelian school - supported, rather than undermined, mystical and vitalist hypotheses explaining inheritance. As Haldane thundered:

I can hardly imagine anything more calculated to make men vitalists of the old school than a contemplation of all the orderly facts relating to the behaviour of chromosomes in cell-division and fertilisation, with the related phenomena of hereditary transmission, together with the fact that we cannot form even the foggiest mechanistic conception of how these phenomena are brought about. To regard them as throwing light on any 'mechanism' of heredity seems to me to be only ludicrous.³

Conversely, and not surprisingly, Haldane was quite enthusiastic about Woodger and Russell, who represented a younger generation of scholars that was developing, and even improving, his own insights. Woodger, Haldane declared; "...carries me with him in nearly all his criticism, and his references to my own writings are very friendly, I can only express the hope that his book will be widely read...His criticisms", Haldane concluded, "of the use of both mechanistic and vitalistic ideas are even more thorough, and considerably more detailed, than my own; and he arrives at a conclusion in which I am in entire agreement with him..."⁴

Haldane also praised Russell's book, which he considered: "...a very scholarly and extremely interesting critical discussion of the theories which have, at various periods in the history of biology up to the present, been held on the subject of heredity and embryology. It is a book which can be very confidently recommended to the careful consideration of all those interested, not only in the subject, but

³ As Haldane continues: "Professor Hogben begins his book with the assumption that biology deals with 'living matter', and not simply with life. The detailed phenomena of hereditary transmission do not seem to me to take him any farther in showing how his assumption is consistent with biological observation, or how biology can dispense with the 'holistic' assumption that life means inherent coordinated maintenance of structure and activity, which we can observe, measure, and treat scientifically, but which necessarily eludes us if we attempt to resolve it into mechanism or relate it to a coexisting physically interpreted world." (Haldane, 1931, p. 148)

⁴ Haldane, 1931, pp. 149-150.

in its general philosophical implications.”⁵ Even though the organismal approach that Russell defended - an approach that, as Haldane himself recalled, was first developed by Ritter in the US - was totally in agreement with Haldane’s view, Haldane complained that Ritter’s and Russell’s position overlooked, sometimes, the importance of the environment. In fact, to Haldane, the unity of the organism should be extended to the environment too; both the individual organism and the environment in which it is immersed must be considered one unique inseparable unit. Furthermore, Haldane praised the critical discussions that Russell had undertaken about contemporary theories of heredity; Russell’s harsh critiques of Weismann’s germ-plasm and Mendelian genetics were as beautiful music to Haldane’s ears.

In short, Haldane, the elder statesman, not only fully supported new and more accurate versions of the theoretical biology he had taught throughout his long career, he also backed and encouraged new generations of scholars in improving what I have dubbed the ‘neo-Kantian biophilosophy’.⁶ In this chapter we will see that both Russell and Woodger, albeit from different perspectives and interests, took seriously all the post-Kantian tenets discussed in the second and third chapters: denial of both vitalism and mechanism; the acceptance of living organisation as a postulate; the use of teleological explanations; the prominence of function over structure; the essential organic relation of parts to the whole; and the fundamental interrelatedness of organism and environment. However, whereas Russell sought only to formulate an original and coherent framework — what he called “functional biology” — in which all these positions had their place; Woodger aimed to do nothing less than clarify and eventually solve all the biggest controversies affecting biological thought. In other words, more than a formulation of an alternative biology, Woodger preferred a critical biology in the Kantian sense; a theoretical biology that, with the new powerful tools provided by the analytic philosophers, aspired to unravel the presuppositions, assumptions and dogmas preventing or hindering any form of agreement among opposing schools. At the same time, and with the same analytic tools, Woodger tried to provide a logical and strong foundation to ‘organismal’ biology: a biology centred on the notion of organism as

⁵ Ibid., pp.152-153.

⁶ As he concluded: “The books of Mr. Woodger and Dr. Russell represent critical and constructive efforts to refashion biology on more secure theoretical basis.” (Haldane, 1931, p. 165)

organised hierarchical system.⁷ In the next sections I will introduce Russell's biological thought and his context, then I will focus on Woodger's background and his early theoretical biology. We will see that both were well connected, philosophically, socially, and institutionally, with the scientific community of their time; in other words, they did not represent a small silent minority, but a rather noisy minority.

4.2: E. S. Russell: the International Diffusion of Organismal Biology

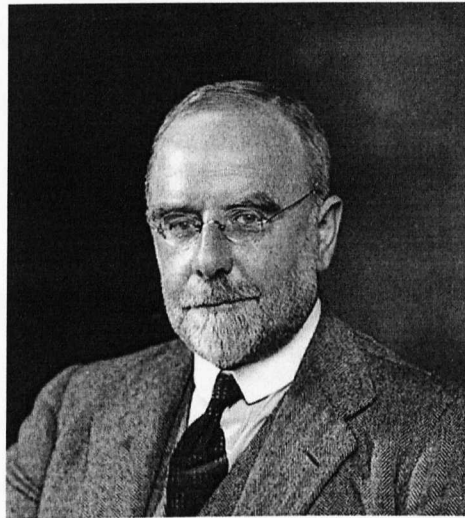


Fig. 4.1, E. S. Russell, 1887-1954⁸

The conception of the organism as essentially a unified whole is of course a very old one. It was clearly stated by Aristotle, and Kant has formulated it at great length in the Critique of Judgment.⁹

E. S. Russell

That we cannot explain or account for the directiveness and creativeness of life need make no difference to our projected functional biology; we must simply accept the immanent teleology of

⁷ As Nils Roll-Hansen well characterises these views, as well as the prominence of both men: "E. S. Russell and J. H. Woodger were among the most influential philosophers of biology in the English-speaking world in the second third of this century [C20th]. They were among the principal authorities on the subject among philosophers and biologists interested in the philosophy of science. Both were trained as biologists and were at some time active in biological research. While Woodger worked with embryology, Russell was a naturalist engaged in fisheries research...Despite their philosophical differences, Russell and Woodger were joined in a broad anti-mechanist biology. Biological phenomena should be taken at face value, not explained away by underlying physico-chemical mechanisms. The idea of particulate material genes, some kind of complex chemical molecules lodged along the chromosomes, was to both men unscientific speculation." (Roll-Hansen, 1984, p. 408)

⁸ Source: <http://icesjms.oxfordjournals.org/content/60/6/1169.full>.

⁹ Russell, 1930, p. 173.

organic activities as, so to speak, the basis or background of our biological thinking...because organic teleology is not mechanical, it is not therefore something miraculous and supernatural.¹⁰

E. S. Russell

Russell's fame as biologist and philosopher went well beyond British borders; when, in 1930, he published *The Interpretation of Development and Heredity*, biologists in both the German-speaking lands and the US knew him, and enthusiastically commented on his work. This is evident especially if we consider a letter that, in 1931, Ritter sent from San Diego to a young Viennese philosopher who, after Second World War, would become the initiator and promoter of the 'General System Theory': L. von Bertalanffy. Ritter had previously advised von Bertalanffy to read Russell's book; in turn, von Bertalanffy replied that he had already read it — indeed, Woodger himself had sent a copy to Austria:¹¹

It is very nice on your part to bring to my attention Russell's 'Interpretation of Development'. I knew that book already, Dr. Woodger sent me a copy of it. While I was reading it, I was quite amazed by how similar the book is — in content and order — to my "Critical Theory of Morphogenesis" (which was published almost 3 years ago). Since there is no reference in his work, Russell does not seem to know my publication; however, this is for me a remarkable proof of the "publicity of the case" and, again, it proves how much our "organismic" train of thought is in the air today. You will be further convinced of the striking parallelism between Russell's book and mine once it comes out in English, which, as you know, will happen very soon. In any case, I see the English edition of my "Critical Theory", and especially my "Theoretical Biology", as a formulation of the "organismic" view that

¹⁰ Russell, 1945, p. 176.

¹¹ The translation of the letter is my own. The original text in German of von Bertalanffy is: "Es ist sehr freundlich, dass Sie mich auf Russell's 'Interpretation of Development' aufmerksam machen. Ich kannte das Buch bereits, da Dr. Woodger mir ein Exemplar davon schickte. Beim Lesen war ich geradezu verblüfft, wie sehr dies Buch meiner „Kritischen Theorie der Formbildung“ (die fast 3 Jahre früher erschienen ist) sowohl in Disposition als auch inhaltlich ähnelt. Da Russell – indem er auf meine Publikation keinen Bezug nimmt, - mein Buch nicht zu kennen scheint, so ist mir das ein erstaunlicher Beweis der „Publizität der Falle“ und beweist mir aufs Neue, wie sehr unsere „organismischen“ Gedankengänge heute „in der Luft liegen“. Sie werden sich von der Parallelität des Russelchen Buches und des meinen Überzeugen können, sobald das letztere englisch herauskommt, was ja, wie Sie wissen, in Bälde der Fall sein wird. Ich hoffe übrigens, dass diese englische Ausgabe meiner „Kritischen Theorie“ und vor allem die von mir vorbereitete „Theoretische Biologie“ die Formulierung der „organismischen“ Auffassung ein gutes Stück über meinen früheren und Russels Standpunkt fordern wird.

represents a synthesis of a large part of my stances expressed in the past and Russell's position on the matter.¹²

When the English edition of von Bertalanffy's book came out in England in 1933 (in a version translated by Woodger himself and titled *Modern Theories of Development*), he expressed, in the introduction, his enthusiasm about the fact that the organismic view in biology was shared among many biologists and philosophers in many different countries; it was in the air because great books and articles, he continued, had been written on such a subject and figures such as Russell in the UK and Ritter in the US led the way. Even a reviewer of von Bertalanffy's book considered his author as "one of a small band of people who are paving the way to a new conception of the organism, a new orientation of biological thought."¹³

Although Russell's *Interpretation* further established him internationally, this cosmopolitan recognition was not new; he was already known in Italy where, in 1909, he had collaborated on a newly founded international journal directed by two Italian philosophers, Eugenio Rignano and Federigo Enriques. Indeed, in 1907, Rignano, Enriques, and other fellows based in various Italian Universities edited the first edition of *Rivista di Scienza* (renamed *Scientia* in 1909), aiming to offer an interdisciplinary platform where scientists from different countries, and interested in many different disciplines, could show and discuss their own specialities before an international audience. The editors defined the journal as an international organ of scientific synthesis and, in order to further such an international character, articles and reviews were presented in four different languages (French, German, Italian, and English). As well as von Bertalanffy himself, who, like Russell, worked regularly for the journal,¹⁴ famous contributors included scientists and philosophers such as Freud, Neurath, Carnap, Driesch, and Einstein (to mention just a few).¹⁵

¹² Letter from von Bertalanffy to Ritter, October 22th, 1931, Ritter Papers, 71/3 c, Box 6, Folder, Bertalanffy 1901, Bancroft Library Archive, University of Berkeley, California.

¹³ Quoted in von Bertalanffy, 1933, p. 4.

¹⁴ Von Bertalanffy, though less so than Russell, gave several contributions to the journal; especially in the form of reviews.

¹⁵ In biology, C. M. Child, Y. Delage, E. Rabaud, C. L. Morgan, R. Semon, R. Goldschmidt, C. S. Sherrington, J. Needham and others were published in *Scientia*. For a general history of the Journal see S. Linguetti 2005.

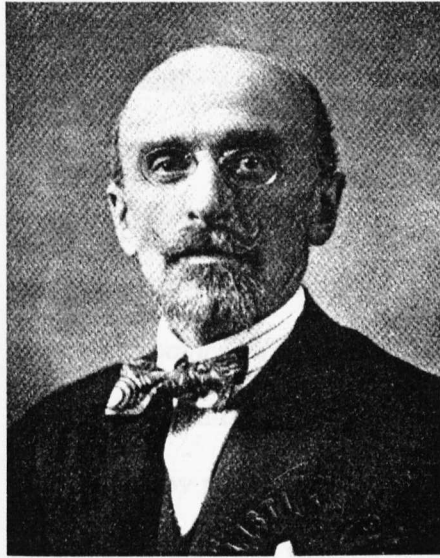


Fig. 4.2, Eugenio Rignano (1870-1930)¹⁶

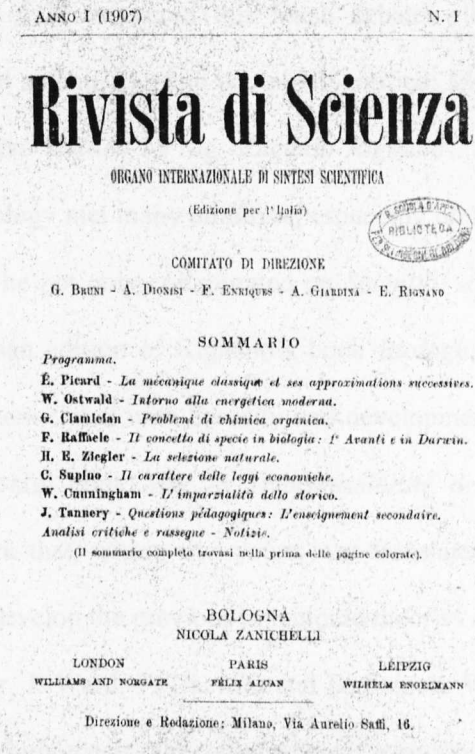


Fig. 4.3, First volume of the International Journal of Science

Between 1909 and 1933, Russell would publish two articles and more than 100 reviews in this journal. Moreover, he shared ideas, views and approaches in biology with Rignano. Above all, Russell was fascinated by Rignano's mnemonic theory of heredity. Rignano was seventeen years older than Russell, born in Livorno (Tuscany) in 1870. He had trained in physics and engineering at the University of Pisa and the University of Turin.¹⁷ From his university years, Rignano had demonstrated deep interests in philosophical issues as related to science and politics. As Enriques recalled, Rignano used to read Spencer and Comte, as well as Mill and Kant.¹⁸ With the new century, Rignano's philosophical and historical interests were increasingly focused on biology and its linked theoretical issues. Lamarckism, the opposition against neo-Darwinism, and holistic, anti-mechanist and anti-reductionist approaches characterised Rignano's bio-philosophy from the beginning. In 1926, he started a debate with Joseph Needham on the nature of life and organism. The book he published under Driesch's auspices, *Man Not a*

¹⁶ Source: Sarton, 1931, p. 2

¹⁷ See E. V. Stonequist, 1930, Eugenio Rignano 1870-1930, *American Journal of Sociology*, Vol. 36, N. 2., pp. 282-284 and Sarton, 1931.

¹⁸ Enriques, 1930.

Machine: A Study of the Finalistic Aspects of Life,¹⁹ triggered this harsh debate with the young Cambridge biochemist who, the next year, published an anti-Rignano pamphlet, entitled: *Man a Machine in Answer to a Romantical and Unscientific Treatise Written by Sig. Eugenio Rignano ...*²⁰. However, Rignano's teleological and organismic views on biology met many admirers, especially on the continent. Von Bertalanffy was one of his allies and friends; he not only collaborated on *Scientia*, writing articles and reviews, but, in 1930, he revised a new German edition of Rignano's book *Biological Memory*.²¹ Rignano's obsession for mnemonic phenomena as associated with heredity and development dated back to 1906, when he published a moderately successful book: *Sur la Transmissibilité des Caractères Acquis : Hypothèse d'une Centro-épigénèse*: a work that, within five years, was translated to German, English,²² and Italian and that aimed to extend and develop the previous mnemonic theories of inheritance as advanced by people such as E. Hering, S. Butler, J. Ward, F. Darwin, and R. Semon. What Rignano tried to do in this book was two-fold: to formulate a hypothesis that could synthesise both preformationist and epigenesist theories of heredity and, at the same time, to propose a Lamarckian mechanism through which acquired characters could be passed to the next generation. To Rignano, the element unifying

¹⁹ Rignano, 1926.

²⁰ Needham, 1927. Both Haraway (1976) and Winchester (2008) have described Needham as holist and organicist. However, according to letters, published and unpublished materials I have consulted, I have noted that Needham was rather criticised by his organismic fellows. I can confidently say that, at least during the early 1930s, he was not part of the organismic crowd, but rather critical of them. I think that Needham's bio-philosophy requires a serious rereading and rethinking because, even though he supposedly supported an organicist stance, it was a very peculiar and idiosyncratic stance.

²¹ E. Rignano, 1931, *Das Gedächtnis als Grundlage des Lebendigen; mit einer einleitung von Ludwig von Bertalanffy*, Wilhelm Braumuller, Wien. In a letter to Ritter on 14th December 1930, von Bertalanffy mentioned that he was working on the book; indeed, in expressing his regret to Ritter for the delay in replying to previous letters, he wrote: "I hope better to deserve your forgiveness when I tell you that I am not only in the midst of a big piece of work, but have also to revise and practically rewrite my book on the 'critical Theory of Morphology' for an English translation (Clarendon, Press, Oxford) and revise the German translation from the French of a book by my late friend Professor Rignano-Milano" (Von Bertalanffy to Ritter, 1930, 71/3 C, Box 6, Bertalanffy Correspondence, 14 December 1930, Ritter papers, Bancroft Library, University of California, Berkeley). The German edition of *Biological Memory*, with von Bertalanffy's introduction, was published after Rignano's death in 1930. The British edition was published in 1926 and introduced by the embryologist E. W. MacBride (1866-1940).

²² Not surprisingly, the English edition was translated in Chicago; indeed, Rignano was quite well known by the biologists based at the Zoological Department of the University of Chicago. As an example of how mnemonic theories of heredity and development were regarded as relevant by the Chicago group, there is an interesting letter from the director, Whitman, in 1909, to the celebrated psychologist and primatologist R. Yerkes (1876-1956). Whitman said: "Mnemonic phenomena are in my opinion at the basis of vital phenomena of every order. Psychology and physiology seem blend here, and I find no point at which they become separate. Yet it may be useful to classify as psychological, actions in which sense organs and brain are conspicuously concerned. On this point I have no right to express an opinion, as you will readily grant." (Whitman's letter to Yerkes, October, 24th, 1909 in Lillie Papers, Box IIA, Folder: 99, MBL Archive, Woods Hole). Relations between psychology and physiology, as well as ontogeny and phylogeny, were all central topics in Rignano's book translated the following year in Chicago.

ontogeny, phylogeny, and the acquisition of novelty in evolution was a mnemonic mechanism; ontogeny recapitulated phylogeny because the fertilized egg retained, in the form of mnemonic traces, all the history of its ancestors. Just as a phonograph 'reads' a disc producing sounds that were previously recorded, development represented to Rignano a progressive unfolding of mnemonic traces 'recorded' during phylogeny.

Russell was quite enthusiastic about Rignano's attempt; in 1910 he wrote a paper for *Scientia* in which, following Rignano, he dismissed both preformationist and epigenesist theories of heredity and development, assuming that the only hypotheses logically coherent and in agreement with scientific data were the mnemonic theories which: "...do not find many supporters among biologists nevertheless the compelling justifications that Semon, Rignano and Francis Darwin have provided long ago...what it is really significant is that these theories virtually introduce a new method in biology, a method that can be recognized as properly biological, whereas the mechanist and morphologist methods preferred in our time are not biological at all."²³

The relation between Rignano and Russell was further established when, in 1911, Russell travelled to Bologna in order to participate in the Fourth Congress of Philosophy; there, Russell read a paper soon to be published on *Scientia*:²⁴ a paper aiming to reject both vitalism (and its new forms) and neo-mechanism and, at the same time, proposing a third "attitude": an organismal approach. As Russell explained: "One may concede the universal validity of physical and chemical laws and yet hold that the laws of biology cannot be reduced to their level. To admit the physico-chemical determinism of life is not to admit that physico-chemical laws are adequate to explain life."²⁵ Like Haldane before him, Russell believed that life presented and exhibited peculiar phenomena; phenomena necessarily irreducible to physico-chemical mechanisms: "...while many of the phenomena presented by living things are thus to be explained as the direct result of simple physical and chemical relations, there still remain a vast number of

²³ Russell, 1910, p. 225, my translation from the French. Yet, in 1912 Russell reviewed Rignano's English edition and concluded that: "We are convinced that the solution for the problem of heredity and development must be sought in the particular phenomena that Rignano, with a rare acquaintance, has chosen as specifically important, and we deeply recommend his work, which constitutes to our eyes the best attempt so far to produce a simpler and more rational solution in the framework of a positive philosophy."(Russell, *Scientia*, Vol. 11, 1912, p. 439), my translation from the French.

²⁴ Russell, 1911, pp. 329-345.

²⁵ *Ibid.*, p. 330.

facts of life which cannot be explained by any direct reference to chemical laws. They present truly biological problems which can be solved only by biological laws.”²⁶ It is not surprising that one of the central phenomena that Russell deemed unexplainable in physico-chemical terms was the migration of eels. Indeed, in 1909 Russell joined the Board of Agriculture and Fisheries; working at the Aberdeen Laboratory, his research involved, among other things, studying the effects of intensive fishing. In particular, the fisheries department was committed to formulating censuses based on statistical observations of fish populations in various areas of the ocean. The fluctuations of fish populations, their distribution and migration in relation to the environment (without overlooking food chains and behaviour) provided precious information for a rational exploitation of the seas’ resources; vital information for the national economy.²⁷ As a skilled observer of marine biological phenomena, Russell maintained that knowledge about all these issues had to remain on purely biological basis.

In fact, to Russell, the fact that eels migrated, during the breeding season, from Northern and Western Europe to the warmer, saltier and deeper water of the Atlantic represented an irreducible living phenomenon because:

...even if we knew the exact chemical mechanism of muscular contraction, and of nervous conduction, for muscular movement is dependent upon nervous stimuli, we should not be a whit nearer an explanation of the fact that eel was taking this long journey to a particular area of the North Atlantic for the purpose of spawning. The fact is that the laws of metabolism and of the physico-chemical side of life lose by their very generality all power to explain concrete facts of higher order.²⁸

In short, migration ‘emerged’ from all the chemical and physical elements put together in forming a higher order of phenomena; as Russell concluded:

In the case of the eel it is possible to decompose the act of migration into a large number of acts of a different order, into the chemical reactions occurring in muscular movement, in nervous conduction, in

²⁶ *Ibid.*, p. 332.

²⁷ See Russell, 1932.

²⁸ Russell, 1911, p. 336.

the stimulation of peripheral sense organs, but by doing so one cannot but lose sight of the interconnection of these single acts, the interconnection which really binds together all these acts into the single act of migration.²⁹

At the Bologna conference Russell concluded that biology was an independent and irreducible science, not because living organisation required entelechies or vital principles, but because it dealt with phenomena of a peculiar order. In the following years, in reviewing and criticising more than 100 books in the pages of *Scientia*, Russell would state over and over again such a position. His vitriolic reviews against Mendelian genetics and all books propagandising a mechanistic view of life (including, in his opinion, Bateson's, Morgan's and Loeb's books) established him as an organismic biologist. There are very few doubts that Russell's publications in *Scientia* contributed in no small part to his international fame.

However, in the next sections we will see that Russell's plan throughout the years — from the publication of his first book, (*Form and Function*), to his last contribution (*The Directiveness of Organic Activities*) — followed a very coherent and reasoned line of thought. Both history and philosophy had to support his own conception of biology; a conception that, as we will see, was based on functional and integrated organic activity. Yet Russell's theoretical biology was employed concretely to deal with many different issues, from the interpretation of animal behaviour to regeneration, and from the physiology of digestion to comparative anatomy. But especially, it was used to tackle the classic problems of biology since Aristotle: development and heredity.

²⁹ Ibid., p. 336.

4.3: Russell's Agenda: Making History of Science an Integral Part of Contemporary Science

We need to look at living things with new eyes and truer sympathy. We shall then see them as active, living, passionate beings like ourselves, and we shall seek in our morphology to interpret as far as may be their form in terms of their activity. This is what Aristotle tried to do, and a succession of master-minds after him, we shall do well to get all the help from them we can.³⁰

E. S. Russell

Although Russell would eventually be committed throughout his life to the study of marine biology as related to fisheries issues, becoming first director of Fisheries Investigation, Ministry of Agriculture and Fisheries and, in 1940, President of the Zoology section at the British Association and President of the Linnaean society; he is mainly remembered for one of his classic books: *Form and Function: A Contribution to the History of Morphology*. The book was published in 1916, when he was twenty-nine, and represented a general excursus through the history of biology — a history that, nevertheless, had to support Russell's biological agenda. In fact, more than anyone else I have mentioned before or will bring up later, Russell was fully aware of being part of a venerable tradition: the post-Kantian tradition. As a keen historian, he selected his sources wisely and formulated a coherent narrative supporting and legitimising his own preferred option: the triumph of functional biology over the so-called “aberration” of the 19th century: materialism. After all, Russell's conclusions reflected his social concern too; to him scientific materialism was not a result of a wrong philosophy, but the outcome of the “...over-rapid development of a materialistic and luxurious civilization, in which man's material means have outrun his mental and moral growth.”³¹ In short, materialism was not only wrong as a scientific interpretation, it was a dangerous ideology to be fought against: history and science were the tools Russell chose to fight that battle.

The main argument characterising and ordering Russell's book was the idea that the history of morphological sciences (or morphological thought) could be divided into three different schools: the functional or synthetic school (to which Aristotle, Cuvier and von Baer belonged), the formal or

³⁰ Russell, 1916, p. 390.

³¹ Ibid., p. 373.

transcendental school (of which Geoffroy Saint Hilaire was a representative), and finally the materialist or 'disintegrative' school (which was founded by the Greek atomists). In Russell's passionate narrative, Cuvier emerged as a hero: after Aristotle, he was the first truly comparative anatomist because, as Russell claimed: "...like Aristotle, like the Italian anatomists, Cuvier studied structure and function together, even gave function the primacy."³² Cuvier, he added, was a teleologist in the wake of Kantian bio-philosophy; indeed, as he explicitly reported: "...there can be no doubt that [Cuvier] was influenced, at least in the exposition of his ideas, by Kant's *Kritik der Urteilskraft*, which appeared ten years before the publication of the *Lésons D'Anatomie Comparée*. Teleology in Kant's sense is and will always be a necessary postulate of biology."³³

Even though Cuvier's principles of correlation and condition of existence represented, to Russell, two fundamental pillars supporting what he would eventually dub, "functional biology" or the "psychobiological approach", he thought that other figures had made central contributions: Goethe, the German transcendentalists, and Richard Owen in Britain.³⁴ However, another giant surfaced in the history of biological thought: K. Ernst von Baer: "Von Baer reminds one greatly of Cuvier. There is the same sheer intellectual power, the same sanity of mind, the same synthetic grip. Von Baer, like Cuvier, never forgot that he was working with living things; he was saturated, like Cuvier with the sense of their functional adaptedness."³⁵ According to Russell, von Baer was influential well beyond his own country. In fact, not only was he behind Darwin's phylogenetic tree because: "...Darwin interpreted von Baer's law phylogenetically,"³⁶ but he influenced different generations of scholars who, like J. Muller, disapproved of cell theory and its atomist interpretations, and, like T. Huxley, defended the notion of ideal type.

In 1911, at the conference in Bologna, Russell had stated that living organisms were different from inert matter because, among other things, they were historical entities; activities, forms and

³² Ibid., p. 45.

³³ Ibid., p. 49.

³⁴ Owen first introduced the distinction between analogical and homological organs which represented, Russell argued, a distinction between structure and function: indeed, function, as a teleological property, characterised analogical organs.

³⁵ Russell, 1916, p. 145.

³⁶ Ibid., p. 257. Russell here is referring to the law according to which the structures visible during the earlier stages of ontogeny are more common among all organisms than structures appearing in later ontogenic stages. This subject is treated in Richards, 1992.

structures were necessarily shaped and related to their experiences and, therefore, any living being could only be understood comprehensively by knowing its phylogenetic past.³⁷ Now, five years later, Russell was arguing that knowing organisms' past would involve the understanding of hereditary transmission; indeed, knowledge about heredity would help to distinguish which characters were acquired and which simply inherited during evolutionary history. However, with hereditary transmission Russell did not intend gene transmission or any particulate theory of heredity; he intended a functional science of heredity linking together embryology and morphology. As a Lamarckian, Russell was convinced that functional activities of the organism slowly changed its structures while structural change could be fixed and transmitted to the next generations. Indeed, the enormous appeal that mnemonic theories of heredity had for Russell, and that closed his celebrated and ambitious first book, derived from his Lamarckism. Because structural variations depended on the organism's functional responses to the environment and functional satisfaction of its needs, structural changes emerged from those functional activities that, in some way and under different forms, were 'stored' in the germ cells and became hereditary. Samuel Butler, together with Orr, Cope, Rignano and Francis Darwin were enlisted in supporting such a view (although from slightly different perspectives). In sum, to the young Russell, mnemonic theories of heredity and development were the only hypotheses coherent with a functional and organismal understanding of biology.

Russell's biological agenda — an agenda now justified from his historical account — found further support in his theoretical biology (and its philosophical foundations). Indeed, in 1924, Russell published a new book simply titled: *The Study of Living Things*; a work aiming to "outline" a method for biological investigation that would eventually avoid both materialist approaches and vitalist speculation.³⁸ Haldane's influence on Russell's second book was particularly evident; in fact, as we have seen in the previous chapter, during the second decade of the 20th century, Haldane became a prominent figure among scientists, philosophers, and laymen. After the publication of his *Mechanism, Life and Personality* (1913), *Organism and Environment as Illustrated by Breathing* (1917), *The New Physiology* (1919), and *Respiration* (1921), Haldane represented a flag symbolising a campaign against mechanist and

³⁷ In Russell's own words: "we must regard the organism as an historical being and interpret its present structure and activities in the light of its past history." (Russell, 1911, p. 343)

³⁸ See Haldane, 1924, p. VII.

reductionist interpretations of physiology and biology. Russell did not hide this; as he clearly pointed out in the book's preface: "I owe much to the writings of J. S. Haldane..."³⁹ This was not, though, a mere vague acknowledgement, because Haldane's ideas were effectively reported and positively discussed throughout Russell's book; indeed, to him, Haldane's work represented the ideal method to follow in biological investigations:

The finest modern exposition of a 'biological' method, which should mediate between physics and psychology, is that set forth by Dr. J. S. Haldane in a series of recent publications. In considering his powerful plea for an independent biology with laws and concepts of its own we shall see how irreconcilable are his views with the mechanistic theory...⁴⁰

In his epistemic treatment of life sciences, Russell distinguished five different methods: methods that had been applied and used in different historical periods. There was a morphological, a physiological, a vitalist, a psychological, and a biological method. The first assumed that an organism's activities could be deduced from observation and knowledge of its structure, so that function was an 'effect' of the organism's material structure. Yet, Haldane in England and Delage in France had convincingly rejected such a method: it betrayed an antiquated "habit of thought", it supported the misleading machine analogy, it sustained a static view of living entities, and it backed particulate theories of heredity. The second 'attitude' instead, although recognising the primacy of function upon structure, overlooked the organism's unity, its individuality and 'relative' independence' from the environment:

Materialist physiology...goes to the opposite extreme from morphology. While the morphologist studies the form and structure of the organism in almost complete isolation from its environment, the physiologist merges it completely into its surroundings and robs it of all independence...it cannot consider the organism as a living and independent whole. Its laws have no reference to individuality.⁴¹

³⁹ Russell, 1924, p. VII.

⁴⁰ Ibid., p. 46.

⁴¹ Ibid., pp. 12-13.

The third method was quickly dismissed; indeed, vitalism was defined by Russell as pure materialism with the addition of a mystical, speculative and unintelligible force. The fourth viewpoint represented a positive step toward the 'right' method; it assumed the individuality and unity of organisms and presupposed their abilities to perceive the environment and behave accordingly. Finally, the fifth approach represented the best so far; it was Haldane's approach. It regarded organisms as persisting, real and individual wholes.

However, Russell advocated a mixed method: both psychological and biological approaches could be used together, they could make a psychobiological method, which was dubbed simply "functional biology". Such an approach had to assume not only that organisms were perceptive systems, but also that they were irreducible purposive individualities. Living things always have 'instinctive tendencies' to maintain such a system intact; they strive, struggle and fight to stay alive. Such a set of instinctive tendencies was named by Russell "hormé":

The objective purposiveness of organic activity, which is the outcome of *hormic* impulse, or tendency, is not, like the purposiveness of a machine, a fixed and automatic thing, but on the contrary is self-regulatory and adjustable to a wide range of circumstance. A completely blind, unalterable and automatic activity would soon destroy itself... adjustability, flexibility, of response is essential.⁴²

Therefore, both biological and psychological approaches were strictly related because organisms, according to Russell, acquired their specific individuality and structure through active perception of their environment and, accordingly, through their responses and adjustments to it. In sum, in the same way as functional activities made structure, so psychological activities constituted biological forms.⁴³ The characterisation of organisms as '*hormic* interconnected systems' was beautifully described by Russell with a very Kantian analogy between works of art and natural products (Kant's *Naturzwecke*):

⁴² Ibid., p. 57.

⁴³ Russell: "...it is mainly through perception that life becomes individualized and separates itself out from the environing flux. Through perception the organism clears, as it were, a space around it in which to live, and disposes of time in which to protect itself against the surrounding influences which would imminently destroy it." (Russell, 1932, p. 59)

There is an unanalysable unity in a work of art – the parts form an individualized whole or unity and have a meaning only in relation to the whole. So also in the living thing. As works of art are static organisms, so organisms are dynamic works of art. It follows that living things can, no more than works of art, be exhausted of their content by the analytic and superficial description offered by the physical sciences. They are the sounds and the shapes and the colours, but they are more, as works of art are more. They differ from works of art being self-creative, or created by Nature as Artist.⁴⁴

The functional method advocated by Russell was readily applied to specific biological problems: first of all, to the interpretation of the behaviour of the simplest organisms. In fact, in contrast to Loeb's rigid and mechanist interpretations, Russell noticed that organisms such as *Amoeba* or *Pelomyxa* did not show very stereotyped or fixed behaviour; in the actions involved in capturing motile preys, they manifested creative and unexpected activities. If organisms reacted in unexpected ways to old or new situations (old or new stimuli),⁴⁵ a mechanical interpretation based on an automatic or determined responses had to be rejected.⁴⁶ To Russell, both *Amoeba* and *Pelomyxa* responded not to a physico-chemical stimulus, but to a perceived and interpreted stimulus; in other words, the best way to interpret creative behaviour is to assume that external stimuli were 'perceived' as directly 'significant', and not as mere external physico-chemical stimuli: "What is responded to is not the stimulus *qua* physico-chemical, but the stimulus as perceived, and not the stimulus merely as perceived, but as interpreted. Response is really to the meaning of the perceived stimulus, not to the stimulus itself."⁴⁷

⁴⁴ Russell, 1924, p. 61.

⁴⁵ Russell reported several examples of creative behaviour among Protista and unicellular organisms, see Haldane, 1924, pp. 65-81.

⁴⁶ Russell, in referring to the work of Kepner and Edwards on *Amoeba* and *Pelomyxa* feeding habits (W. A. Kepner, W. C. Whitlock, 1917, Food-reactions of *Pelomyxa carolinensis*, *Journ. Exper. Zool.*, vol. XXIV, pp. 381-404), stated: "From this review of the feeding responses of *Amoeba* and *Pelomyxa*, as observed with care and without prejudice by skilled and competent workers, it is apparent how much simpler and adequate is the psychological interpretation than a materialistic. Any attempted restatement in terms of surface tension or rigidly determined tropisms would be lame and hypothetical in comparison." (Russell, 1924, p. 76)

⁴⁷ Russell, 1924, p. 77. On the way to study animal behaviour in general, Russell proposed a list of rules that the functional biologist should follow: 1) actions are responses of the organism as a whole, 2) actions must be studied in relation to the reciprocal influence of the *hormic* impulse and the perceived situation, 3) the living organism must be studied in his natural environment first, 4) in an experimental setting, the responses of an organism must always be interpreted as if the organism was responding to stimuli happening in its natural setting, 5) the analysis of physical stimuli must be centred on the analysis of the 'meaning' of the overall situation in the environment, i.e., what is important to the organism or what is not etc., 6) any response of an organism has a goal or aim toward an object; it is significant, 7) the aim of an action can be found in observing the results of specific responses, or from the observation of the all chain of actions bringing to satisfaction of cessation of the activity, 8) responses can be

In addition to Haldane, Russell included D'Arcy Thompson too in his broad biological agenda; in fact, although functional biology entailed a study of 'perceived' stimuli and functional adaptations, it did not overlook the so called 'material condition of life'; that is to say all the properties of life that are contiguous with physics and chemistry. Because functional activities required specific substances to work and were constrained by determined physical forces, a knowledge about what Russell dubbed "the negative condition of functional activity" was essential; and Thompson's *Growth and Form* pointed in that direction. Of course, Russell deemed the physico-chemical investigation quite a secondary interest for biologists; after all, physico-chemical processes — elements such as temperature, various chemical substances essential to life, light etc. — represented a mere background in which organisms actively moved and against which they creatively reacted. However, like Haldane and Thompson before him, Russell maintained that investigation in biology required both analysis and synthesis; therefore, both knowledge of the organic parts constituting the whole (physico-chemical as psycho-biological knowledge), and how the whole produces or shapes its parts. The physico-chemical understanding of the organism represented only a small step toward a comprehensive understanding of the nature of life.

Even though animal behaviour, together with the so-called 'negative conditions of living', were both important parts of Russell's functional biology, one of the most significant theoretical consequences that functional biology entailed was its incompatibility with Weismann's germ-plasm theory and with Mendelian genetics. To Russell, all of these theories (i.e. hypotheses based on the assumption that some well-defined particles could explain, in principle, the transmission and development of morphological characters) were based on pure speculation or presupposition. Russell did not question the idea that there was a material continuity among generations or races; he only questioned that such a continuity could be explained by determinants or genes. Functional biology must interpret both heredity and development from a very different perspective; firstly, heredity did not consist in the transmission of material stuff but in the transmission of tendencies (namely, potential functions); secondly, and as a consequence, development was the process through which these tendencies or potential functions became, gradually, actual functions: "What is essentially transmitted is not structure but potential function, a bundle of

classified as instances of aims without any respect to the physical nature of the stimulus. See Russell, 1924, pp. 79-80.

habitual tendencies which gradually become actualised in structure.”⁴⁸ The link between functional or organismal biology and its bearing on the interpretation of heredity and development assumed a central position among the interests of Russell. After all, functional biology was precisely thought to tackle all the fundamental activities concerning living organisms i.e., development, heredity, physiology and evolution. Indeed, in 1930, Russell would publish an entire monograph focussed on the interpretation of heredity, development and their mutual relations. Probably, from a historical viewpoint, such a monograph represents one of the most vigorously anti-Weismannian and anti-Mendelian books written in that period, on British soil at least.

4.4: Heredity and Development without Genes.

Delage’s criticism of particulate theories is in fact unanswerable. If the cell and the developing organism are regarded as physico-chemical systems in constant metabolic relations with their environment, external and internal, there is absolutely no place for independent and isolated material units which represent or determine certain characters or groups of characters. No part of the cell can exist in isolation from the whole; to imagine such is to create a conceptual fiction to which nothing corresponds in reality.⁴⁹

The gene is a word, which enables a complicated happening to be briefly denominated.⁵⁰

E. S. Russell

To Russell, *The Interpretation of Development and Heredity* (IDH) represented the consequent and most natural application of the organismal or functional biology he had previously established, both historically and philosophically in previous books and articles. For many years indeed, he had expressed his ideas on these topics in reviews of French, German and English books in *Scientia*. In 1914, for example, he reviewed Bateson’s *Mendel’s Principles of Heredity* and Plate’s *Vererbungslehre mit besonderer Berücksichtigung des Menschen (Heredity, with Special Reference to Man)*. Bateson’s book was

⁴⁸ Russell, 1924, p. 132.

⁴⁹ Russell, 1930, p. 82.

⁵⁰ Quoted in Russell, 1930, p. 67. The original article is Dembowski, 1926, pp. 216-147.

published the previous year and represented the third edition of a successful textbook. Russell praised the clear exposition of the Mendelian doctrine; he liked the illustrations and pictures, and appreciated both Mendel's biography and the translation of two of his papers. However, a few lines later, Russell was much less enthusiastic; of course, he partly accepted Bateson's suggestion according to which hereditary units could be thought of as things similar to enzymes, but he warned that Mendelian analysis was going too far:

For now, Mendelians manifest a certain overconfidence, too much enthusiasm, about the universal application of their ideas...Mendelism should regard the only appropriate place convenient to itself, which is that of a very precious method of analysis applicable to some modality of hereditary transmission; it could not be considered as a complete solution to all problems of heredity.⁵¹

In the next review Russell was less diplomatic; indeed, he complained that: "The conception of the organism as a set of character-units is dogmatically seen as the only possible alternative, and the study of heredity is arbitrarily defined as the study of gene's mutual relations (or determinant of unit-characters)."⁵² In the following years Russell would remain loyal to this idea. Reviews of T. H. Morgan, M. Caullery, L. Doncaster, H. F. Osborn and others betray his uneasiness with a gene-centric or unit-centric approach to many problems of biology, from sexual determination to human intelligence, from development to evolution, from morphology to adaptation. In sum, Mendelian genetics had to be considered only an aspect, a portion, a tiny section of a bigger discipline or larger framework exemplified from the studies of heredity, development and evolution. When, in 1930, IDH was published, Russell intended to reinforce this idea: heredity cannot be defined as Mendelian genetics because heredity was much more than that; indeed, heredity deals not only with stochastic variations among populations, but also with the reproduction of individual organic form through development:

The broad fact of repetition of type has tended of recent years to become lost from sight, because of the excessive attention paid to the laws of transmission of such slight variations or differences as are

⁵¹ My translation from the French, see Russell, 1914b.

⁵² My translation from the French, see Russell 1914.

no bar to successful interbreeding; the study of heredity has come to mean in practice the study of the modes of inheritance of minor differences. But clearly there is this major problem which is practically untouched by genetic or statistical studies, and equally clearly, repetition of type must be regarded as one of the main characteristics of development, not as separate and independent problem.”⁵³

It is important to notice that 1930 was also the year in which Ronald Fisher published the *Genetical Theory of Natural Selection*, a successful book which propounded the very opposite conception of heredity — a conception totally based on populations rather than individuals. In fact, qualitative individual changes could be ascribed to the selection of small measurable and quantitative variations within populations: variations inherited and selected. Neither evolutionary change nor heredity has anything to do with individuals and their development; but with the transmission of genes as statistically measured within populations. In sum, organic form passed at second hand; it became a mere epiphenomenon of gene-pool variations within populations. Such a doctrine would eventually lead to the establishment of a new discipline called population genetics; indeed, it would be one of the milestones of the modern evolutionary synthesis.

However, Russell had a very different modern synthesis in mind; a synthesis based on his conception of functional or organismic heredity as the expression of developmental forces; in fact, the whole of IDH presents a long and critical argument against Morgan’s idea that heredity itself could be severed from development. Aristotle, Russell argued, was the first to recognise: “...the important point that the explanation of hereditary resemblances is dependent upon the explanation of development, that this resemblance is a feature of development rather than a separate problem.”⁵⁴ In Russell’s interpretation, von Baer’s whole notion of ‘Wesenheit’, the essential nature of the animal, spoke against the idea that embryogenesis could be disconnected from hereditary processes, in principle at least. In fact, for von Baer, reproduction was defined as: “the taking on by a part of the potentialities of the whole,” i.e., an organic part, a bud or egg, broke the domination of the whole and developed into a new individual

⁵³ Russell, 1930, p. 8.

⁵⁴ *Ibid.*, p. 24.

organism.⁵⁵ The formation and development of this new individual was driven by the ‘Wesenheit’, the *essential nature*, which guided the organism from a fertilized egg towards its *complexification* and increasing individuality. The whole process was conceived as intrinsically developmental throughout: “...it is not the matter, in its mere arrangement, but the essential nature of the procreating organism that rules the development of the offspring.”⁵⁶ We could interpret the ‘Wesenheit’ as the variable x that organisms transmit to their offspring, generation on generation; however, this hypothetical x could never be severed from development because development was the actual and explicit manifestation of ‘Wesenheit’. In sum, to Russell, the idea that heredity could be studied only through development had a very old *pedigree*. And the modern theories, the particulate theories, run against such a tradition.

Furthermore, Russell, in common with many organismal biologists, considered both Weismann’s germ-plasm theory and Morgan’s theory of the gene as lying on a similar conceptual framework; in fact, the notions of determinant and of gene had some interesting similarities, although their existence was deduced in different ways: “The gene theory in its original form was linked up with the concept of unit characters. The process of thought is the same as that which led Weismann to postulate the existence of separate determinants to account for the independent heritability of small definite, discontinuous characters.”⁵⁷ In 1926, T. H. Morgan had published *The Theory of the Gene*, a book in which he synthesised many of the results achieved to date by him and the group of students working at the Columbia lab. Morgan summarised his theory succinctly: the exposition of the Mendelian laws of segregation and dominance was followed by the hypothesis that genes were physically aligned along chromosomes. The phenomena of crossing over, linkage and mutation were explained and illustrated, the statistical, quantitative and physical studies on gene activity highlighted and praised. The book was certainly one of the best popular formulations of the gene theory so far and, for this reason, a central target for Russell.

Russell’s critiques, both of Weismann’s germ-plasm and Morgan’s genetics, will be discussed in more detail in the conclusions; here, I will rather describe Russell’s alternative. To begin, Russell compared Johannsen’s conceptions of genetics, genes and heredity with Morgan’s. Wilhelm Johannsen

⁵⁵ The similarity between von Baer’s and Child’s conception of reproduction is striking.

⁵⁶ Von Baer quoted in Russell, 1930, p. 35.

⁵⁷ Russell, 1930, p. 59.

(1857-1927) was a Danish botanist who first coined the term 'gene'. In 1923, he published a very short article that Russell took as a source of inexhaustible inspiration.⁵⁸ The article was published in *Hereditas*, a journal that was originally edited by *Mendelska sällskapet i Lund* (the Mendelian Society of Lund), and it represented a formidable attack against the Mendelian agenda. Firstly, Johannsen was sceptical about ontological interpretations of genes, as material or physical entities aligned on chromosomes stored in cell nuclei; in other words, as Churchill reminds us, Johannsen did not believe in the "...cytological efforts to bind Mendelian patterns of segregation to chromosomal phenomena."⁵⁹ Secondly, his notion of gene betrayed a developmental conception; to Johannsen, genes were not things but correlated chemical *reactions*, whole organic reactions that had nothing do to with the notion of unit-character: "from a physiological or chemico-biological standpoint we must *a priori* in characters or developed parts of organisms see *Reactions* of the (I should say geno-typical) constitution belonging to the zygote in question; and from this point of view there are no unit-characters at all!"⁶⁰ Thirdly, genetics was affected by misleading terminology guiding a confusing train of thought: "...in the language of genetics we meet with some unhappy old-fashioned expressions, relics and obsolete conceptions – the worst of all these relics is probably the expression *Transmission* where no transmission exists but where continuity is found!"⁶¹ Fourthly, the hope of reducing the genotype to a set of particles was pretentious and unsupported by observed facts; as Johannsen himself emphatically put it:

We are very far from the ideal of enthusiastic Mendelians, viz. The possibility of dissolving genotypes into relatively small units, be they called genes, allelomorphes, factors or something else. Personally I believe in a great central 'something' as yet not divisible into separate factors. The pomace-flies in Morgan's splendid experiments continue to be pomace-flies even if they lose all 'good' genes necessary for a normal fly-life, or if they be possessed with all the 'bad' genes, detrimental to the welfare of this little friend of the geneticists. Disregarding this (perhaps only provisional?) central

⁵⁸ As Russell described it: "In a short but fundamental paper he lays [Johannsen] his finger on the limitations of modern genetical theory, and assesses its general significance in masterly fashion." (Russell, 1930, p. 63). As F. Churchill reports, Johannsen was also harshly critical of the British school of biometricians, as exemplified by Weldon and Pearson. He used to say indeed: "We must pursue the science of heredity but not as mathematics", Johannsen, quoted in Churchill, 1974, p. 8.

⁵⁹ Churchill, 1976, p. 18.

⁶⁰ Johannsen, 1923, p. 136.

⁶¹ *Ibid.*, p. 136.

something we should consider the numerous genes, which have been segregated, combined or linked in our modern genetic work. But what have we really seen? The answer is easily given: we have only seen *differences*.⁶²



Fig. 4.4, W. Johannsen (1857-1927)⁶³



Fig. 4.5, T. H. Morgan (1866-1945)⁶⁴

The very same distinction between genotype and phenotype that Johannsen first made was essentially developmental; to him in fact, the phenotype represented the reaction of the whole genotype in interaction with the environment: "...however far we may proceed in analysing the genotypes in separable genes or factors, it must always be borne in mind, that the characters of the organisms – their Phenotypical features – are the reaction of the genotype *in toto*. The Mendelian units as such, taken *per se* are powerless."⁶⁵

To Russell, all this closely fitted his own conceptions; Johannsen's central 'something' could easily be interpreted as von Baer's 'Wesenheit'; heredity was 'something' that, in principle, could not be cut and sliced, because it was a property of the whole organism. The gene theory instead reified and endowed: "...with material existence what are merely differences, and it does this by postulating a gene for every heritable difference found."⁶⁶ In sum, Morgan, together with Mendelian geneticists, invented or posited fictional entities to explain the differences observed in *Drosophila* eye colour. In so doing, they

⁶² Johannsen, 1923, p 138.

⁶³ Source: *The History of Biology* de Erik Nordenskiöld, Ed. Knopf, 1928.

⁶⁴ Source: <http://ihm.nlm.nih.gov/>

⁶⁵ *Ibid.*, p. 139. Then Johannsen concluded: "...the phenotype being the reaction of the genotype (nature) with the ambient conditions (nurture)." (Johannsen, 1923, p. 141)

⁶⁶ Russell, 1930, p.31.

sliced the organism into abstract parts. On the one hand heredity, with its fictional, discrete and separate particles; on the other development; conceived as mere effects of those particles and their arrangements. However, not only was Mendelian genetics inadequate as an explanation for the mechanism of heredity in general; it also focussed on unimportant or secondary phenomena.

As Albert Brachet (1869-1930), one of the leading figures in the Belgian school of embryology, had famously distinguished, development dealt with two different kinds of hereditary potencies or tendencies: those characterising *general heredity* and those making *special heredity*, the former has to do with the laws or causes producing the whole individual belonging to a species; the general type, so to speak. The latter instead concerned small individual variations; or, in other words, all the variations or deviations added to the *general heredity*.⁶⁷ In Brachet's, as in Russell's mind, special heredity represented a secondary sub-section of general heredity; which denoted the study of heredity *par-excellence*. Now genetics, in dealing with small or superficial variations, with special heredity, overlooked the production and reproduction of the organism's type i.e., general heredity. In other words, genetics was unable to shed any light on one of the oldest issues in biology: how like begets like.⁶⁸ Furthermore, drawing on F. R. Lillie (see chapter 5),⁶⁹ Russell added that gene theory, as it was formulated, was of no help in understanding how organisms develop. Positing imaginary entities equally stored in the cell nuclei did not advance our knowledge of the way that cells differentiate, indeed, differentiation was probably a phenomenon tied to cell cytoplasm and internal cell interactions in connection with whole individual organism. In the end, Morgan's gene theory was considered by Russell inferior even to Weismann's germ-plasm.

⁶⁷ See Brachet, 1917, see also Mulnard, 1992.

⁶⁸ As Russell claimed: "It is these *special* resemblances and differences that have been the subject of the modern study of heredity, whether by biometrical or by genetical methods. The broad general resemblances of type give no hold for experimental or statistical treatment, and have accordingly on the whole been ignored. But it is this general hereditary resemblance which constitutes the main problem. We saw in discussing the gene theory that it deals only with differences between closely allied forms, and with the modes of inheritance of these differences; it leaves the main problem quite untouched as to why, for example, from a pair of *Drosophila* only *Drosophila* arise. It takes for granted the inheritance of Johannsen's 'great central something' – the general hereditary equipment of the species." (Russell, 1930, p. 270)

⁶⁹ In particular Lillie's "The Gene and the Ontogenetic Process", an article published in *Science* in 1927. In this paper Lillie had argued that gene theory could not help to embryology and developmental theories.

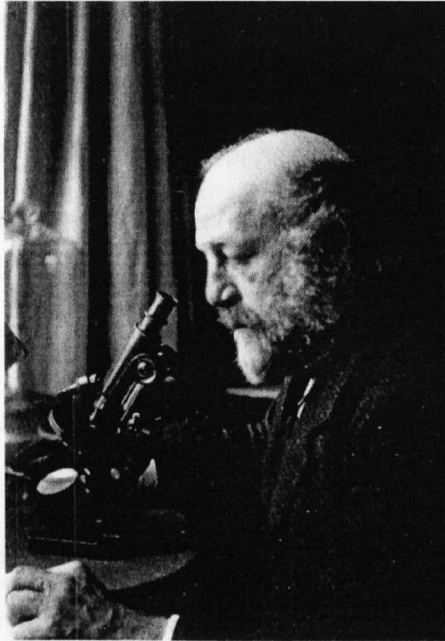


Fig. 4.6, Albert Brachet (1869-1930)⁷⁰

In Russell's project to empty heredity and development of particles, both historical figures and contemporaries scientists were enlisted:⁷¹ Aristotle, von Baer, Haldane, Johannsen, and Lillie of course, but also C. Bernard, Y. Delage, D'Arcy Thompson, C. O. Whitman, C. M. Child, C. Sedgwick C. Sherrington, E. G. Conklin, H. Woodger, W. E. Ritter and others. Ritter was particularly important; Russell had borrowed from him the term 'organismal biology' and, as he stated: "It will be seen that Ritter's point of view is essentially the same as that taken here, though he has arrived at it by a different route. I take this opportunity of acknowledging my indebtedness to Ritter..."⁷² Bernard clearly upheld and disseminated the organismic view in medicine and biology.⁷³ Delage too deserved a special mention in Russell's intellectual geography. In 1895 he had published a large volume, *L' hérédité et les grands problèmes de la biologie générale*: a book that went through three editions and that influenced subsequent generations of scholars.⁷⁴ Delage had introduced the term 'organismic biology', had formulated a violent

⁷⁰ Source: <http://www.md.ucl.ac.be/histoire/vancamp/brachet.htm>.

⁷¹ Russell also included in his list Whitehead, who, as a philosopher, had provided the theoretical scaffolding for organismal theory.

⁷² Russell, 1930, p. 177. See chapter 6.

⁷³ Russell referred to Bernard's *La Science Experimentale*, a book published in 1890 where Bernard effectively admitted: "In saying that life is a directive idea or an evolutive force of being, we simply convey the idea that there is an unity in all morphological and chemical changes that are produced, at beginning, by the germ until the end of life", my translation from French, see C. Bernard, 1890, p. 430.

⁷⁴ As Russell wrote of the book: "He exhibits throughout a clarity of thought, fidelity to the facts of observations, and a sobriety of hypothesis that make his book one of the finest contributions to general biology ever written"(Russell, 1930, p. 84). See also Introduction and chapter 5 of this thesis.

critique against particulate theories of heredity, and had proposed an epigenesisist hypothesis of heredity and development; all achievements that Russell found highly significant. D'Arcy Thompson had successfully criticised the morphological, structural approach to understanding heredity and development; to Thompson heredity, as we have seen in the previous chapter, had to do with energy and its manifestation and not with bare matter. Yet, to Thompson, heredity was a property belonging to the nucleus, cytoplasm and the cell as a whole. Furthermore, Thompson had also conceived organisms in a Kantian way: as individual wholes where the sum was more than the parts.⁷⁵ Finally, with Whitman and Conklin, Thompson had condemned cell theory; the individual organism was not a mere colony of cells, because cell organisation was itself a product of the whole organism. Furthermore, Child had clearly shown that ontogeny was triggered and directed by a whole system of reactions; Neither particles nor vital entities were required. The organism was seen as an indissoluble unity in both heredity and development.⁷⁶ Both Sedgwick and Sherrington had stressed the functional integrity of the organism as a whole; the former in his embryological observations, the latter in his studies of the nervous system. Finally, Woodger, had analysed the meaning of some central notions belonging to organismal biology.⁷⁷

Russell was a synthesiser; he gathered information from many different sources, discussed the pros and cons of several theories and built his own coherent system of thought — a system based mainly on a strenuous critique of mechanist, materialist, and reductionist interpretations of living phenomena. Like Haldane, he believed that scientific materialism had dangerous social consequences, as Roll-Hansen explains:

He [Russell] sees the refutation of reductionism in biology as part of a crusade against materialism.

But he believes mechanism to be a failure in biology, as well as philosophically untenable and socially

⁷⁵ As Russell specified: "All parts and organs are, as Kant would say, reciprocally means and ends, and all cooperate in the life of the organism as a whole. For, as D'Arcy Thompson, 'the life of the body is more than the sum of the properties of the cells of which it is composed.'" (Russell, 1930, p.148)

⁷⁶ See Russell, 1930, pp. 92-93. As Russell emphasised: "This principle of unity, or action of the organism as a whole, corresponds to Whitman's concept of organization...the same view, that development is essentially an activity of the organism as a whole, has also been upheld by others — by Conklin and Child for instance, and by Ritter..." (Russell, 1930, p. 244)

⁷⁷ See Russell, 1930, p. 189.

harmful. Mechanism had dominated nineteenth-century biology, and now it was time to formulate a fundamentally different methodology.⁷⁸

However, Russell's theoretical system — his organismal discourse — was not entirely original. Indeed, as von Bertalanffy had mentioned in his *Modern Theories of Development*, organismic or organismal biology was a fairly widespread movement, both in Europe and in the USA:

If one may use a pictorial catchword the development of science in the last decades may be characterized by an 'organismic revolution' which has taken place...the reader on this side of the Atlantic will easily detect the parallelism with Whitehead and other American authors who, at this time, were very little known in Europe. This 'revolution', though, was not merely a development of philosophy but most definitely in science itself.⁷⁹

The "organismic revolution" mentioned by von Bertalanffy had its origins, in fact, in a venerable and long tradition; a tradition that increasingly became philosophically convincing and internationally recognised. The application of such a philosophy to the problems of heredity and development provided radical and controversial results. The tenets of post-Kantian tradition clashed with the so called "modern" hypotheses of heredity and development; as Russell explicitly concluded, genetics, together with all particulate hypotheses had to be rejected, first and foremost, on theoretical grounds:

If we hold fast to the principle that the whole cannot be completely explained in terms of its parts, that the modes of action of higher unities may be conditioned, but cannot be fully accounted for, by the modes of action of lower unities, it follows that no substance and no sub-cellular unities can be invoked as sufficiently accounting for the phenomena of development and heredity, which are essentially phenomena manifested by whole organisms – unicellular or multicellular.⁸⁰

⁷⁸ Roll-Hansen, 1984, p. 409.

⁷⁹ von Bertalanffy, 1933, p. VII.

⁸⁰ Russell, 1930, p. 192.

Organismal biology, with its essentially neo-Kantian framework, required that chromosomes were starters of catalytic processes in an integrated hierarchical system, they did not alone cause development and differentiation; they were not alone responsible for hereditary characters. Indeed, if the higher activities of the organism were not fully reducible to its lower actions, the activities of the whole could only be transmitted by the whole itself, namely by the whole fertilized egg.⁸¹ Therefore, the notion of hierarchical system became central when dealing with organic phenomena; heredity was no exception, it was a property of the whole and had to be investigated as such. Heredity had to be seen as the *actual* functional exhibition of *potential* tendencies; tendencies that could be identified only through the study of development. Even after the triumph of the chromosome theory of heredity, Russell would continue to support mnemonic, Lamarckian and developmental interpretations; interpretations that were increasingly enriched by the strong belief that organic phenomena were understandable as hierarchical — partially reducible and essentially interrelated — phenomena. However, it would be Woodger who, more than anyone else, would dedicate — with the relatively new logical tools provided by analytic philosophers — the greatest attention to formulating a coherent and well-grounded model of the organic hierarchical system.

4.5: Woodger's Philosophical Agenda: What Biology Required

What biology requires is a better ventilation of its thought and a more critical scrutiny of its concepts; more openmindedness and more careful consideration of the relation between investigation and theoretical interpretation. But above all we need a wider recognition of the value of thought itself. Biologists have taken the celebrated saying of John Hunter: 'Don't think; try' too literally...you must think first and *then* try. And you must think about the right things. In biology we require to think primarily about biological facts, not about hypothetical billiard balls. But even thinking about biological facts is not enough. We must scrutinize our ways of thinking too, in order to try to overcome the limitation of those two grooves into which thought

⁸¹ As Russell explained: "If the activity of the organism as a whole is not completely reducible to the modes of action of its parts, then it follows that the modes of action of the whole, whether actual or potential, can be transmitted only by a whole, i.e. by the egg in its entirety, which at very beginning of development *is* the new individual. Subordinate parts of the egg-organism can transmit only their own particular modes of action, and not the modes of action of the whole; they cannot transmit even their own modes save as integral parts of the whole." (Russell, 1930, p. 283)

has been confined since Descartes, from which it has resulted that a specifically biological way of thinking has hardly been so much as considered...at present the application of logical and epistemological principles to the critique of biological knowledge is not at all understood in English-speaking countries. Since our biologists are only trained to be good investigators we can hardly expect them to be good thinkers.⁸²

J. H. Woodger



Fig. 4.7, J. H. Woodger, CA 1920⁸³

Russell had argued that the difference between organic and inorganic world reposed on a direct, evident, and obvious perception derived from common sense.⁸⁴ “Uncritical common sense”, argued Russell, “distinguishes sharply between living things and lifeless things”, yet human common sense could so easily distinguish animals from stones or clouds because organisms: “...possess a power of individualized activity. The living thing is active and individual, the lifeless thing is passive and unindividualized.”⁸⁵ To Russell, it was common sense perception of living phenomena that guaranteed, *prima facie*, the independence of biology from other sciences; biology was different and had its own ‘rules’ and ‘laws’ because organisms were *evidently* different, ontologically and epistemically diverse, from stones or clouds. In sum, to reduce biology to physics implied denying common sense experience and, therefore, assuming an ideological position. The philosophy of common sense, based on a simplified and naïve empiricism, was also part of Woodger’s theoretical baggage with respect to the epistemology of biology;

⁸² Woodger, 1929, *BP*, p. 487.

⁸³ Source: Woodger papers, UCL Archives, Category G, Photographs.

⁸⁴ Roll-Hansen highlighted this aspect of Russell’s bio-philosophy. Russell’s epistemology of biology was: “...supported by a typically British commonsense philosophy, inspired by Aristotle as well as the radical empiricism propagated by Bishop Berkeley.” (Roll-Hansen, 1984, p. 410)

⁸⁵ Russell, 1924, pp. X-XI.

his recurrent quotation of Bacon, Hume or Locke clearly demonstrate his fascination for empirical philosophies and common sense attitudes. However, although Woodger maintained that experience, as characterised through careful observations and detailed experiments, was an essential part of the scientific enterprise, he also held that a critical and theoretical analysis was required in any scientific investigation, including biology. By using an effective analogy, he introduced his major philosophical work, *Biological Principles* (BP), in the following way:

Modern natural science may be likened unto a crab which has grown too fat for its shell. The process of ecdysis is slow and painful. The old shell, which has matured and hardened for some three hindered years, has done good service. No wonder the crab is loath to part with it. But it has already begun to crack, and some bits have even dropped off. What is to be done?⁸⁶

In the crab analogy, the internal matter, the meat, represented the data — all the evidence scientists had gathered so far — whereas the shell symbolised the philosophical framework ordering and systematising that data into a coherent whole. To Woodger, the philosophical background was collapsing under the relentless and disorganised accumulation of data. What was to be done? Woodger believed that a possible solution lay in a new philosophy, a philosophy able to match a Kantian critical approach with the new tools offered by analytic philosophy. Indeed, what biology required was not more evidence, but more thought — more criticism, more philosophy and more logic. A Kant scholar, Ernst Cassirer, had shown how important the theories of knowledge had been in the history of physics linked to experimental analyses; methodology and experimental investigations went hand in hand in Galileo's, Kepler's and Newton's scientific revolution.⁸⁷ But while in physics, for historical or philosophical reasons, theoretical speculations were considered part of scientific investigation, in biology philosophical treatments were dismissed, criticised or, at least, regarded as suspect. Woodger aimed to reverse that situation and to show that theoretical biology was essential in solving issues that remained unsolved, even with the help of further planned experiments and specific observations. Many biological issues, indeed, rested on

⁸⁶ Woodger, 1929, *BP*, p. I.

⁸⁷ Woodger quoted Cassirer's *Einstein's Theory of Relativity considered from the Epistemological Standpoint*, Open Court, 1923. The reference to Cassirer was very indicative; indeed Cassirer investigated the connection between Einstein's relativity and Kant's theory of knowledge.

conceptual ambiguity and theoretical misconceptions; misunderstandings waiting for philosophical clarification. In Woodger's opinion, the philosopher of biology, before choosing one theory rather than another, one approach over other methods, had to investigate all assumptions, presuppositions, and postulates supporting those hypotheses or methods: "His duty [the philosopher] is simply to examine the logical procedure and ontological assumptions involved in them, and to show how far the difficulties ordinarily felt in regard to such rival theories depend upon such assumptions."⁸⁸

The philosophical method Woodger employed was essentially Kantian;⁸⁹ identify a controversy between two factions and undertake an analytic investigation into the assumptions that each party accepted. In Woodger's hands, the Kantian critical philosophy became the analytic investigation of intellectual controversies: Structuralists against Functionalist, Preformationists against Epigenesists, Vitalists against Mechanists, Organism against Environment, and Inherited against Acquired characters; all debates that Woodger analysed by dismantling, through a detailed *exegesis* of the arguments involved, the hidden postulates making disagreement possible. Of course, as we will see, Woodger's theoretical philosophy was much more than that; indeed, as I will show in the next sections, Woodger provided an analytic and solid foundation for organismal biology.

4.6: Towards an Unsuccessful Analytic Biology: From Practice to Theory

The difficulty of avoiding 'teleological' modes of expression in biology rests partly upon the fact that in an organism the parts constituting it are so related to one another and to environmental events that typically the organism endures.⁹⁰

J. H. Woodger

Roll-Hansen defined Woodger as: "...a logical empiricist, drawing inspiration from Kant's philosophy of science and from linguistic analysis."⁹¹ I would slightly change the order of Roll-Hansen's sentence and

⁸⁸ Woodger, 1929, *BP*, p. 6.

⁸⁹ As Kant's Antinomies of Pure Reason. Woodger explicitly mentioned that his method recalled Kant's approach to philosophical investigation: "Criticism as here intended (in the sense in which it was first introduced into philosophy by Kant) is a disinterested examination of traditional conflicts with a view to the discovery of their roots, and the removal of difficulties created by an uncritical use of the notion of unreflective thought." (Woodger, 1929, *BP*, p. 7)

⁹⁰ Woodger, *BP*, 1929, p. 440.

⁹¹ Roll-Hansen, 1984, p. 408.

define him as essentially a Kantian at heart “drawing inspiration from logical empiricists and from linguistic analysis.” This is not a matter of trivial detail; it makes a substantial difference to our interpretation of Woodger’s bio-philosophy. Indeed, logical empiricism, however defined, was only one aspect of the complex and heterogeneous philosophy of the young Woodger. Of course, in the late 1940s, his interests increasingly narrowed toward a classic logical positivism *a la* Carnap. In fact, after the Second World War, Woodger attempted to provide an effective, though vain, axiomatisation of biological thought.⁹² However, when we consider Woodger’s overall earlier contributions, we get a quite different and more complicated picture. In Woodger indeed, there were two related agendas; a *critical* bio-philosophy aiming to clarify terms, notions and unsolved issues; and a *positive* bio-philosophy, which aimed to support and clarify the notion of organism as an integrated and teleological hierarchical system.⁹³

Woodger’s philosophical insights had few followers; like Haldane, D’Arcy Thompson and Russell before him, he founded no school or tradition continuing his work, either in philosophy or biology. As Joe Cain rightly argues: “...Woodger can scarcely be described accurately as well known or prominent among biologists. A. R. Jonckheere (Psychology, University College London), who knew Woodger since the nineteen forties, recalls Woodger thought of himself as a minor figure in the English intellectual scene and on the periphery of biologist communities.”⁹⁴ Furthermore — and contrary to Smocovitis’ opinion — Woodger’s philosophy had no impact on the modern synthesis movement and its advocates, and this not only because we have no evidence attesting the link between Woodger and any of modern synthesis’ actors; but also because, as Cain claimed:⁹⁵

...his project to ‘unify’ biology also was an enterprise *different in kind* from the intellectual projects long identified with synthesis actors. His criteria and methods for unification were fundamentally different from what counted as ‘synthesis’ among evolutionists. Their epistemic concerns sharply

⁹² See, for instance, Woodger’s *The Axiomatic Method in Biology*, Cambridge University Press, Cambridge, 1937.

⁹³ Again, Woodger’s critical philosophy was not only characterised by the methods employed by analytic philosophers; of course, part of Woodger’s aim was to clarify, logically or linguistically, the terms used and notions supposed by biologists or physicians; but, nonetheless, Woodger also provided a strong critique against phenomenalist philosophies and advanced his own alternative based on Whitehead’s philosophy of the organism. Furthermore, he developed a broad theoretical position based on the notion of organism as hierarchical system.

⁹⁴ Cain, 2000, p. 539.

⁹⁵ See Smocovitis, 1992, and Smocovitis, 1996.

contrasted. There is no evidence to suggest that the holism Woodger sought was of any interest to synthesis actors.⁹⁶

Woodger not only remained a secondary figure in the British intellectual world but, as Roll-Hansen argues, his proposal to formulate an alternative to reductionist and mechanist philosophies was a failure; a failure that, in my view, represented not only Woodger's unsuccessful strategy, it represented the failure of a whole tradition; the neo-Kantian tradition.

As I will further demonstrate, Woodger's agenda was extremely distant from what the modern synthesisers were proposing, at least until the late 1930s. This should not be surprising given Woodger's complex background. Indeed, he was a biologist primarily trained in embryology; he gained a degree in Zoology at the University College London in amniote embryology and physiology in 1914. After spending a great part of the First World War in the Norfolk battalion in Mesopotamia, he was appointed protozoologist at the Clinical Laboratory in Amarah, where he was occupied in studies concerning plague rats and other local medical issues. In 1919, he went back to England and began research in embryology with his former teacher J. P. Hill (see chapter 2). In 1922 he was awarded a University Readership in Biology at the Middlesex Hospital Medical School. There he taught biology, human histology and other medical disciplines; indeed, during his stay at the Middlesex Hospital, he published a textbook for medical students: a book that, as we will see, anticipated his organismal beliefs.⁹⁷ In 1926 he worked in Vienna for few months, with Przibram at the Biologische Versuchsanstalt (Institute for Experimental Biology), also known as the 'Prater Vivarium'.⁹⁸ The brief experience there must have been important for the intellectual formation of Woodger; indeed, once back in England Woodger wrote in a short sketch of his biography (intended for his CV): "On my return to England in May 1926 I came to a decision which, for a time, involved a departure from the usual pursuits of biologists."⁹⁹ Indeed, after 1926 and against his previous exclusive experimental style of investigation,¹⁰⁰

⁹⁶ Cain, 2000, p. 541.

⁹⁷ Woodger, 1924,.

⁹⁸ See Edwards, 1911.

⁹⁹ Woodger J. H., 6 January 1930, The Academic Registrar, University of London, C 1/3, Miscellaneous, Woodger papers, UCL Archives. For a biographical sketch see also Gregg and Harris, 1964.

Woodger embarked on a deep philosophical discussion about the fundamentals of biological thinking. His stay in Vienna was certainly relevant for his decision to ‘depart’ from what he considered the ordinary path of biologists. And if we look at the intellectual context of the Vienna Vivarium, we can better understand this shift in his career.

The ‘Prater Vivarium’ was founded by Hans Przibram and other two friends: L. Von Portheim and W. Figdor in 1903.¹⁰¹ Przibram had graduated in Zoology under the supervision of B. Hatschek (1854-1941), a morphologist and embryologist who had been a student of both Haeckel and Leuckart.¹⁰² After spending a brief period in Leuckart’s laboratory in Leipzig, Przibram travelled to Strasbourg to study with the physiologist F. Hofmeister (1850–1922). Once back in Vienna, Przibram purchased the old zoo-aquarium located in the large public park known as Prater. In fact, the old aquarium was sold due to bankruptcy in 1902 and Przibram converted it into an international experimental laboratory.¹⁰³ Przibram worked as director of the Zoology Department, Figdor as director of the Botany Department and W. J. Pauli (1869-1955)¹⁰⁴ was appointed director of the Physical and Chemical Department. Finally, P. Kammerer (1880-1926) was in charge of the Prater’s terrarium and aquarium. The explicit goal of the institution was, as Przibram himself recalled: “to tackle all the big questions of biology”.¹⁰⁵ Przibram’s vision was to create an institution where many different disciplines and approaches could find common ground; a synthesis between physics, chemistry, biology, and physiology. As Pouvreau describes, the Prater Vivarium tended towards:

...interdisciplinary and experimental studies on morphological issues, which overlooked a merely descriptive and comparative biology and highlighted all the researches based on causal explanations.

In particular, experiments on animal regeneration, transplantation, on the effects of temperature on

¹⁰⁰ The first papers that Woodger published were rather technical and essentially descriptive. See ‘On the Relationship between the Formation of Yolk and the Mitochondria and Golgi Apparatus during Oogenesis’, *Journ. Roy. Micro. Soc.*, pp. 129-156, 1920; ‘Notes on a Cestode occurring in the Haemocoel of House-flies in Mesopotamia’, *Annals of Applied Biology*, Vol. III, pp. 346-351, 1921; ‘On the Origin of the Golgi Apparatus on the Middle-piece of the Ripe Sperm of Cavia’, *Quart. Journ. Micro. Science*, Vol. 65, pp. 265-291, 1921; ‘Observations on the Origin of the Germ-cells in the Fowl, studied by means of their Golgi bodies’, *Quart. Journ. Micro. Science*, Vol. 69, pp. 445-462, 1925.

¹⁰¹ On the Vienna Vivarium see Cohen, 2006.

¹⁰² See Stork, 1949.

¹⁰³ See Edwards, 1911.

¹⁰⁴ The father of Wolfgang Pauli (1900-1958), the Nobel laureate in Physics.

¹⁰⁵ Przibram quoted in M. Drack, W. Apfalter, D. Pouvreau, 2007, pp. 357.

biological processes, and those concerning comparative embryology were tackled. The institution was generally characterized by the opposition to Darwinian and neo-Darwinian theories, accepting, of course, evolution, but denying the idea that natural selection alone could explain evolution and the preformationist conception of heredity proposed by Weismann (1834-1914): the dominant conception was that the organism had to be conceived as a system in an active relationship with its environment, and that the organism's morphogenesis had to be seen as the result of epigenesis processes.¹⁰⁶

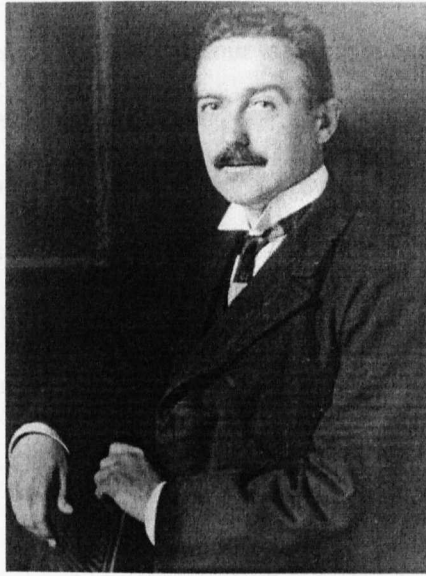


Fig. 4.8, Leo Hans Prizbram (1874-1944)¹⁰⁷



Fig. 4.9, Prater Vivarium in Vienna, CA 1940¹⁰⁸

¹⁰⁶ My translation from French, D. Poivreau, 2006 , p. 13.

¹⁰⁷ Source: Drack, Apfalter, Pouvreau, 2007.

Among other things, Przibram's agenda included mathematical studies on organic morphogenesis; in particular, he aimed to understand the physical forces shaping the organism's development through a quantitative approach encompassing physical, chemical and physiological knowledge. For Przibram in fact, as for many post-Kantian bio-philosophers, developmental processes showed how the whole constantly shaped its composing parts; now, he was convinced that such a relation of whole/parts could be understood through the help of mathematics: "...the influence of the 'whole on the 'part' turns out to be accessible to mathematical processing, grounded on our ideas from exact natural history."¹⁰⁹

Przibram's project for a mathematical morphology had many similarities with D'Arcy Thompson's approach; after all, as we have seen in the previous chapter, the mathematical approach to morphology marked the Goethean tradition.¹¹⁰ When, in 1924 Kammerer left the institution following the famous accusations of fraud,¹¹¹ Paul Weiss (1898-1989) succeeded.¹¹² Weiss had been a student of Hatschek too, and his PhD was supervised by Przibram himself. Therefore, his anti-mechanist and holist approach toward developmental problems reflected his background in Vienna. Weiss's studies on regeneration and transplantation, together with the discussions on mosaic and epigenesis mechanisms operating in ontogeny, brought him, eventually, toward a *systemic* conception of the organism and its development; a conception that influenced the young philosopher von Bertalanffy who, even in his doctoral dissertation, had begun to speculate about how organisms, conceived as entities belonging to a superior hierarchical level of complexity, could be studied and understood in their own individuality.¹¹³ In sum, when in 1925 Woodger arrived in Vienna, anti-mechanism, anti-reductionist and holistic approaches to biology, especially characterised from a hierarchical perspective, marked and dominated the Vivarium.

A few months before departing for Vienna, Woodger deemed it prudent to find more information about the Austrian institution. As was well known, D'Arcy Thompson had special ties with Przibram, having sent or recommended students to go there. Indeed, in late 1925, Woodger sent a letter to

¹⁰⁸ Source: Ibid.

¹⁰⁹ Przibram quoted in M. Drack, W. Apfalter, D. Pouvreau, 2007, p. 5.

¹¹⁰ See chapter 3 p. 63, although Przibram criticised Thompson's models, which he accused of being too inductive and of little predictive value, see M. Drack, W. Apfalter, D. Pouvreau, 2007, p. 6.

¹¹¹ See Arthur Koestler, 1971. See also Gliboff, 2006.

¹¹² See Overton 1997, and Brauckmann, 2003.

¹¹³ On the intellectual relations and contacts between Weiss, von Bertalanffy and the Vienna Vivarium, see M. Drack, W. Apfalter, D. Pouvreau, 2007, on von Bertalanffy's PhD dissertation and life, see Pouvreau, 2007.

Thompson — a letter which demonstrates his acquaintance with the Scottish professor and offers, at the same time, a nice glimpse of how that institution was considered behind closed doors. Thompson was indeed enthusiastic about the place but also wary about the research done there; as Thompson wrote to Woodger:

Przibram is a very good fellow, he has been extraordinarily kind to the fellows I have sent out to him, and though his Laboratory is (or lately was) a trifle impecunious and out-at-elbows (like everything else in Austria) its deficiencies did not prevent a lot of work being done. But I am not sure that I shall send any more men out there. Przibram, like Kammerer, is a trifle too sanguine; he too often thinks he has got hold of a big things, and sticks to it after it is pretty plainly a mare's nest. I do not believe at all in the eye-transplantation experiments...For a man like yourself that would not matter; you could make full use of the Lab, and be none the worse for any slight peculiarities on the part of the Professor. But (between you and me) I no longer think that Przibram, good friend of mine as he is, is the best of guides for the younger men.¹¹⁴

Despite Thompson's warnings, Woodger's trip would represent a turning point in his academic life. The Prater Vivarium offered an exciting environment where experimental biology and philosophical discussions about the nature of life went hand in hand. Weiss' theoretical biology, based on system theory, and von Bertalanffy's lifelong friendship marked Woodger's intellectual development.¹¹⁵

4.7: Woodger's Organismal Biology: Analysis, Relations, and Hierarchies

Biologists, in their haste to become physicists have been neglecting their business and trying to treat the organism not as an organism but as an aggregate. And in doing so they may have been good

¹¹⁴ D'Arcy Thompson to Woodger, 29th November, 1925, Box C1/3, Folder Correspondence D'Arcy Thompson, Woodger papers, UCL Archive, London.

¹¹⁵ Przibram himself, as expressed in a letter of recommendation, praised Woodger's achievements: "...I have read his book 'Biological Principles', written with much temperament and the thorough will to 'see it through'. Those who have, like myself, watched closely and with rising uneasiness, the biological theories and especially the ultra-selectionist's views of evolution, must welcome heartily Woodger's efforts to replace vague terms and loose reasoning by stringent definitions and good logic. We will also agree with him in his attempt to refute sterile warfare between vitalists and mechanists, preformationism and epigenetism, causation and teleology" Przibram, December 14th, 1929, Box C1/3, Folder: Miscellaneous, Woodger papers, UCL Archive, London.

chemists but they have not been good biologists, because they have been abstracting from what is essential to the biological level.¹¹⁶

J. H. Woodger

According to my view the properties of the whole in an organism are the outcome of the properties of the parts of particular kinds in their particular relations, and the properties of the parts are the outcome of the sort of part they are and of the relations in which they stand to one another., i.e. according to the place they occupy in the whole. With different parts in the same relations, or with the same parts in different relations we have a different whole. The whole is a multiple relation between its parts. The properties of a cell are not entities standing to it in a two-termed relation. They are the outcome of what it is and of its surrounding. i.e. – partly intrinsic and partly relational.¹¹⁷

J. H. Woodger to L. von Bertalanffy



Fig. 4.10, L. von Bertalanffy (1901-1972)¹¹⁸

Of course, before going to Vienna, Woodger was not ignorant of the organismal tradition or holistic approaches to biology. As a student of Hill at UCL, he may well have apprehended the long embryological tradition characterising organismal attitudes (from Huxley to the Scottish school). The discussions he had with Ian Dishart Suttie, a Scottish psychiatrist who was one of his comrades during his stay in Mesopotamia, could also have introduced some elements of the holistic tradition.¹¹⁹ Whatever the case, from 1924 Woodger was a sure supporter and admirer of Haldane's functional biology and

¹¹⁶ Woodger, BP, 1929, p. 291.

¹¹⁷ Woodger to von Bertalanffy, Box D/4, 20th July, 1930, Folder: Ludwig von Bertalanffy, Selection Hypothesis, Woodger papers, UCL Archive, London.

¹¹⁸ Source: http://www.eoearth.org/article/Von_Bertalanffy,_Ludwig

¹¹⁹ See Gregg and Harris, 1964, p. 2.

organismal physiology. His medical textbook, published in 1924, fully demonstrates that. First, he introduced the book with a quotation from Haldane about the strict relation between function and structure, and how this relation brought further knowledge about what is normal and what pathological in medicine.¹²⁰ Second, the whole organisation of the textbook reflected the typical organismal approach; it started with the whole organism, its function and organs, then treated the organisation of tissues and finally discussed the properties of the cell: it emphasised to young students that the whole organism's organisation comes before its constituents. After all, the celebrated 19th century German botanist Heinrich Anton De Bary (1831-1888) had coined a famous and successful aphorism: *Die Pflanze bildet Zellen, nicht die Zelle bildet Pflanzen* (The plant forms cells; the cell does not form plants). Such an organismic statement represented a warning against Schleiden's approach of beginning textbooks with the cell rather than the whole organism. Third, the conception of the organism and its relation to the environment mirrored Woodger's holist beliefs, taken from Haldane; as he wrote:

Biological problems always involve a threefold relation. First as we saw at the beginning, the living organism is the seat of ceaseless activity, it is always *functioning*; secondly, its functions are always manifested through some material *form*; and finally, these functions, sooner or later, directly or indirectly, have reference to the surrounding of the organism, that is to say, to its *environment*...Just as the organism is more than the sum of its material parts, so it is more than a bundle of functions. Just as its parts are organized and unified, so are its functions in reality not separable but all interconnected and coordinated, so as to result, in the living animal, in one great function – the behaviour of the animal as a whole. Any complete account of the organism must take this fact into consideration; in other words we must not only analyse, pulling the animal to pieces, separating its functions, but also synthesise, putting it together again if we can — and seeing how the parts are related to the whole.¹²¹

In sum, when Woodger arrived in Vienna, he was fully receptive to the novelties and new directions that organismal approaches were taking. However, one central notion emerged from his stay at the Prater: the notion of hierarchy. Such a concept indeed required clarification and Woodger would spend several years

¹²⁰ See Woodger, 1924, p. 2.

¹²¹ Woodger, 1924, pp. 457-458.

in pursuit of this. More than the philosophical discussions about mechanism or vitalism, preformation or epigenesis, phenomenalism or possible alternatives, structure and functions and the organism and environment, the philosophical notion of hierarchy occupied a central place in Woodger's bio-philosophy. Organic hierarchy would represent Woodger's original contribution to organismal biology; it would unify several problematic notions: heredity (inborn) or environment (acquired), genetics and embryology, living organisation, synthesis and analysis in biology, and a general critique against reductionism and mechanism.

Woodger introduced the notion of hierarchy, and its related issues, in his early *magnum opus*, *Biological Principles*. However, before setting up the theoretical elements making an organic hierarchy, he proposed his own ideas about biological explanations. Indeed, his epistemology reflected the ontological fact that organisms were hierarchical systems where causes and effects were indissolubly interrelated. Therefore, in biology, any explanation required four conceptual elements: 1) the things or objects requiring an explanation, 2) the ways through which those things can be analysed, 3) the relationships in which those objects stand to each other and 4) the relationships in which those objects stand to each other and which can be also analysed (reduced) to simpler relations. Now, in biology Woodger conceived two kinds of explanation: explanation by analysis and explanation by relation.¹²² Biological analysis involved, in turn, *perceptual analysis* (specific distinction of characters), *manual analysis* (the anatomical distinctions such as organs, tissues and cells, etc.), *physiological analysis* (the study of the mutual relation of anatomic parts) and *chemical analysis* (the study of chemical compounds as related to life's processes). Although, as he taught his medical students, the different forms of analysis were central in biological or physiological explanation and essential in biological investigations, biology was essentially a science of relations. In biological phenomena, *relations* between organisms and their environment, between organisms and other organisms in the environment, between organism and its parts were essential to understand life's 'mechanisms'. And yet, according to Woodger, the concept of *relation* was strictly related to the notion of living organisation itself: "Biological explanations...always involve far more than simple analysis but will have to deal with the complex relations between the various *relata* revealed by the analysis. Thus a theory of biological explanation requires a preliminary study of what we

¹²² See Woodger, BP, 1929, p. 273.

are to understand by organization, a question which, curiously enough, is rarely discussed in biological books.”¹²³

Woodger would never give a clear-cut definition of ‘organisation’ because he thought living organisation was a result of organic relations among lower and upper levels of organic complexity; in other words, organisation was all that emerged from dynamic hierarchies; his definition was given, so to speak, *ostensively*. Organisation implied two kinds of hierarchies: hierarchies concerning what Woodger dubbed *relata* (composing parts), and hierarchies concerning relations among *relata*: “...the organism is analysable into organ-systems, organs, tissues, cells and cell-parts. There is a hierarchy of composing parts or *relata* in a hierarchy of organizing relations. These relations and *relata* can only be studied at their own levels and not simply in terms of the lower levels since these levels do not constitute *unit relata*.”¹²⁴ But organisation, as the manifestation of hierarchical relations, entailed also a temporal and spatial element: “...a living organism is analysable into a hierarchy of parts in a hierarchy of relations, but neither its parts nor their relations are unchanging since it is differentiated temporally as well as spatially.”¹²⁵ In sum, organisation emerged from the spatial relations among hierarchies in temporal differentiation. As we will see, Woodger’s scepticism about genetics and his criticism of gene concepts did not derive from his “excessive empiricism”,¹²⁶ but from his pervasive notion of organism as hierarchical system and his critical views on the notion of ‘causal determination’ in embryology and genetics.

Between 1930 and 1931, Woodger published three articles in a new journal, *The Quarterly Reviews of Biology*. The journal was founded by Raymond Pearl (1879-1940) in 1926 and it was intended to be an intellectual platform for discussions related to historical or philosophical issues in biology, and book reviews. Pearl was an American biologist who had studied biometry with Karl Pearson in England; once back in the US he became a widely known populariser of science, especially on issues concerning population control and eugenics policies. He admired Woodger’s philosophical attitude and helped to support his career as main referee. When, in 1930, Woodger applied for a chair in Social Biology at the London School of Economics, Pearl wrote a glowing letter of recommendation: “I know of

¹²³ Ibid., p. 275.

¹²⁴ Ibid., p. 293.

¹²⁵ Ibid., p. 311.

¹²⁶ As Roll-Hansen (1984) and M. Ruse have argued. See M. Ruse, 1975.

no young man in either England or America who approaches Mr. Woodger in fitness in this respect for the peculiar and important requirements of this post.”¹²⁷ Even though Woodger did not get that job, Pearl’s admiration for him was further demonstrated when he invited the young scholar to publish a large manuscript in the *Quarterly Reviews*: the manuscript had been divided by Woodger into three parts and treated one of the hottest topics of the time: the relationship between embryology and genetics.

The notion that connected both embryological and genetical studies was the concept of the organism as an integrated system of hierarchical levels. In the first part of the manuscript, Woodger began to define and describe in formalist language an organic hierarchy. His treatment, based as it is on an axiomatic system, is sophisticated and complex but essential to an understanding of Woodger’s reformulation of the notion of heredity as the expression of developmental tendencies. A hierarchical order was first characterised as a whole integrated entity W , analysable into composing members M and m belonging to two different sets : the set L (levels) and the set of assemblages A (set of M and m). Now, both L and A were correlated by a fundamental relation Rh so that every member belonging to a specific level L was analysable into an assemblage A in which every component in A was in Rh relation to A . The relation Rh defined therefore an irreducible level of complexity although other forms of relation were conceived too: relations Rl among levels and relations Ra among members M and m belonging to specific assemblages A ; for instance, a cell was analysable in cell-part assemblages and cell-part assemblages could be analysed in term of chemical compounds; yet, although a relation between different levels could be established in principle (so to analyse the cell in terms of chemical compounds), there was not, in Woodger’s scheme, a fundamental lowest level *explaining* or *causing* all higher ones: “We thus have to get out of the habit of regarding only the supposed ‘ultimate’ components as ‘really real’. Otherwise it is quite arbitrary to stop at cells, or genes, or molecules, or even atoms. We are required to do justice to each level in the hierarchy of levels.”¹²⁸

¹²⁷ R. Pearl’s letter of recommendation to Woodger, Box C1/3, Folder: Miscellaneous, Woodger papers, UCL Archive, London.

¹²⁸ Woodger, II, 1930, p. 452.

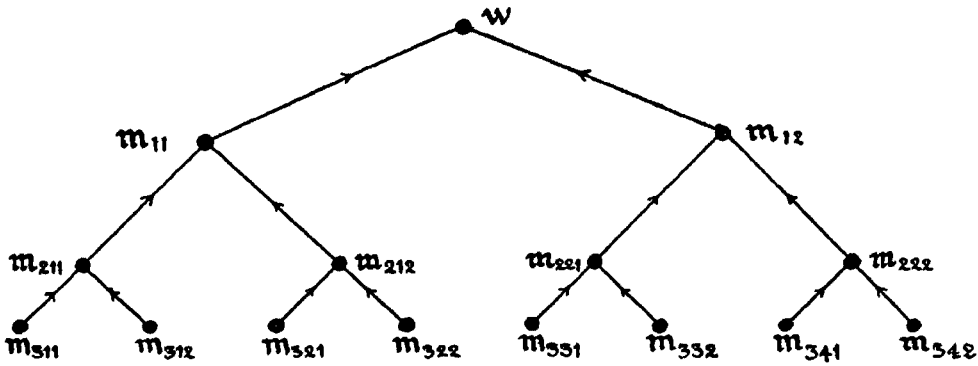


FIG. 1. GRAPHIC SYMBOL OF A SYSTEM OF ENTITIES IN HIERARCHICAL ORDER

The suffix numbers indicate (1) the level, (2) the assemblage within the level, to which a member belongs, and (3) the third number distinguishes one entity of an assemblage from the others. In the first level, where there is only one assemblage, the second suffix number is omitted. In a regular hierarchy in which the number of entities in a level is constant, if N is this number then the number of members of any level L_n is N^n , and each member of L_n stands to W in the relation RH^n .

Fig. 4.11, Woodger, II, 1930, p. 448

Woodger defined the concept of hierarchy as applied to the notion of organism more and more analytically. Organic hierarchies not only involved different relations and levels, but also entailed diverse kinds of hierarchies; division, spatial and genetic hierarchies described, through their own specific relational properties, all possible forms of cellular organisation. Yet, diverse hierarchies were not only composed of things and their various relations, they were also characterised by temporal and spatial parts: to Woodger, a temporal slice or event was always associated with a spatial part; however, he further distinguished between *components* and *constituents* of spatial parts: the former was defined as assemblage A of level L (i.e. the nucleus is a component of the cell or the cell a component of tissues); the latter was thought as a contingent part without any relation to the level or hierarchy (a beef-steak is a constituent of the cow). To Woodger an organism was a four dimensional entity; in fact, the temporal dimension defined the kind of relations that the whole system established in different temporal slices between levels L and between members of A . As a consequence, living organisation was defined in terms of relational properties; an organism was alive if some specific relational properties between levels and members were established.

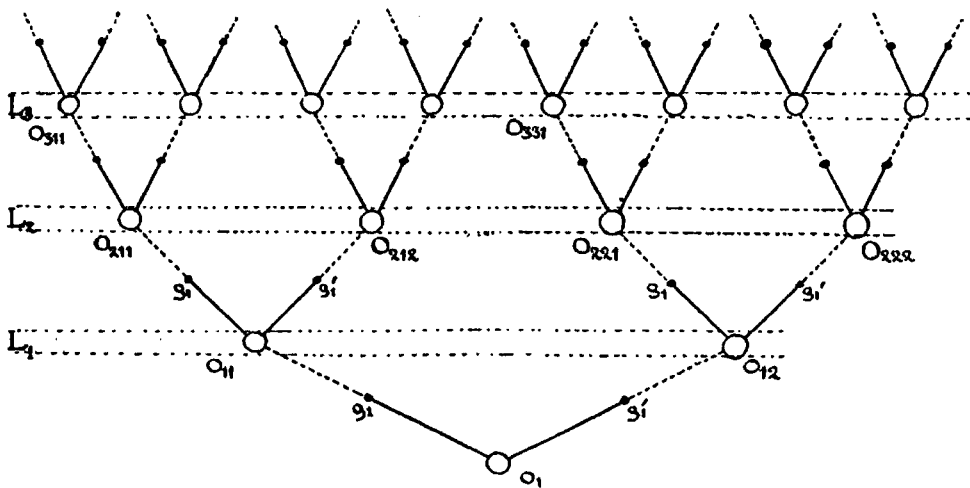


FIG. 7. GRAPHIC SYMBOL OF A GENETIC HIERARCHY WITH RESPECT TO THE ZYGOTE O_1

The relation $R_H(g)$ is a relation between zygotes, but this relation is the relative product of two relations, namely the converse of R_H^P (between a given zygote and a certain gamete g_1 , belonging to its cell-posterity), indicated by the broken lines, and the converse of R_f (between g_1 and the zygote into the constitution of which it enters), indicated by the continuous lines. Consequently, although the gametes are not terms in the relation $R_H(g)$ and are not members of the hierarchy, they are shown in the figure as the intermediate terms in the relative product. Durations are not indicated, but it is evident that the members of a given level L_n (although they may belong to different durations) will extend through durations all of which are earlier than durations extended over by members of levels higher than L_n , and later than durations extended over by members of levels lower than L_n .

Fig. 4.12, Woodger, II, 1930, p. 460

Components, organised according to specific relations in a whole W divided in levels L_n , characterised, among other things, the differences among organism. What biologists did was to compare different wholes (for instance W with W_1) or analogous slices of related wholes. So, while taxonomists compared wholes of diverse hierarchies, embryologists compared analogous time slices of related wholes, geneticists compared characters of an adult organism with related characters of another: "We might, for example, be comparing a particular shade of gray under the determinable colour of the skin of the adult rabbit A, with the particular shade of brown under the determinable colour of the skin of the adult rabbit B."¹²⁹ Of course, the differences, observed from different perspectives, by taxonomists, embryologists and geneticists reflected both *intrinsic* (or immanent) and *relational* properties that an organism, during its development, exhibited during different temporal slices. Although intrinsic and relational properties could be translated as heredity and environment, Woodger preferred to avoid the word heredity altogether because he considered it vague and misleading; as he had warned in his *Biological Principles*: "from the very diverse definitions of this word [heredity] given in biological literature it seems clear that the word

¹²⁹ Woodger, 1931, p. 180.

stands for an indefinable abstraction, and in the interests of precision it could be banished from scientific terminology with advantage. It is a vague term borrowed uncritically from common sense.”¹³⁰

The distinction between intrinsic and relational properties in a hierarchical system allowed Woodger to reformulate the sharp opposition between hereditary or acquired characters, and between inherited or environmental factors. Indeed, intrinsic properties could be thought of as acquired relational properties during development, once ontogeny was defined as the progressive increase of the different relations in an organic hierarchy:

If two cells, which are assumed to have ‘equal’ nuclei behave differently in the same environment, we should say that they differed intrinsically in their cytoplasm, since their relations are supposed to be the same. But that intrinsic cytoplasmic difference may have been acquired in consequence of relational differences during development, and would therefore be an acquired relational property. But since it now persists in spite of changed relations (since by hypothesis both cells are in the same environment now) we should have to call it an acquired intrinsic property.¹³¹

In sum, with the aid of the notion of organism as hierarchical system, Woodger hoped to reconfigure the whole debate between embryologists and geneticists and, therefore, between preformationists and epigenesists. Variations between hierarchical systems (so organisms) were due to both intrinsic and relational properties; however, there was no neat division between ‘inborn’ and ‘acquired’ properties. Indeed, intrinsic properties were, in truth, ‘persisting’ relational properties as ‘acquired’ by the hierarchical system as a whole. In the end, Woodger’s theoretical framework left open the way for a Lamarckian interpretation.

Yet, as we will see in the next section, his new theoretical approach met the approval of most developmental biologists and was quite critical about genetical sciences; genetics, he wrote (in a document probably intended as a lecture to deliver in the late 30s): “...is the branch of biology which is concerned with the way in which the classification of the beginning of a life depends on the classification

¹³⁰ Woodger, BP, 1929, p. 384.

¹³¹ Woodger, I, 1930, p. 15.

of its parents and their environment.”¹³² To Woodger indeed, whereas genetics dealt with classifications, comparisons, variations and differences; ‘heredity’ was the science dealing with immanent and relational properties as manifesting during the different temporal and spatial slices characterising the whole organism’s development. In sum, to him, genetics was not the science of heredity.

4.8: What Genes Cannot Do: Heredity as Result of Immanent and Relational Properties

...each parent produces a gamete, these gametes unite to form a single cell, and this cell in an environment develops into a human embryo. But neither gamete is simply a mass of genes. Each has parts which are neither genes nor parts of genes.¹³³

But the molecules with which the biochemists deal do not exist at all ‘in nature’. They are always either constituents of a biological hierarchy or they are ‘artefacts’ i.e. made by human beings. Now just as molecules (even if we take them naively) have different properties from their atoms, so do organized parts of the organism which are self-propagating have characteristic properties which can only be discovered by studying such parts themselves, not only by studying their constituent molecules. Moreover, these parts-chromosomes, etc. – are themselves incapable of independent existence but are subordinate parts of a larger organic whole.¹³⁴

Thus chromatin takes the place of Descartes’ God as the ‘controlling mechanic’.¹³⁵

One of the most important legacies of Woodger’s stay in Vienna was his acquaintance with animal regeneration phenomena; indeed, initially, he had planned to go to the Prater Vivarium to study transplantation in worms.¹³⁶ After all, Przibram was internationally recognised for his experiments on animal regeneration and transplantation and Woodger certainly benefited from that. Among his papers,

¹³² Woodger, ca 1935, Box D3, Folder: Antitheses between Heredity and Environment, Woodger papers, UCL Archive, London.

¹³³ Woodger, 1929, *BP*, p. XVII.

¹³⁴ *Ibid.*, p. 288.

¹³⁵ Woodger, *EG*, part I, 1930, p. 18.

¹³⁶ Apparently, when Woodger arrived in Vienna, the worms he found there were not appropriate for transplantation experiments. See Gregg and Harris, 1964, p. 3.

conserved at the UCL Archives in London, is a draft of a translation from German of Przibram's "*Regeneration und Transplantation im Tierreich*" ("Regeneration and Transplantation in the Animal Kingdom"),¹³⁷ a paper that Woodger probably drafted after his return in England. The phenomena of transplantation and regeneration offered Woodger powerful theoretical support for his organismic approach and his arguments against genetics and any preformistic view. To him, Przibram, Weiss¹³⁸ and later Spemann had shown, through their experiments, that hereditary determination depended on intrinsic properties, spatial and temporal relations: "In such an organism as a newt, in which a high regenerative ability is retained throughout his life, what is regenerated depends not only upon the spatial relations of the regenerating tissues but also on the temporal slice of its history which has been realized, in other words what is regenerated depends on the state of development to which the organism has reached."¹³⁹



Fig. 4.13, P. A. Weiss (1898-1989)¹⁴⁰



Fig. 4.14, H. Spemann (1869-1941)¹⁴¹

According to Woodger, the experiments on animal transplantation, which involved cutting specific part of animals and embryos parts and pasting them into the bodies of other animals or embryos, demonstrated the plasticity of the organism's reactions; both in the parts and wholes. In fact, only rarely were the transplanted parts strictly determined at the beginning because, once they were pasted, their activities

¹³⁷ H. Przibram, 1913, *Regeneration und Transplantation im Tierreich*, *Kultur der Gegenwart, Band Allgemeine Biologie*, pp. 347-377. The draft translation is: Woodger papers, Box D4, Folder: Embryology, pp. 17, UCL Archive, London.

¹³⁸ On Weiss's experiments, see Haraway, 1976.

¹³⁹ Woodger, 1929, BP, p. 355.

¹⁴⁰ Source: www.nap.edu/readingroom.php

¹⁴¹ Source: <http://www.sciencephoto.com/media/228650/view>

changed according to the new 'environment'. In sum, the activities of transplanted parts always depended on the activity of the whole system in which these new elements were inserted.¹⁴²

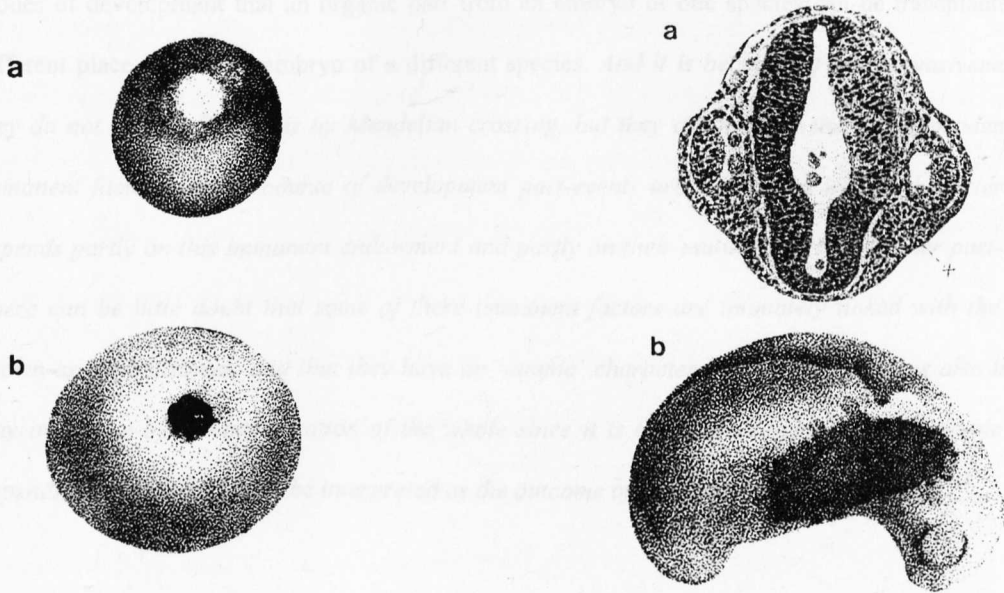


Fig. 4.15, Woodger referred to the Spemann's famous heteroplastic (interspecific) transplantation experiment.¹⁴³ *Triturus teaniatus* gastrula (a, left) has a white spot in the middle representing a transplant of tissue taken from a *Triturus cristatus* gastrula (b, left), and vice-versa. The original tissue transplanted in (a, left) would normally become epidermis, but it behaves according to the new environment into which is inserted; so it becomes eye and part of the brain (a, right). Likewise the original tissue transplanted in (b, left) would normally become forebrain and eye, but in the new environment it forms epidermis. The last figure (b, right) represents the *Triturus cristatus* embryo at an advanced stage of development. Note the black pigmented cells in the gill area.

Furthermore, both regenerative and transplantation phenomena provided excellent instances of normal development. Then, to Woodger, development itself appeared to be quite incompatible with Mendelian genetics. Indeed development, given its extreme plasticity and variability (likewise regeneration and the activities related to tissue transplantations), could not be controlled directly by gene activity.¹⁴⁴ In other words, because development was seen by Woodger as an open, regulative and plastic process resulting from intrinsic and extrinsic factors, it could never be ascribed to fixed or determined hereditary particles:

¹⁴² On Spemann's experiments see Hamburger, 1988.

¹⁴³ Source: see Spemann, 1919.

¹⁴⁴ In 1926, T. H. Morgan had published a well-known paper in the *American Naturalist* arguing, amongst other things, that genes, if considered as protein bodies, could produce enzymes and therefore 'affect' development. See Morgan, 1926.

Development is a process in which with temporal passage new spatial parts come into being all with the same genetic endowment. As development proceeds they do not lose 'factors' but selection is made from their possibilities and this depends on their mutual relations, on the relation of the whole to the environment, as well as on their immanent endowment. It is because of the pervasiveness of the earlier modes of development that an organic part from an embryo of one species can be transplanted to a different place in another embryo of a different species. *And it is because of this pervasiveness that they do not admit of analysis by Mendelian crossing, but they are not any the less dependent upon immanent factors...in the course of development part-events are elaborated whose characterization depends partly on this immanent endowment and partly on their mutual relation to other part-events. There can be little doubt that some of these immanent factors are intimately linked with the events known as chromosomes, and that they have an 'atomic' character. But this atomicity is also in some way overcome by the organization of the whole since it is the characterization of the whole which depends on them and cannot be interpreted as the outcome of the doings of unrelated cells.*¹⁴⁵

However, like Lillie before him, Woodger did not simply dismiss genetical sciences; he only argued that they could not be of great help in understanding development. Geneticists were not interested in the organic process of 'realisation' but only in statistical distributions of the final outcome. Morgan's theory of the gene was not: "...concerned with development but with genetical ratios...the numerical data here primarily concern the number of individual organisms having a certain character in a given generation. The gene is designed to explain the distribution of the characters among such a generation of whole organisms."¹⁴⁶ Therefore, the real challenge lying before genetical science was neither to explain or elucidate embryological issues, nor to formulate an all — comprehensive theory of heredity; it was rather to gain knowledge about the law-like distribution of characters among individuals belonging to different generations.

To summarise, the model of development that Woodger presented was totally unsympathetic to genetic interpretations; it was essentially based on a hierarchical model in which new organised relations emerged temporally. As he clearly explained, in accepting a hierarchical model of development:

¹⁴⁵ Woodger, 1929, *BP*, p. 376.

¹⁴⁶ *Ibid.*, pp. 365-366.

“...there is no need to regard the zygote as a mystery-bag of ‘potencies’ which, at their appointed hour, proceed to blossom out into the ‘characters’ which they are said to be ‘for’.¹⁴⁷ As a consequence, the notion of ‘hereditary characters’ was considered by Woodger old-fashioned and belonging to a “...pre-scientific stage in the history of genetics.”¹⁴⁸ In fact, his new terminology and notions based on intrinsic and relational properties restated, on a new basis, the old debate about nature and nurture. In an organic hierarchical system, asking what was natural and what was ‘acquired’ was equivalent to asking how much the volume of a gas was due to its temperature or its pressure.¹⁴⁹ In brief, to Woodger heredity had nothing do to with discrete things but with organised systems as a whole; intrinsic properties emerged in a hierarchical system where relational properties and environment worked together. Yet, even if genes existed, Woodger added, they were “...clearly not the things that geneticists are talking about.”¹⁵⁰ Genes could only vaguely denote all that makes different cells; whether what made this difference was a gene, an entelechy or a mnemonic element, did not matter as long as it brought new useful knowledge. But, whatever genes could be or do, the organismal biology Woodger advocated prevented him from seeing any kind of ‘hereditary character’ as the main causal factor behind the production of organic form — the organism — as Kant and his followers (including two of the most influential figures on Woodger’s philosophy; Haldane and Whitehead) had taught, was that the parts were reciprocally cause and effect of the whole.

¹⁴⁷ Woodger, 1931, p. 203.

¹⁴⁸ Ibid. p. 205.

¹⁴⁹ See H. Woodger, 1931, III.

¹⁵⁰ Ibid., p. 206.

4.9: Conclusion : Against Mechanism, Against Capitalism

My point is, therefore, that we should cultivate the habit of regarding ourselves as parts of an organism of a higher order than that of the cellular individual unit. It is the antithesis of the attitude which is expressed in the saying that an Englishman's home is his castle; for a castle suggests a moat, drawbridge and portcullis – an elaborate attempt to shut out the outside world.¹⁵¹

Although Russell, as we have seen, was concerned about the social and political consequences of materialist, reductionist and mechanist sciences, he never developed an explicit and wide critique of society and political interventions as being based on a false or mistaken science. Woodger did. As one of the main members of the Theoretical Biology Club in Cambridge during the 1930s, Woodger shared the company of some of the most left-wing, radical scientists active in that period in England.¹⁵² Even though, as Haraway recalls, the club was committed to:

...bringing to biology the power of logic and mathematical explanation previously enjoyed in the physical sciences, but they were not merely a modern variant of workers operating on a mechanist paradigm. They shared also the view that hierarchical organization, form, and development were the central concerns of a new biology...its members were importantly involved in the transition to an organismic, non-vitalist paradigm for developmental biology.¹⁵³

The members participating in the meetings — people such as J. B. S. Haldane, J. D. Bernal and J. Needham — were scientists also fully committed to a political cause: socialism.¹⁵⁴ Woodger himself was interested in the influence of science on society in general. As he wrote in his *Biological Principles*: “...the results of scientific enquiry sometimes have application to other aspects of human life, and some

¹⁵¹ Woodger CA 1945, Woodger papers, Box E/3, Typescript ‘A Biological Approach to Socialism’, UCL Archive, London.

¹⁵² See P. Abir-Am, 1987.

¹⁵³ Haraway, 1976, p.4.

¹⁵⁴ Werskey defines the Theoretical Biology Club as: “...one of the most important underground scientific enterprises of the 1930s.” See Werskey, 1978, p. 80.

of these applications have, and are likely to continue to have, a profound influence upon it.”¹⁵⁵ However, as a philosopher of science, Woodger was not so much interested in technological applications to society but in how biological ideas could be used to support a socialist ideal. Although, to my knowledge, Woodger never published any pamphlet, book or article with explicit political contents, he did speak about these topics in lectures and speeches. In particular, in the UCL archive, is a typescript about a paper given at the Middlesex Medical School Socialist Society, apparently in 1945. This extraordinary document, entitled ‘A Biological Approach to Socialism’, demonstrates how, even twenty years after Haldane’s address at the Institution of Mining Engineers, the analogy of the society as a collective organism persisted.

As Woodger presented, the biologist, as any common citizen, is heated by the “...disgust with the poverty and sickness or an outraged sense of justice at the inequalities, which capitalism inevitably brings in its wake, may impel us towards socialism.”¹⁵⁶ Now, he continued, some biological ideas could give support to socialism and, at the same time, condemn capitalism. The conception of the organism, for example, which conveyed the idea of association and cooperation among parts for the sake of the whole. Indeed, apart from properties or activities such as respiration, excretion, nutrition or movement, organisms show other fundamental properties such as aggregability, divisibility and diversifiability. By aggregability, Woodger meant that all living things tend to form units of higher order; from multicellular organisms to societies. For divisibility, Woodger intended reproduction or, at the social level, migrations. For diversifiability, he referred to Milne-Edwards’s division of labour; organisms are divided into functional specialised regions. A characteristic deriving from these three properties is that when a part of an organism was severed from the whole, both the part and the whole behave differently.¹⁵⁷ In sum single

¹⁵⁵ Woodger, 1929, BP, p. 66.

¹⁵⁶ Woodger CA 1945, Woodger papers, Box E/3, Typescript ‘A Biological Approach to Socialism’, UCL Archive, London, p. 2.

¹⁵⁷ Woodger used once again the analogy with animal regeneration and transplantation: “It is a very familiar fact that when a part is removed from an organism both the part removed and the part which is left undergo change. It may be that both parts perish, or that one perishes and the other survives, or again, both may survive after going through regenerative processes. Thus the parts of living organisms are mutually dependent on one another, their properties are different in isolation from what they are in their organic relations. This is exemplified not only at the cellular level but also at the social level. A steward on board ship and a coal miner develop different properties in accordance with their different social relations, and both lose these special properties if they are cast upon a desert island, just as cells tend to de-differentiate when isolated in tissue culture. Again an English child brought up in a French society will develop the property of speaking French and will lose this if it is transplanted to an English unit,

organisms, as well as whole communities, manifest a mutual dependence on each other: "I express this mutual dependence of organic parts by saying that they need each other, or that they supply each other's needs. This relation of needing is a fundamental biological relation. The whole of physiological investigation consists in the experimental analysis of the way in which the parts supply each other's needs."¹⁵⁸ To Woodger indeed, the connection between the organism's properties and society was evident.

However, he made clear that with his organismic conception he did not intend to support the Hegelian State doctrine. The dependence of the individual on the whole society was not so high as the case of cells in an organism; the social organism should always be thought of as constituted from free individuals, i.e. human beings freely cooperating, for the sake of both the whole and themselves. Unfortunately, capitalist societies perverted the beneficial relations of part to whole or individual to individual; in fact:

...society is regarded largely as an arena for individual struggle and competition, in a capitalist society leisure and opportunities provided for the satisfaction of human needs are enjoyed by comparatively few while the burden of toil which makes such leisure possible falls so heavily on the vast mass of the population that, as we all know, their conditions of existence do not even provide adequately for their biological needs. In biological terms we have an organism in which one set of parts is permanently parasitic on the remainder.¹⁵⁹

When, in 1931, Haldane, Russell and Woodger (though not D'Arcy Thompson) participated in the Second International Congress of the History of Science in London — a meeting that, as Werskey records, was characterised by a strong Soviet and socialist propaganda — questions about materialism, mechanism and reductionism in biology were not just abstract issues, but conveyed a strong political charge.¹⁶⁰

just as cells from one embryo, or to another region of the same embryo, where their mutual relations with other cells are different." Woodger, 1945, p. 5.

¹⁵⁸ Woodger, 1945, p. 6.

¹⁵⁹ *Ibid.*, p. 9.

¹⁶⁰ See Werskey, 1978, p. 138.

We will see that in the United States too, the diffusion of organismal biology was accompanied by a similar political charge. In fact, it was not casual that W. E. Ritter, as we have seen, chaired the 1931 session at the London Congress. However, in the following two chapters I will show how organismic approaches and conceptions were received in the US; a very different context from Britain. We will see that in the US, the organismic metaphor, more than inspiring personal or individual agendas, influenced entire institutions.

5.0: Neo-Kantian Biology in the USA: Chicago and Beyond

5.1: Introduction

In the second and third chapters we have seen that, in Europe, the neo-Kantian tradition, known as organismic biology, spread through different idiosyncratic ways in each country and was accepted by a number of investigators with very diverse backgrounds. However, in the United States, the diffusion of such a tradition was less complex and more straightforward. Even though important figures such as Louis Agassiz¹ had established an important European outpost of research and education on American soil since 1848 – in organising, amongst other things, an important museum of Comparative Zoology in 1860 at Harvard University, an institution shaped according to his bio-philosophy and pedagogic convictions² and which, at that time, provided the training of some of the leading 19th century American naturalists³ – the great philosophical speculations or syntheses in biology that are part of my story came later and, as I have already mentioned, from other sources. One of the most important intellectual sources was certainly Leuckart and his school at Leipzig. However, as we will see later on, although Leuckart and his school, as well as other European figures and distinct British, German, and French institutions, inspired and shaped the biological knowledge of many American investigators, biologists in the new continent developed, and sometime transformed in an original way, what they had learned abroad. In sum, since the very late 19th century, American biology – as Benson and Maienschein argue⁴ – had its own intellectual space and therefore its own peculiarities. This is not really surprising: the New World biologists knew each other personally or knew each other's work; they exchanged new ideas through their own specialist journals, their international conferences, their private letters; they worked in similar US institutions and often had similar training. In brief, there were all the necessary social conditions, facilitating national connections and local networks, to support a quite original version of biological research. In fact, the American

¹ See Lurie, 1960.

² Winsor 1991, and P. J. Pauly, 2000.

³ Among others, J. Le Conte, A. Hyatt, D. S. Jordan, A. P. Packard.

⁴ See Benson, 1988 and Maienschein, 1985. See also Rainger, Benson, Maienschein, 1991.

organismic tradition I will sketch in this chapter and the next, like American biology in general, was not a mere copy of the European biology; it retained its own originality. Nevertheless, it shared styles, methods, and key-principles with Continental investigators.

In this chapter we will see that, within the US context, persons, traditions, ideas, institutions, research methods, all interacted in different ways. In particular, when we analyse the development of the American organismic tradition, we find it difficult to uphold, without reservation, the idea – current among some sociologists of science – according to which institutions and structures of power shape, for example, style of inquiry, ideas, research traditions and theoretical outcomes.⁵ For example, Jonathan Harwood, in his authoritative book *Styles of Scientific Thought*, argues that differences in styles of thought depend on the kind of organisation or institution in which the investigator works: “Which problems are defined as central to a discipline”, wrote Harwood, “is determined not by an internal logic but by the structure of power in and around that discipline”⁶. In fact, turning to the particular case Harwood analyses, he pointed out that stylistic differences between American and German genetics reflected different structures of power and interest: “The key to understanding why genetics was defined more broadly in Germany than in the United States, I have argued, lies in the differing structures of their respective universities and other research institutions. And the qualitative effect of university structure upon the scope of genetics was intensified by quantitative differences in the rate of institutional expansion before 1914, and especially by German economic crises after 1918”⁷. German geneticists were more open-minded about different mechanisms of inheritance, cytoplasmic inheritance, for example, than their American colleagues; and they were also less inclined to focus on transmission genetics, keeping an open eye on developmental issues. This was, Harwood argues, partly because in Germany, unlike the US, scarce resources and low growth of the higher education system prevented the establishment of new institutions in which new disciplines could be carved from broader fields. On the other hand, Harwood explains, “...Rapid growth of resources within an educational system...makes institutional innovation easier. Instead of competing with better-established fields for scarce resources, new fields can set up

⁵ See Hangstrom 1975; and Ben-David and Sullivan, 1975.

⁶ Harwood, 2003, p. 177.

⁷ Ibid., p. 178.

independently of older ones. Geneticists who inhabit chairs or departments designated for genetics, for example, will be freer to define their own research agenda.”⁸.

Of course, Harwood identifies other reasons underlying the different research styles and diverse approaches to genetics, such as the organisation of the German institutions and universities, i.e. their external connections with industry and agriculture, for example, and also the power of the faculty or a single professor over the development of departments. In sum, following the best sociological tradition exemplified by Mannheim, and the institutional approach of Joseph Ben-David, Harwood reduces scientific styles to specific interests, institutions or “basic intentions”. In such a scheme, ideas and traditions are in fact mere secondary elements of an underlying social structure which directs and filters the intellectual experiences of the social actors.

Such an institutional difference between American and German genetic communities reflected, as Harwood explains, two kinds of methodological approach to science: a pragmatic and a comprehensive viewpoint. Americans, in virtue of their history and institutional organisations were more prone to solving concrete and affordable issues whereas Germans were more inclined toward wild theorisations. The experiences of German émigrés in the US confirmed this: the New World held, as Hofstadter⁹ claims, a strong anti-intellectualist component, an aspect totally alien to the German culture: “In such a society”, Harwood points out, following Hofstadter, “knowledge was generally valued not as a route to wisdom, but as the means to utilitarian ends. The man of knowledge was respected, not as a culture-bearer in the German mould, but as someone whose expertise could solve practical problems.”¹⁰.

I linger on Harwood’s work because it represents, in my opinion, a very clear and convincing model of sociological explanation;¹¹ a model that sheds light on the reasons why different styles of

⁸ Ibid., p. 156.

⁹ Hofstadter, 1963.

¹⁰ Harwood, 2003, p.190.

¹¹ The opposition *pragmatic* vs *comprehensive* has been used by Harwood not only to flag national differences between Germany and the US, but also to describe some intra-national divergences within Germany. Therefore, in order to integrate an institutional explanation about styles of research within a more traditional sociological framework, Harwood distinguishes between two different types of German biographies which shaped particular attitudes toward science. Within the German community of geneticists, *comprehensives* were investigators with wide knowledge in biology and other scientific and humanist disciplines, scientists generally aiming for broad syntheses and particularly bent toward holism. *Pragmatics* instead represented figures supporting an instrumental, materialist and reductionist scientific methodology able to control and predict phenomena. Such different attitudes reflected, according to Harwood, diverse biographies, i.e., different experiences and social class. As he concludes: “I have shown how comprehensive and pragmatic styles of thought reflected the differing class backgrounds and

reasoning succeed and thrive. However, although the Harwood scheme may be true regarding its own context, it would be inappropriate if applied to my case study or, to put it in another way, I think that my case study represents a disproof of Harwood's model as well as a confutation of many approaches in history of science heavily based on institutional reconstructions.¹² Indeed, when we turn to my story, we see that even though American biologists such as Child, Conklin, Harrison, Wilson, Whitman, Ritter, Just etc. worked for the greater part of their lives within American institutions, they still maintained a Continental style and viewpoint in biology; i.e., many first-rank American investigators indulged in broad speculations and theorising as did their German and European colleagues. Furthermore, even though original and innovative, their concepts and ideas – in general biology, then in embryology, heredity, morphology, evolutionary studies, their methods and experimental practices – were not in contradiction with European standards, nor did their approaches to science necessarily have a pragmatic end. If we look at American biology from a larger perspective – one not based on the Morgan school or Mendelian tradition in general – we see that Harwood's distinction between comprehensives and pragmatics is much more difficult to accept.¹³

If a larger picture of the American context relativises national styles of thought – in showing that there is not always a direct and smooth connection between institutions, styles and ideas – then, we could argue that perhaps scientific traditions, ideas, and methodological styles can enter people's minds notwithstanding strong social and institutional filters. I think that my American case-study demonstrates that people and ideas may come before institutions and structures of power. In other words, persons, ideas and traditions can profoundly shape institutions and structures of power rather than be shaped by them.

experience of two sectors of the Germans academic community during a period of rapid social change" (Harwood, p.313). Therefore, both institutional differences – national and intra-national - and biographies could account, according to Harwood, for the differing styles of thought, diverse cognitive patterns entailing different interests and methodologies; and, of course, distinct final theoretical outcomes.

¹² I mean all models that regard the development of scientific ideas as mere epiphenomena of institutional or social organisations, structures of power, economical constraints or interests, or "basic intentions". That does not mean I consider all externalist approaches unhelpful or useless; I only question the idea that any tradition, style of thought or theoretical result has a direct and reducible relation with its social and institutional environment.

¹³ It is also important to remember that several first-rank American biologists, during the first three decades of the 20th century at least, accepted different theoretical versions of cytoplasmic inheritance. Of course, many American geneticists were sceptical about cytoplasmic heredity, but, as I hope I have already demonstrated, geneticists were not the only group working on heredity but that they were part of a bigger context in which cytoplasmic inheritance was generally admitted. Historians of biology should accept the idea that Morgan did not hold the monopoly on the study of heredity in the US, at least not until the 1940s.

In the next section I will introduce my first case-study: the zoology department at the University of Chicago. I shall focus my research on two figures having important relations with such an institution: F. R. Lillie and his pupil E. E. Just. We will see that the bio-philosophy upheld by these figures – and therefore their holist and organismic approaches to biology – had its roots in Europe; in the post-Kantian agenda I have described in the previous chapters. Then, in the next chapter, I will introduce my second case-study: the Scripps Marine Association in San Diego and the relation between the founder of this institution, W. E. Ritter and another Chicago biologist: C. M. Child. At the end of my discussion I hope to have demonstrated that both these institutions were shaped according to the scientific ideas and philosophical conceptions of their founders and employees rather than the other way around.¹⁴

Finally, where, in the second chapter, I have explained the diverse connections tying together American biologists with European traditions, in this chapter I shall focus on the Americans' positive program, i.e., discussions, ideas, theory and scientific results. In sum, once established that their bio-philosophies were rooted in the neo-Kantian tradition in Europe, we need to understand in what ways they had been original, what kind of positive discourse they proposed and which scientific agenda they supported.

5.2: Persons and Ideas Shaping Institutions: The Organismal Style at the Zoology Department of the University of Chicago

Organic functionalism, with its focus on how individual parts were integrated and organized into purposeful wholes, formed the core of the interactionist paradigm in the life sciences at Chicago, a paradigm in which physiology served as the model science.¹⁵

G. Mitman

The University of Chicago opened in 1892. Thanks to the financial backing of J. D. Rockefeller and the organisational skills of a young classicist, W. R. Harper, the institution started, as Newman records,¹⁶ as a “fully-fledged” university. In fact, in the same year, Charles Otis Whitman was appointed Head Professor

¹⁴ I think that Ritter's case, probably more than Chicago and Woods Hole, represents a sheer vindication of the history of ideas because, as Ritter's documents on the foundation of the San Diego Marine Association attest, the institution was conceived and built according to the bio-philosophical conceptions of its founders: in sum, people and ideas come first and institutions follow.

¹⁵ Mitman, 1992, p. 71.

¹⁶ See Newmann, 1948.

of Biology and Professor of Animal Morphology in the brand new Department of Zoology; a department that, as we will see, would represent a very important place for the development of organismal philosophies in the US. Whitman was born in Nord Woodstock, Maine, in 1842.¹⁷ He received a largely classical education in local schools and, in 1868, after taking his BA degree from Bowdoin College, he taught classic and modern languages, as well as mathematics, at Westford Academy. It was through E. S. Morse, a zoologist who taught at Bowdoin College and was a former student of Agassiz, that Whitman changed his interests towards zoology. Indeed, he was among the few students attending the unlucky Louis Agassiz's school of natural history at Penikese Island. After this brief experience, Whitman sailed toward Europe, in order to work as a PhD student, at Leuckart's school in Leipzig. The German experience made him a prominent embryologist and, after two years spent as a teacher at the Imperial University of Tokyo, he concluded his training abroad, working at the Naples zoological station in 1881. During the following years, Whitman would change and direct different institutions: from Assistant Zoologist at Agassiz's Museum in Harvard to Director of the Milwaukee Lake Laboratory, from professor of Zoology at the Clark University to the first director of the new marine biological laboratory in Woods Hole in 1888. When in 1892 he became head of the department in Chicago, he was already a star: he was the first editor of one of the most important American Journal for biologists; the *Journal of Morphology* and founder, together with one of his Chicago colleagues, W. M. Wheeler, of the *Biological Bulletin*. In sum, Whitman is not only a prominent figure in my story but he has certainly been a central figure in the development of American biology as a whole.

The presence of Whitman in Chicago was decisive in fostering an organismal and 'neo-Kantian' approach to biology: both institutionally and philosophically. As Mitman observed, his:

...concept of organization was one that permeated not only his institutional plans but his biological research as well. Organization did not just emerge from a combination of cells or faculty members. Nor was it merely responsible for the maintenance of the organism or institution. Organization instead preceded development; it resided latent within the egg as a potentiality of structure passed on through heredity that awaited actualization. Hence, the highest function of organization was to 'create and

¹⁷ Morse, 1912.

direct', not 'to adapt and conform'. Organization was thus a guiding force of development and ensured progress along the way.¹⁸

Indeed, looking at the people Whitman appointed and trained, the kind of works that were published under his supervision, it is easy to see how he shaped the institutions that he directed according to his received ideas and approach to biology.¹⁹ After all, it was thanks to him that figures such as G. Baur,²⁰ W. M. Wheeler,²¹ C.M. Child and F. R. Lillie were appointed there.²² In sum, Whitman was able to use his power as an administrator to create an intellectual environment dominated by an organismic style or approach to biology:²³ a neo-Kantian style having many similarities with the European tradition he had absorbed during his stay abroad.²⁴ With Agassiz, Whitman's department represented the second important European pole of research and education on American soil. After his death in 1910, a young biologist that he had trained took his place; that was F. R. Lillie.

¹⁸ Mitman, 1992, p. 22.

¹⁹ Pauly too stressed this point: "...his organicist belief that biologists like organisms, would interact to produce a whole larger than the sum of the parts and would thereby individually become enriched. Success, while natural, would not be automatic. It depended on a favorable environment, the right people, intimate associations, and continued autonomy" (Pauly, 2000, pp. 153-154).

²⁰ A German biologist and morphologist. See W. M. Wheeler, 1936, "George Baur's Life and Writings", *Amer. Nat.*, 33 (1900), 15-30 and Rainger, 1981.

²¹ See Evans and Howard, 1999.

²² Lillie had earned his PhD in Zoology at the same institution.

²³ J. Maienschein, 1991b.

²⁴ Regarding Whitman in Chicago, Newman states that: "By way of summary of the Whitman period, it may be said that it was under the domination of one great leader in American Zoology who ran the department single-handed in more or less autocratic style, that he was interested almost exclusively in research and looked upon class work and executive routine as merely an interference with research." (Newman, 1948, p. 223)

5.3: Disseminating Organicism: F. R. Lillie (1870–1947)



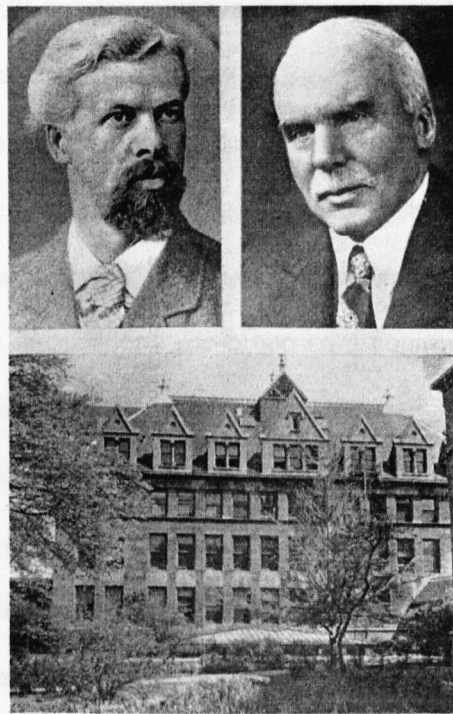
Fig. 5.1, 1901, Department of Zoology, University of Chicago, from left to right standing: F. R. Lillie, C. M. Child and C. O. Whitman²⁵

Frank R. Lillie earned his PhD under Whitman's supervision and Whitman's influence on Lillie's biophilosophy is evident from the earlier stages of his career. That Whitman was a constant source of inspiration for the young Lillie is already evident, in particular, in the first important papers Lillie published on *Unio*²⁶ and *Chaetopterus*.²⁷ Although specialist and very focused pieces, the central lesson Whitman had advanced in his classic papers such as "The inadequacy of the cell-theory of development" and "The Seat of Formative and Regenerative Energy" is easily discernible; the whole organised entity we call the organism (or parts of it as the cells), in all its complex functions, could not be understood by considering its composing elements alone, insofar as we require a "principle of unity" able to explain how those elements are disposed in such an organised manner. In brief, the whole organism comes before its composing elements and life resides not in these elements but in their peculiar disposition and dynamic organisation.

²⁵ Source: Mitman, 1992, p. 33.

²⁶ Lillie, 1901.

²⁷ Lillie, 1906.



Charles Otis Whitman (upper left), Frank Rattray Lillie (upper right),
Hull Zoological Laboratory (below)

Fig. 5.2, C. O. Whitman and F. R. Lillie²⁸

Lillie was born in Toronto in 1870. The son of wealthy parents, he studied first religion then science at the University of Toronto.²⁹ In 1891 he gained his BA degree and began working at the Woods Hole Marine Laboratory where, from 1900, he was assistant director under Whitman. Apart from a brief interlude at the University of Michigan and Vassar College, Lillie spent most of his career between Chicago and Woods Hole. Although a prolific author, skilled teacher and widely recognised figure by his contemporaries, he was also a keen administrator and organiser.³⁰ In 1908 he became director³¹ at Woods Hole, after Whitman's retirement. As Newman explains, Lillie³² was: "...the prime mover back of the development of the Marine Biological Laboratory from a small affair housed in a few frame buildings to the present large and commodious laboratory that is now recognised as the leading marine laboratory in

²⁸ Source: Newman, 1948.

²⁹ See Willier, 1957 see also Lillie, "My early life" (a biography written for Lillie's children in 1944), Lillie Papers, Box II I, Folder 8, MBL Archive, Woods Hole.

³⁰ As Lillie's obituary reported: "As an organizer and administrator, Lillie has played a leading role in the advancement of science throughout the present century. His greatest monument, perhaps, is the Marine Biological Laboratory at Woods Hole, Massachusetts, a unique experiment in a democratic organization, owned and operated by its members who represent colleges and universities throughout the United States, and many foreign institutions. In Lillie Obituary, 1947, Lillie Papers, Box II I, Folder 7, MBL Archive, Woods Hole.

³¹ See Lillie, 1944.

³² See also Peters, 2000.

the world.”³³ From 1935 to 1939 he also maintained presidencies of both the National Academy of Science and the National Research Council.

A practical man, as Kenneth Manning³⁴ describes him, he was not particularly inclined to philosophical speculations. Indeed, careful experiments, detailed observations and very limited working hypotheses characterised his scientific enterprise. Expert in general embryology, his name is especially remembered for his research on fertilization.³⁵ He proposed a controversial theory according to which fertilization is essentially a chemical reaction happening between three elements: sperm, egg and a supposed substance Lillie called fertilizin; a substance present on the egg’s surface which, once “activated” by the sperm, triggered the developmental processes.³⁶ This theory was harshly criticised by people such as Jacques Loeb during the first decades of the 20th century.

Like all the figures belonging to the organismic tradition I am discussing, Lillie linked his organismal biology with his beliefs about heredity and development. From 1906, when he published the aforementioned paper on the embryonic development of *Chaetopterus*,³⁷ he argued that it was through embryonic development that heredity manifested itself; in other words, it was through detailed observations on ontogeny – and all the careful experiments aimed to divert normal development – that hereditary phenomena become visible: “...I make no apology for entering into details, because there is no other explanation of heredity than a complete account of development, and one cannot describe even a small part of so complex a thing without many words, unless one knows in advance what is essential and what is not.”³⁸

Yet, the careful investigations on *Chaetopterus* development also supported other important conclusions, notably that complex hereditary phenomena “...cannot be reduced to the operation of any single factor.”³⁹ The complex relations between the nucleus and cytoplasm as well as the apparent structural differences among chromosomes left the door open to diverse interpretations. What seemed to be clear though was that both the intra-cellular Darwinian theory of pangenesis and the Weismannian

³³ Newman, 1948, p. 229.

³⁴ Manning, 1983.

³⁵ Farley, 1982.

³⁶ Lillie, 1914.

³⁷ Lillie, 1906.

³⁸ *Ibid.*, p. 154.

³⁹ *Ibid.*, p. 246.

theory of determinants were substantially “unwarranted” insofar as: “The whole economy of nature forbids us to believe that each cell possesses arm, leg brain, liver lung etc., chromosomes of which only one class enters into activity in any given tissue, the remainder lying idle.”⁴⁰ Although the breeding experiments practiced with the Mendelian methods could help to establish the relation between chromosome-characters and inherited “proportions” (at that time Lillie could not use the conceptual distinction Wilhelm Johannsen made in 1909 and 1911 between genotype and phenotype),⁴¹ our knowledge about hereditary material might nevertheless advance little; in fact, insofar as there is no real resemblances between “phenotype” and “genotype” but only a possible correspondence: “...any imaginable degree of knowledge of the unit species-characters would not furnish a particle of information as to the nature of the original germinal characters.”⁴² To put it in another way, even though we are able – through the observations of Mendelian ratios obtained through breeding experiments – to find a correspondence between specific characters (such as colour or albinism) and chromosome-characters, we still remain ignorant about the true nature of chromosomal structures. Once again – as we will see as a common objection to genetics – to say that a specific adult observable character (height or hair colour) is related to an unobservable unit-character contained in the chromosome adds almost nothing to the knowledge about such germinal characters.⁴³

Lillie’s recurring synthesis of Whitman’s organismal philosophy with heredity reflected a common refrain among the community of organismal biologists. To them, the cells were: “...subordinate to the organism⁴⁴, which produces them, and makes them large and small, of a slow or rapid rate of division, causes them to divide, now in this direction, now in that, and in all respects so disposes them that the latent being comes to full expression.”⁴⁵ If the organism was the primary source of organisation and guided complex processes happening at the lower organic levels, the morphological characters could not be linked to discrete material hidden within the nucleus of the cell, because any visible character, from the simpler to the more complex, is the result of the whole organisation and not the outcome of

⁴⁰ *Ibid.*, p. 250.

⁴¹ Johannsen, 1909; 1911; see also Churchill, 1974.

⁴² Lillie, 1906, p. 251.

⁴³ This last point will be developed further on.

⁴⁴ Whitman had pointed out such a hypothesis in his article “The Inadequacy of the Cellular Theory of Development” published in 1893.

⁴⁵ Lillie, 1906 p. 252.

direct expression from chromosome-character to the species-characters. In particular, the embryological mosaic theory of development⁴⁶ – a theory which assumed the existence of predetermined factors narrowly and firmly related to specific morphological parts – had to be replaced, “...by the view that there are certain properties of the whole, constituting a principle of unity of organization, that are part of the original inheritance, and thus continuous through the cycles of the generations, and not arise anew in each.”⁴⁷

To summarise, particulate theories of inheritance – as intended by Weismann’s followers and as interpreted by Mendel’s advocates – appeared totally unjustified in the light of the organismal conceptions of biology as seen by some Chicago investigators (but not only there). Anticipating a topic that would become dear to Ritter, Lille pointed out: “The organism is primary, not secondary”, i.e., the organism is not an epiphenomenon of unspecified germinal particles. The organism “...is an individual, not by virtue of the cooperation of countless lesser individualities, but an individual that produces these lesser individualities on which its full expression depends.”⁴⁸ Not surprisingly, many issues we found among European biologists, in earlier chapters, concerned Lillie too. In effect, the organism not only acted as a whole toward its own parts, but any part was also a result of the interaction between contiguous elements and the external environment.⁴⁹ All visible morphological characters were therefore the outcome of these dynamic processes happening at different levels of complexity, plus the environment. Given such a framework, Lille could conclude, once again, that “...characters are not due to “unfolding” of the potencies of determinants but are results of morphogenetic reactions between two or more formative stuffs. The “characters” need no more be preformed in the reagents (formative stuffs) in the case of a morphogenic than in the case of a chemical reaction.”⁵⁰

Yet, such a theoretical position was often mingled with epistemic prescriptions: not only did the idea that the nucleus contained all the necessary particles representing adult characters contradict the

⁴⁶ See Maienschein, 1991, pp. 43-59.

⁴⁷ Lillie, 1906, p. 251.

⁴⁸ *Ibid*, p. 252.

⁴⁹ Lillie distinguished between the “action of the whole organism”, in which the entire organism “...exercises a formative influence on all of its parts” and “correlative differentiation” which involved “...all actions of the intraorganic environment”. The action of the whole organism on its parts was, after all, a qualitative extension of the more limited correlative differentiations.

⁵⁰ Lillie, 1906, p. 258.

available evidence, it was totally unconvincing as a possible scientific explanation: Nägeli, De Vries, Weismann and Wilson, all were accused of sustaining such a controversial hypothesis: “According to these writers...all the characters that are ever to be impressed by the nucleus on the cytoplasm are represented by original preformations in the nucleus. Such a conclusion appears to me to be practically a negation of the evidences of our senses.”⁵¹ After all, Lillie argued, if all the structural diversity we observe in the adult organism was already present in the chromosomes, it ought to be clearly visible and assessable by “...our senses, by variety of behaviour or reaction”. Not only was such a complex structure not observed but even its supposition contrasted with the known “laws of chemical combination”. In short, when a hypothesis was neither supported from evidence nor coherent with other reliable knowledge, it should be rejected: “It seems to me that all *a priori* consideration should be ruled out of court, unless we are willing to transform biology into a branch of metaphysics dealing with potencies and latencies”.⁵² The charge against the particulate theory of inheritance was serious; indeed, Lillie believed that all those advocating for these theories spoke a medieval language,⁵³ accepted *a priori* assumptions, and overlooked the clear evidence: in a word, they broke the elementary requirements of an empirical science.

Lillie’s bio-philosophical agenda became more and more clearly articulated in the following years. In 1909, he published a paper in which his philosophical and scientific ideas were exposed in a popular style.⁵⁴ In this paper, Lillie presented the embryo as a more or less stable individual on which the environment acted in different ways. Once again he stressed the importance of both “intra-organic” and “extra-organic” environmental factors during the whole morphogenetical process⁵⁵ and ascribed to such a dialectic the difficulty for any preformistic hypothesis in heredity: “...an immense part of we call inheritance is inheritance of environment only, that is, repetition of similar developmental processes under similar conditions.”⁵⁶ Furthermore, to Lillie, the difference between a particulate theory of

⁵¹ *Ibid.*, p. 260.

⁵² *Ibid.*, p. 260.

⁵³ Potencies and latencies as dominant and recessive.

⁵⁴ Lillie, 1919.

⁵⁵ As Lillie instantiated: “...the constancy of distribution of peripheral nerve is not due to the transmission of nerve-branching determinants from generation to generation, but is a function of the intra-organic environment in each generation”, *Ibid.*, p. 244.

⁵⁶ *Ibid.*, p. 245.

inheritance and a physiological theory of heredity appeared evident once these theories were confronted with some relevant observations. For example, the different colours of mammals did not depend on the presence or absence of specific determinants in the germ cells, but on a specific power of the protoplasm to oxidize: “The development or inheritance of colour...can certainly not be due to the presence of black or brown or red or yellow determinants in the germ, assumed for theoretical purposes by some students of heredity, but to a specific power of oxidation of the protoplasm.”⁵⁷ Hence, to him, all the problems of heredity and organic variation had to be tackled within a physiological and developmental framework because, as we have seen, understanding how a morphological character developed was equivalent to explaining inherited and multiple expressions.

The particulate theories of heredity that Lillie was criticising included also what he called the theory of “unit-character”, a theory supported by De Vries and Bateson among others. In fact, while Lillie remained sceptical about the supposed relation between germ-character and visible-character (genotype and phenotype), he actually questioned the definition of “character” *tout court*. He regarded the notion, especially as defined by the early geneticists, as in contradiction with all that the physiology of development had taught. Indeed, Lillie felt it important to specify that, contrary to the received opinion of many zoologists or botanists, “characters” cannot be seen as anatomical stable units because⁵⁸: “...they simply represent the sum of all physiological processes coming to expression in definable areas or ways, and they may thus represent a particular stage of a chemical process.”⁵⁹ “Characters” are like “...shells cast up on the beach by the ebb and flow of the vital tides; they have a more or less adventitious quality,”⁶⁰ Lillie concluded, quoting Thomas Huxley.

In revealing the depth of Huxley’s analogy, Lillie was expressing his organismal faith: if we ignore the nature of vital tides, we also ignore why a shell lies in one position rather than another. But, if we could understand more about the tide’s movements – therefore, by analogy, more about the physiology of protoplasm – we could also shed light on the hidden mechanisms of heredity for the simple reason that any character has its own developmental history. Mendelian factors then – just as any other

⁵⁷ *Ibid*, p. 248.

⁵⁸ Again, “characters” do not represent static and definite entities because: “...in the study of heredity and development we are dealing with biological processes”, p. 250.

⁵⁹ *Ibid*, p. 250.

⁶⁰ *Ibid*, p. 250.

kind of hereditary factor – cannot be conceived as representative units of definite morphological parts but, at most, they “...must be factors in the development of the entire organism”.⁶¹ In sum, genes may trigger developmental processes but they cannot be the direct “cause” of any morphological character. With many European biologists, Lillie strongly believed that there was a profound conceptual continuity between Weismannism and Mendelism and that both were in contradiction with organicism.

5.4: Embryos, Feathers, Genes and Hormones: Lillie’s Epistemic Pluralism

Lillie, unlike many other figures belonging to the tradition I am describing, did not attempt to formulate a large synthesis of genetics, embryology, physiology and evolution but, rather, he looked for a mutual “cease-fire” between respective disciplines in the name of a methodological pluralism. Indeed, during the first years of the development of genetical sciences, while Morgan and his students were framing a new paradigm of heredity, some embryologists and cytologists in Europe and the US felt the need to propose a convincing synthesis of studies on inheritance and development.⁶² However this attempt never succeeded and the clash between two different scientific approaches about the understanding of hereditary mechanisms ended in favour of the geneticists who, as Scott Gilbert emphasises, were able to translate the greater part of embryological issues into genetical terms, i.e., so undermining the pluralism advocated by Lillie.⁶³

Not surprisingly, Lillie seemed to be quite sensitive to these themes. In 1927 he published a paper in *Science* in which he evaluated the extent of the separation between these scientific disciplines: “Since Weismann, physiology of development and genetics have pursued separate and independent courses...there can be no doubt, I think, that the majority of geneticists, and many physiologists certainly, hope for and expected reunion. The spectacle of the biological sciences divided permanently into two camps is evidently for them too serious a one to be regarded with satisfaction.”⁶⁴ In the late 1920s genetical sciences were too important to be so easily dismissed as Lillie did in his early papers.

⁶¹ *Ibid.*, p. 252.

⁶² Allen, 1985b.

⁶³ See Sapp, 1987, and Gilbert, 1998.

⁶⁴ Lillie, 1927, pp. 361-368.

Furthermore, prominent scientists increasingly considered genetic knowledge to be an essential element for a deeper understanding of the physiology of development.⁶⁵ It was for precisely these reasons that Lillie tried to assess to what extent – given the assumed importance of genetics for organic development – the concepts put forward by the Mendelian school were compatible with the concepts set out by embryologists.

Lillie began by defining the notion of the germ and its progressive unfolding. First, as Delage had argued several years before, the germ was characterised as a simple entity which manifested itself through the irreducible and dynamic duality between nucleus and cytoplasm. Furthermore, it was a physiologically integrated entity which could encompass different units: from a single cell to a polarized individual with one or more metabolic gradients.⁶⁶ At this point, Lillie distinguished between two different consequential processes: on one hand was embryonic segregation, which denoted the establishment of definite “primordia” at the beginning of embryogenesis, and implied the existence of well-delimited regions with determinate developmental potencies. On the other hand, especially during the later stages of development, such potencies ‘emerged’ in forming definite tissues (histogenesis) and further “functional differentiations”.

The concept of embryonic segregation was of paramount importance.⁶⁷ It implied a progressive, dynamic, and ordered movement from simpler and undifferentiated “primordia” to the more complex, and highly specialised, structures – a movement ending with the definitive genetic restrictions that anticipated the consequent histogenic processes. While the first stages of embryogenesis were characterised by a quite dynamic and flexible pattern; this flexibility was progressively lost when development entered the phase Lillie called “closed terms”. In other words, the diverse developmental branches, exemplified by the open potencies, were now limited to just one possible realisation.⁶⁸ Once the organism had reached this stage, its morphological parts possessed a relative independence from the whole organism, so that, to use an analogy current at the time, the parts increasingly became independent from the tyranny of the whole.

⁶⁵ Lillie mentioned Morgan, Spemann and Goldschmidt.

⁶⁶ Lillie accepted Child’s theory of metabolic gradients.

⁶⁷ This will be discussed more extensively in the next section.

⁶⁸ Lillie would extend this model in another paper published in 1929: “Embryonic Segregation and Its role in the Life History”, which I will discuss later on.

Once he had provided the theoretical framework in which embryologists were immersed, Lillie tried to evaluate what contribution geneticists could make to such a discussion. Lillie held that genetics could certainly shed light on some biological issues. First, to Lillie, geneticists not only had "...brilliantly demonstrated that genes are concerned in phenotypical realization at different stages of the life history, and it is therefore a reasonable postulate that this is true of all phenotypic realisation,"⁶⁹ but they also showed that the expression of many morphological characters could be *Mendelized*, i.e., it could be statistically demonstrated that a relationship between the development of some phenotypes and genes existed. However, Lillie concluded, regarding embryology, genetics could be more misleading than helpful, in principle at least. Indeed, the reconciliation between embryology and genetics was mainly impeded by the enormous conceptual gap that separated a conception of heredity defined as pure reiteration of an individual organism's life (the physiological conception of heredity) and a conception of heredity seen as the statistical recurrence of specific characters generation over generation. A profound divergence, Lillie asserted, instantiated in different method of investigations, different epistemic approaches and experimental traditions.

Secondly, although genetics could give some contributions in understanding the physical and chemical nature of the germ, it was of no help in working out the process of individuation: indeed, as we have seen, this process was conceived as a complex event strongly mediated by external and internal organic environments. Third and finally, genetics could not help to improve a possible definition of embryonic segregation for the simple reason that geneticists held that each cell possessed the same genetic material. In other words, if all hereditary material was more or less homogenous, genetics could not explain how very different and heterogeneous forms and structures were formed at different stages of development. Hypotheses which supposed some alleged complex models of interactive genes meant putting the cart before the horse; indeed, Lillie argued these invoked processes supposed what they pretended to explain.⁷⁰ Lillie concluded that, unless some surprising and unexpected progress were made in the near future, the possibility that genetics could be of any help with the phenomena of embryonic

⁶⁹ *Ibid*, p. 366.

⁷⁰ Lillie in particular criticised the Goldschmidt' attempts to formulate a physiological theory of development positing a complex mechanism of gene activations at different times. The Goldschmidt's model indeed "...presupposes an underlying mechanism adequate to almost ultraphysically precise regulation in the germ, for which no model can be suggested: at the most it shifts the difficulty one step further back" (Lillie, 1927, p. 365).

segregation was small: "...I don't know of any sustained attempt to apply the modern theory of the gene to the problem of embryonic segregation. As the matter stands, this is one of the most serious limitations of the theory of the gene considered as a theory of the organism", if any cell possessed the same genetic material "...the phenomena of embryonic segregation must, I think, lie beyond the range of genetics."⁷¹

Hence, Lillie maintained a position of principle: if genetics remained as it was, i.e., in accepting the particulate theory of inheritance, for example, and assumed the existence of fixed representative characters linked to specific morphological structures, it could be of very little use for embryologists. After all, the chief methods and approaches of genetics left out completely the phenomena in which embryologists were more interested: it showed the *alpha* and *omega*, namely the relation between the gene and its realisation (phenotype), but it overlooked what happened in the middle; all the complex universe of causes and effects that lay between the hereditary factors and their visible manifestation. Between genotype and phenotype dwelled a black box which geneticists deemed too complicated to open.⁷² It was precisely for this reason the two fields were still destined to remain separated: they looked at different things with different methods and approaches. They revealed dichotomous aspects of the life history, two irreconcilable perspectives based on two different conceptions of biology: one underlined the firm and unchanging characteristics of the organisms whereas the other emphasised the constant and always dynamic changing of the living matter: "The dilemma at which we have arrived appears to be irresolvable at present. It is the apparent duality of the life history as exhibited in the associated phenomena of genetics and ontogeny: on the one hand the genes which remain the same throughout the life history, on the other hand the ontogenetic process which never stands still from germ to old age."⁷³

This duality underlined by Lillie was particularly evident in his studies dedicated to bird feathers in his later works; publications that, as we have seen, were particularly admired by D'Arcy Thompson. The morphogenesis of feathers and the development of particular patterns and pigments demonstrated how a genetical approach could be too "one-sided". From 1932 indeed, Lillie began to

⁷¹ Lillie, 1927, p. 366.

⁷² We know that Morgan in his *The Theory of the Gene* published in 1926, clearly admitted this last point: "Between the character (phenotype), that furnish the data for the theory and the postulated genes, to which the characters are referred; lies the whole field of embryonic development. The theory of the gene, as here formulated states nothing with respect to the way in which the genes are connected with the end-product, or character". Morgan 1926b, p. 26.

⁷³ Lillie, 1927 p. 368.

explore the complexity of the morphology of the Brown Leghorn fowl's feathers in a long series of papers.⁷⁴ The experiments and observations Lillie undertook aimed to establish, in particular, which factors played a central role in the development of the feather forms, patterns and pigments. In other terms, in these papers he tried to answer a typical embryological question: how feathers, with their sophisticated structure and colours, come to be. The methods of investigation Lillie used consisted, generally, in a nice combination of morphological observation and experimental manipulation. The observation of normal feather development was then used as base to assess how experimental intervention diverted natural morphogenesis.⁷⁵ For example, Lillie noted that injections of thyroxin or female hormone had the power to change feather patterns.⁷⁶ Moreover, experiments on transplantation and recombination on the papillae (the sections of tissue at the base of the developing feather) showed that the latter controlled general feather development.⁷⁷

Generally, the accurate experimental manipulation led Lillie to consider the relationship between specific substances such as hormones, the growth-rates in different feather regions and patterns and morphology of the feather. In other words, quantitative doses of hormones provoked some changes in patterns development; albeit these changes were mediated by the different growth-rates in the different feather regions. Therefore: "Slowly growing feathers react to a smaller dose of hormone than rapidly growing feathers. As rate of growth is a fixed property of the different feather's tracts...it is possible to produce birds, by means of suitable administration of female hormone, with female feathers in the slowly growing tracts, and feathers of male character in the more rapidly growing tracts."⁷⁸

Lillie drew some interesting theoretical consequences from these experimental results. It seemed that female hormones had a specific function such as unlocking: "...the potentiality for female development resident in the constitution of the feather germ. The hormone exteriorizes the morphological and physiological characteristics of the female cell; but both these are the attributes of the cell, determined in their entirety and only dependent on the hormone for expression."⁷⁹ To summarise,

⁷⁴ Lillie and Juhn, 1932, then Lillie, 1938.

⁷⁵ Lillie, 1941.

⁷⁶ Lillie, 1932.

⁷⁷ Lillie, 1941 and Lillie, 1942.

⁷⁸ Lillie and Juhn, 1932, pp. 177-178.

⁷⁹ *Ibid*, p. 175.

departing from the same physiological conditions and assuming the existence of the same hereditary material in the cell nucleus (and in the feather's germ to use the Lillie's terminology), diverse morphological structures were formed; all differences related to the variation of the growth-rates on which, as we have seen, different hormonal quantities could have different influences. As we will see, we are not very far from Child's theory of the metabolic gradients: as well as the action of cyanide or alcohol depended on the metabolic rates the specific region of the planaria's body possessed, the action of the female hormones acted in function of the growth-rate of the bird's feather: "The various patterns formed by injections of hormones are fully explained as to their form by the gradients of growth-rate."⁸⁰

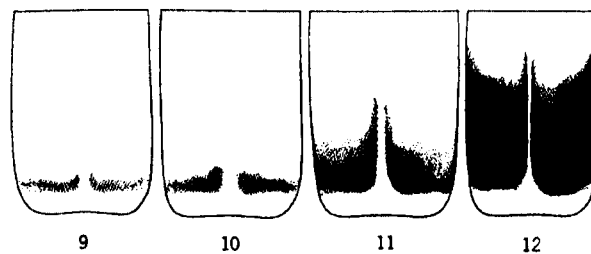


Fig. 5.3, Illustration of the development of different feather's patterns after injections of 5 mg of thyroxin in one specimen. Fig. 9, 24 hours after injection. Fig. 10, 48 hours after injection. Fig. 11, 72 hours after injection. And fig. 12, 96 hours after injection. See Lillie, 1932, p. 208

I linger somewhat on these details because they offer an interesting window on what Lillie really meant when he distinguished between genetics and the physiology of development and advocated their difficult synthesis. In the specific case, whereas geneticists could observe the transmission of specific feather patterns, forms and colours generation over generation – assessing small variations, statistical recurrences, and distribution of traits in a population – the physiologist tried to identify the mechanisms hidden behind the pattern, form and colour formation. Therefore, from Lillie's standpoint, patterns, forms and colours were not explainable by positing the existence of genes for any of these elements; instead, they were comprehensible by diverting the 'normal' physiological processes and by 'tracking' the causal chain that, starting from a homogenous hereditary substance, brought toward a heterogeneous dynamic structure.⁸¹

⁸⁰ Lillie, 1932, p. 207.

⁸¹ As we have seen with the paper Lillie published in 1909, colour variation in mammals, as well as phenomena related to regeneration, the anatomy of the nervous system, development of the blood-vessel etc. did not depend on the existence of determinants or definite unit-factors, but on dynamic intra- and extra-organic interactions.

Once again, it is possible to conclude that physiology, for Lillie, filled the gap between hereditary materials and their dynamic expression whereas genetics focused on the statistical transmission of traits; i.e., factors totally abstracted from their ontogeny. Genetics and physiology, Lillie argued, were complementary fields that did not contemplate any reciprocal reduction, at least according the knowledge of the time. Any efforts to formulate eventual reconciliations were "...doomed to disappointment", any synthesis irremediably premature and any attempt to consider one field more important than the other misleading.⁸² Probably the wisest option would be to accept their irreducibility and leave things as they were. After all, even this situation would be better than to translate one field into another; i.e., forcing, simplifying or distorting concepts and meanings of different vocabularies, compelling experimental methods into a unique framework, circumscribing scientific approaches according to one monolithic paradigm: what Lillie stood for was an epistemic pluralism.

5.5: Lillie's Supplementary Proposal: Embryonic Segregation and its Bearing on Hereditary Sciences

We have seen that from his earlier publications Lillie thought that genetics could not explain how characters come to be; indeed it could, at most, describe regularities happening generation over generation. Genetical sciences could only predict statistically whether a specific character would be expressed in the next generation given the knowledge about the characters expressed in the previous generations. To reiterate, during the late 1920s, Lillie did not think that genetics was faulty, he only argued that genetical approaches clarified issues that were strangers to embryologists; problems such as ratios and distributions of characters (phenotypes) in different generations or within a population did not touch developmental issues. In fact, as I have previously mentioned, the central concern of the geneticists was not focused on the causal chain characterising the progressive unfolding of the morphological traits during ontogeny; what happened between genotype and phenotype was enclosed in a black box, an heuristic and pragmatic gap that nevertheless rendered gene theory open to some paradoxes. One of these

⁸² "Those who desire to make genetics the basis of physiology of development will have to explain how an unchanging complex can direct the course of an ordered developmental stream" in Lillie, 1927, p. 367.

paradoxes was clearly expressed by Lillie in 1928 when, in a letter to J. Huxley he wrote: “if you will excuse a paradox...gene theory is essentially a theory of phenotypes, i.e., something always static for as soon as it changes it is already another phenotype.”⁸³

Again, from a theoretical viewpoint, Lillie felt the same kind of uneasiness that many embryologists (including Just, Child and Ritter) expressed about the type of scientific explanations geneticists offered: to say that a particular phenotype has such and such characteristics because causally linked to an unobservable genotype seemed to be a trivial explanation:⁸⁴ as if someone would explain pullovers keep one warm because they are made of a fabric that keeps one warm. It is for this reason Lillie maintained that gene theory is in its essence a theory of phenotypes; if the genotype was derived from repeated observations of phenotypes, then the former was in reality only a representative label to denote the latter. However, when, in 1929, Lillie published the paper “Embryonic Segregation and its Role in the Life History”, he tried to formulate a view through which the geneticists’ black box could be partially opened and the relation between the hereditary factors and their dynamic expressions would be partly explained. Within such an explicative context, the provisional and partial bridge which would link heredity and its morphological expression was the notion of embryonic segregation, a notion Lillie had already sketched in the articles mentioned earlier, but that he extended further. Again, this was not a synthesis between embryology and genetics, instead it was an attempt to analyse some aspects of heredity as related to development.

The notion of embryonic segregation was compared by Lillie to the problem German biologists called embryonic determination, an issue which involved the pioneers of the *Entwicklungsmechanik* school.⁸⁵ However, although the phenomenon of embryonic determination dealt with some general problems of embryology, Lillie’s embryonic segregation denoted a more specific and limited process. In general, Lillie portrayed embryonic segregation as: “...the process of origin of the diverse specific potencies that appear in the organism in the course of the life history, which express themselves later in

⁸³ Lillie quoted in Sapp, 2003, p. 136.

⁸⁴ As Sapp clearly explains: “The notion that the gene determines the characteristic was pure tautology in the typical breeding experiments because the presence of genes was inferred by experimental manipulation of phenotypes.”, Sapp, 2003, p. 136.

⁸⁵ See Churchill, 1969.

tissues of specific structure and function.”⁸⁶ In other words, to Lillie, the general process of embryonic development included the particular processes of embryonic segregation. To use an analogy: just as individual words are the prerequisite for the composition of a romance, so embryonic segregation is the prerequisite for the overall embryonic development. For clarity’s sake — because Lillie was introducing a new terminology — he furnished a terminological *legenda*;

The most important notions Lillie introduced:

Segregate: The earliest stage of a part possessing specific potency.

Embryonic segregation: The process of origin of segregates.

Primordium: The earliest morphologically definable stage of a segregate, organ, or region.

Genetic restriction: the restriction of potencies of segregates due to embryonic segregation, as compared with those of the parent segregate.

Phenotypic properties or qualities: The properties or characteristics of any stage, or part of stage, of an organism, whether morphological or physiological, *is esse*, as contrasted with those *in posse*; the existing state either morphologically or physiologically considered.

The general idea that Lillie was describing was that, during embryogenesis, any germinal region possessed some specified potencies (qualities); potencies that were increasingly limited or thwarted as long as ontogeny proceeded toward a critical threshold or phase (in the following Fig.).

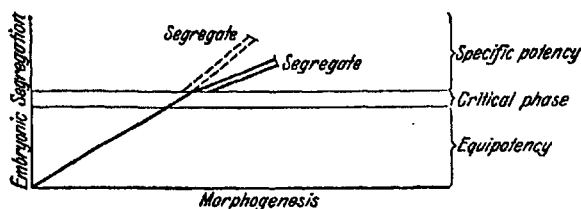


Fig. 1. Embryonic segregation; description in text.

Fig. 5.4, Lillie’s representation of the process of Embryonic segeragtion.⁸⁷

⁸⁶ Lillie, 1929, p. 500.

⁸⁷ Source: Lillie, 1929 .

As the figure shows, at the beginning of development the fate of the different germinal areas were open; in other words, they are almost equipotent. However, once development reaches the threshold Lillie calls the “critical phase”, and the process of segregation is gradually achieving its ends, the open potencies of the different germinal areas reach a “close term”. In effect, embryonic segregation was conceived by Lillie as a rather specific event in time. And yet, because embryonic segregation might express a broad range of Phenotypical characters, it is different from a phenotypic segregation: different morphological characters might be the result of a unique segregate (see legenda).

Furthermore, insofar as development, as von Baer had taught, follows a direction from the simplest to more complex structures, from the homogeneous to the heterogeneous, the development of the segregates (i.e. the embryonic regions still possessing open potencies) was always related to what had happened in the previous stages; in other words, the nature of a segregate is determined by the complexity of the preceding segregates: “Segregates may be designed as complex or pluri-potential so long as they retain the capacity of producing subordinate segregates, and as simple or unipotential when this capacity is lost and only one potency remains.”⁸⁸

Lillie conceived embryonic segregation as a dichotomous process; in the same way that geneticists mentioned dominant and recessive genes, embryologists talked about positive determined segregates and negative determined segregates (remainders).⁸⁹ After all, more than one potency could be related to a specific germ, because developmental possibilities implied a wide gap between potentiality and actuality; i.e., between actualised lines of development and latent ones. This process of segregation was best illustrated, Lillie pointed out, in the observation of cell-lineage. In fact, by following the process of cellular self-differentiation and specialisation, and, therefore, progressive restriction of cellular potencies, the observer could easily detect a dichotomous progression. The mechanism Lillie had in mind was comparable to the mechanism Weismann and Roux described in their theory of mosaic development. However, unlike the mosaic theory, which implied that at any embryonic cleavage the hereditary material was distributed, split and reduced among the cells fixing their fate, Lillie’s hypothesis entailed a quite

⁸⁸ Lillie, 1929, p. 505.

⁸⁹ However Lillie warned that the analogy between dominant and recessive genes and negative and positive determined segregates must not be pushed too far: they were two different phenomena. Indeed the processes related to embryonic segregation concerned the cytoplasm whereas the Mendelian mechanisms referred to the cell nucleus.

flexible process always controlled by the intra-cellular environment. Using the example of the development of *Triton's* eye, Lillie showed that the epidermal *primordium* involved two different segregates: the complex epidermal segregate and more specific “close term” segregate, exemplified by the lens. Because the specific segregations depended also on the extra-cellular environment and not on the fixed hereditary particles alone, the conception of embryonic segregation Lillie defended, unlike the mosaic theory, was an organismal conception of development. It was clearly organismal because, ultimately, it was the organism as a whole which controlled all the formative processes during ontogeny, so that any segregate had to be contextualised within a whole, dynamic developmental system:

In Weismann's theory of development, self-origination is predicated of all segregates; the idea of self-origination is indeed inherent in all determinate theories, and is equally required in all mosaic theories of development, i.e., those theories in which the individual is regarded essentially as the sum of its parts. But the idea of self-origination is foreign to organismal conceptions, such as now dominate the field of embryology, for the reason that segregates are determinably localized within the organism, which thus controls the exact location in which any given segregate is to appear by virtue of certain of its physiological means,” and finally: “...the foregoing analysis of embryonic segregation is based upon an organismal conception of development.”⁹⁰

There was another major difference between the mosaic theory of development and Lillie's hypothesis of embryonic segregation: the latter regarded the relations happening among cells as the result of cytoplasmic interactions. Although Lillie considered the theory of nuclear determination important, he argued that further progress was required to shed light on these phenomena insofar as the available “nuclear theories” – the classic Weismannian or genic ones – were untenable. Jan Sapp has clearly illustrated that, in the first decades of the 20th century, many important American biologists were opposed to nucleocentric theories of inheritance;⁹¹ heredity, according to these biologists, was not an exclusive phenomenon of nuclear substances but it involved also – and in a fundamental way – properties and

⁹⁰ Lillie, 1929, pp. 516- 528.

⁹¹ Sapp mentions, among others, E. G. Conklin, J. W. Jenkinson, J. Loeb, R. Harrison and, of course, F. R. Lillie. See Sapp, 1987.

materials located outside the nucleus. Even more importantly, the cytoplasmatic theories of heredity circulating at the outset of the 20th century highlighted the flexible and dynamic side of organic development; they were veritable epigenetic theories clashing with the supposed Weismannian preformationism: “The individual elementary units comprising a complex organism, e.g., the cells of blastula, were not necessarily predetermined as different parts but could be primarily all alike in constitution. The differences which arose during development were thought to be determined by the action of environmental factors upon whole groups of cells and upon each member of them.”⁹² Lillie’s hypothesis of embryonic segregation was the outcome of this theoretical organismic context.

However, even though the theory of embryonic segregation was not intended by Lillie as an alternative to genetics,⁹³ it could not be overlooked by any broad and convincing theory of heredity. The embryological and physiological studies Lillie undertook throughout his long career – from cell-lineage and regeneration to embryology and fertilization, from embryonic segregation to physiology of bird feathers – convinced him of the unbridgeable gulf separating the conception of heredity as an individual life’s reiteration and the notion of heredity as the statistical transmission of visible characters. Indeed, what Lillie demonstrated, both in his popular writings and orthodox works, was that all hereditary phenomena could be understood under two complementary epistemic categories; two independent and irreducible classes of phenomena. Once again, genetics, Lillie assumed, was the science which tried to figure out how hereditary characters were transmitted, using ratios, rates, and distribution of phenotypes.⁹⁴ The physiology of development instead, in which the theory of embryonic segregation was subsumed, looked at how heredity was manifested and progressively expressed during dynamic and complex processes of individual morphogenesis. Lillie did not confuse heredity with development; he thought that development had a lot to say about heredity from a different perspective than genetics.

The big picture Lillie aimed for led him to divide life history according to three general disciplines or phenomena: morphogenesis, embryonic segregation and genetics.⁹⁵ These were all different and irreducible fields with their own methods, languages and questions. As we have seen, Lillie’s

⁹² Sapp, 1987, p. 7.

⁹³ Just, on the other hand, as we will see in the next sections, regarded Lillie’s theory as an alternative to genetics.

⁹⁴ We have seen that Lillie considered genetics the science of phenotypes.

⁹⁵ Lillie, 1929, p. 507.

epistemic pluralism brought him to conceive heredity as a “multi-faceted” phenomenon. Different experimental and theoretical approaches revealed different irreducible aspects of inheritance: from development to transmission, from ontogeny to phylogeny – in a word, from genotype to phenotype without leaving unanalysed any gap between the two. Genetics was not *the* science of heredity but just one aspect of it. This wide conception of heredity and development was behind Lillie’s failed attempt to create a new Institute at the University of Chicago during the late 1920s: the Institute of Genetic Biology. Such an Institute, which had to formulate a viable alternative to the orthodox eugenics proposals, was meant to provide a research platform where biology could help to solve social problems. As Lillie himself introduced the goals of the Institute:

The future of human society depends on the preservation of individual health and its extension into the field of public health; but it depends no less on social health, that is the biological composition of the population. We are at a turning point in the history of human activity – the age of dispersion and differentiation of races is past. The era of universal contact and amalgamation has come. Moreover the population press on their borders everywhere, and also, unfortunately, the best stock biologically is not everywhere the most rapidly breeding stock. The political and social problems involved are fundamentally problems of genetic biology.⁹⁶

Even though Lillie shared with the eugenicists a fear of the apocalyptic consequences of uncontrolled population increase and disproportionate reproduction by the lowest classes, he was totally against the uncritical and blind application of genetics to eugenics: to him, as to many in Chicago and elsewhere, the environment remained too important a factor in human development. Indeed, as Mitman suggests: “The physiological, epigenetic orientation of developmental biology at Chicago contrasted sharply with the implicit preformationist and deterministic view of development held by geneticists such as Thomas Hunt Morgan”⁹⁷. To Lillie indeed, the individual was much more than his heredity; it was not through the selection of the fittest that a better race could be created, but through the scientific control of development

⁹⁶ Lillie quoted in Mitman, 1992, pp. 98-99.

⁹⁷ Mitman, 1992, p. 100.

(including environmental influences). In sum, it was embryology and not genetics that represented the only salvation for the human kind and civilization. However, such a broad agenda required much financial support which, during the late 1920s – with the world economic crisis – could hardly be afforded.⁹⁸ And, although the Institute never became reality, it shared the convictions, aims and hopes of another institute that during the same years propounded a similar agenda: this was the Marine Zoological Association of San Diego, an institution that will be the subject of the next chapter.

Lillie had been in contact throughout all his life with the director of the San Diego Association, W. E. Ritter. In the very late 1930s, as a retired man, Lillie still kept in contact with him. In their correspondence, they used to talk about scientific as well as philosophical issues. In one of their letters, Lillie illustrated the deep philosophical consequences of his experiments on bird feather development:

There is the same aspect of 'foresight' in the development of the feather that there is in the behaviour of the birds, eliminating of course the aspect of 'consciousness'. Can we have objective criteria of foresight whether accompanied by consciousness or not, and if the answer is negative where is the line to be drawn? What kind of science does this lead us to? It must be something more than a mere return to Aristotle, I would suppose. You probably are acquainted with Spemann's conception of psychological analogies in the processes of development. Ever since I wrote my first paper in 1894–95, where the problem is stated without any consciousness of its implication, this question has been in the background of all my scientific thinking.⁹⁹

The same problem of living organisation, an issue that had obsessed Kant himself, and all post-Kantian biologists, was the line that ran through all of Lillie's scientific life. When, in 1938, Lillie published a paper in *Science*, wondering about the future of Zoology, he stated, once again, the organismic principles that had animated his entire career: "Biology is...committed to a through-going physico-chemical analysis of organic structure and function, but it is not committed to a reduction of its concepts to physico-chemical levels. Biology is an autonomous science in the sense that its problems concern the

⁹⁸ On the history of this Institute see Mitman, 1992, pp. 96-109.

⁹⁹ Lillie to Ritter, November 16th, 1938, Box IIA, Folder 76, p. 1, Lillie papers, MBL Archive, Woods Hole.

level of attainments, both historical and functional, of the living organism.”¹⁰⁰ Lillie had inherited this biological agenda from Whitman who, in turn, had received it from Europe. The same legacy would be absorbed and transformed by one of Lillie’s best students in Chicago, Ernest Everett Just.

5.6: The ‘Un-modern’ Synthesis of E. E. Just



Fig. 5.5, E. E. Just¹⁰¹

Natur hat weder Kern

Noch Schale,

Alles ist sie mit einemale – Goethe¹⁰²

Just had the qualities of genius; nothing whatever turns him aside from his purpose. I have attempted over and over again to get him to conform to the conditions which his race and the nature of university life in America impose. I think now that this attempt was unwise; certainly it was futile.¹⁰³

Lillie to R. G. Harrison

Just was Lillie’s PhD student and Chicago pupil. Although today he is mainly remembered as an icon – as a black hero struggling against the racial prejudices which characterised American society in the first half

¹⁰⁰ Lillie, 1938, p. 67.

¹⁰¹ Source: <http://worms.zoology.wisc.edu/dd2/echino/fert/just/just.html>

¹⁰² My translation: “Nature has neither kernel nor shell. She is both at the same time”, Goethe quoted by E. E. Just, 1939, p. 1.

¹⁰³ Lillie to R. G. Harrison, March 20th, 1939, Box 6, Folder II A 54, MBL Archive, Woods Hole.

of the 20th century, as a brilliant, but underestimated scientist who failed to obtain wide recognition in his time because of his colour,¹⁰⁴ – his scientific ideas have been almost totally forgotten.¹⁰⁵ However, even though his racial background prevented him from fully realising his aspirations, and even though he spent most of his career at the Howard Medical School – a black institution he despised – his life was an intense adventure. From Charleston, South Carolina, the city where he was born in 1883 from very humble origins,¹⁰⁶ he studied at the Kimball Union Academy and then graduated from Dartmouth College in 1907 obtaining *magna cum laude*. In the same year he was hired by the Howard school in Washington where, as early as 1912, he became full professor and head of the department of Zoology. From 1909 Just spent his summers at the Woods Hole Marine Laboratory as assistant to F. R. Lillie who also agreed to supervise Just's PhD at the University of Chicago, where, for instance, he met Wheeler and attended Child's courses in physiology.¹⁰⁷ In 1916, although Just gained his PhD in an important institution with a famous supervisor, his opportunities remained rather limited; no institution, apart from those dedicated to black students, was disposed to accept a black scientist, however highly trained; Just had no other choice than remain at Howard.

In 1929 Just had the opportunity to visit Europe. He went first to Naples, where he studied fertilization in the sea urchin at the Zoological Station and, in 1930, he was invited at the *Kaiser — Wilhelm-Institut für Biologie* of Berlin (today Max Planck institute, which moved to Tübingen in the 1945). Since then, though tied to Howard for funding, Just visited several times Europe, preferring the fascist Italy, the Nazi Germany and the occupied France to American xenophobic society. Although he dreamed to live in Europe, he was never able to get funding to achieve such a purpose.¹⁰⁸ Finally, in 1940 he was working at the French Marine Laboratory in Roscoff when the Nazis arrested and interned him in a camp. He was soon released thanks to the intervention of the father of Just's German wife, who had

¹⁰⁴ Lillie considered Just's scientific career as a "...constant struggle for opportunity for research, the breath of his life. He was condemned by race to remain attached to a Negro institution unfitted by means and tradition to give full opportunity to ambitions such as his", Lillie, 1942, E.E. Just: August 14, 1883, to October 27, 1941, pp. 10-11. S. Jay Gould called his article on Just "Thwarted Genius" to emphasise Just's difficult conditions.

¹⁰⁵ Excepting Gilbert's excellent article "Cellular Politics" in which he compares Just's and *Goldschmidt's* theoretical alternatives to gene-centric hypotheses on heredity and development.

¹⁰⁶ Just's father was son of a slave.

¹⁰⁷ Manning, 1983, p. 85.

¹⁰⁸ In 1936, Just even made a formal request to Mussolini in order to get founded in Italy. See K. Manning, 1983, p. 291.

some important connections with the Nazis. Hence, he was able to get back in America where, once again, he had no other choice than Howard. Just died one year later, in 1941, from a pancreatic cancer.

As I have already mentioned, despite the existence of a discrete number of articles,¹⁰⁹ the publication of an excellent biography, and the several important recognitions attributed to Just, we do not know very much about his scientific achievements.¹¹⁰ Indeed, looking at the existing literature, it seems that his adventurous life overshadows his scientific accomplishments. Therefore, we know quite well about his loves with white women in Europe; in particular about his relation with Margaret Boveri. We know about his numerous attempts to get funding from American foundations and Universities, we know about some of his connections with eminent scientists of his time; with Frank Lillie, with J. Loeb, with Dohrn or Max Hartmann among others. We know about his difficult life at the Woods Hole Station, his happy life in Naples, his travels in Europe etc. However, we do not know very much about the contents of his researches. Of course, we know that he worked with Lillie on fertilization, he was a very able experimenter widely recognised among the Woods Hole crowd, and that he moved – toward the last years of his life – to more philosophical and theoretical issues. We also know that during the last years of his life he published an audacious monograph resuming the researches and ideas on an entire life in University and laboratories.¹¹¹ Finally, we know that he explicitly challenged T. H. Morgan in 1935 on his Chromosome theory of heredity, a theory which eventually led Morgan to get a Nobel Prize in 1933; and about his enthusiasm *a propos* of organismal and antireductionist approaches in biology. However, what we really do not know in detail are his scientific alternatives. In other words, what did Just specifically believe about the organism? What about heredity and development?

In the next sections, I will describe and focus on Just's proposals about what he believed was really relevant in biology; I will also introduce his beliefs and hypotheses about heredity and

¹⁰⁹ With the exception of a recent article written by Jan Sapp (Sapp, 2009), which briefly tackles Just's biology, all the other contributions are mostly popularisation of the individual, and not his science. See S. J. Gould, "Just in the Middle", and "Thwarted Genius", a review of the Manning's book. Byrnes, W. M., and Eckberg, W. R. (2006) Ernest Everett Just (1883-1941) – An Early Ecological Developmental Biologist, *Dev. Biol.* Vol. 296, pp. 1-11, Byrnes, W. M. (2009) Ernest Everett Just, Johannes Holtfreter, and the Origin of Certain Concepts in Embryo Morphogenesis, *Mol. Reprod. Dev.* Vol. 76, pp. 912-921, W. M. Byrnes, (2010) Ernest Everett Just: Experimental Biologist Par Excellence, *ASBMB today*.

¹¹⁰ Since 1927 he was enlisted in *American Men of Science* as among the top of thirty eight zoologists in America. Still in 2002 the black American historian Molefi Kete Asante, a specialist in African American studies, included Just in the list of 100 greatest African Americans.

¹¹¹ Just, 1939.

development; convictions which he developed during the last year of his brief career. With Just, we will see that the neo-Kantian tradition and ideas were well alive even during the late 30s.

5.7: Mutations, Cytoplasm and Evolution

In 1933 Warren Weaver, a prominent American mathematician at that time administrator of the Rockefeller Foundation, sent a letter to Lillie asking for some advices and opinions on the scientific and human skills of E. E. Just. Indeed, in 1932, Just had asked for financial support at the Division of Natural Science of the Rockefeller Foundation and Weaver was gathering as much as information he could get in order to decide for Just's application.¹¹² Lillie answered in an enthusiastic letter: "As regards his scientific work, he has been easily one of the most productive investigators at Woods Hole for the last twelve to fifteen years. His studies have been characterized not only by their care and precision, but also by a very considerable degree of scientific imagination."¹¹³ Just was clearly an excellent investigator and first rank biologist despite his racial problems and his inability to get a position in an important American institution. However, Lillie did not merely discuss Just's skills and problems, he also mentioned Just's theoretical stance about biology, a position shared by Lillie: "Biology is a subject in which schools of thought develop sharply defined controversies. Dr. Just is a rather ardent adherent when his convictions are fully formed. Thus I would say that he is against the extreme Mendelian school and also the extreme mechanistic school of thought in biology. I quite fully agree with his views on these subjects, so far as I understand them."¹¹⁴ It is not surprising that Lillie agreed with Just's bio-philosophy; after all it was the philosophy that animated his own technical papers since 1906, and it was the philosophy that – though now changed and adapted to the new discoveries and knowledge of 30 years of researches – Lillie inherited from Whitman in Chicago. In a word, it was the post-Kantian bio-philosophy.

However, even though Just clearly inherited from Lillie such a philosophy during his training and work in Chicago and Woods Hole, it was only during the early years of 1930s that he formulated his

¹¹² Manning, 1983.

¹¹³ Lillie to W. Weaver, March 6th, 1933, Box 6, Folder II A 54 (Just 1912-41), p. 1, Lillie Papers, MBL Archive, Woods Hole.

¹¹⁴ *Ibid*, p.2.

philosophical speculations. Indeed, between 1932 and 1933, he published, in *The American Naturalist*, two articles tackling different issues: heredity and nature of mutation, then cytoplasm and evolution, all within an organismal framework. In the first paper, Just conceded that the phenomena related to Mendelian inheritance could be accounted for in terms of chromosome combinations and recombinations so that mutational phenomena could be linked to chromosomes themselves.¹¹⁵ However, Just wondered, even though mutations were related to chromosomes, how did mutations happen first? In other words, scientists had established that some external factors such as heat and radiations were able to induce mutations in drosophila, but, Just asked, how did mutations arise in the chromosomes? We will see that such a question, the methods to solve it and the answer, all betrayed a developmentalist and organismal approach. Indeed, Just was not interested in the kind of mutations he could get through external artificial inductions, he was rather interested in the phenomena of cellular regulation that brought mutation to be expressed. That was not a geneticist's issue but an embryologist's curiosity. Second, the methods Just deemed necessary to undertake were embryological; in other words, he described the experimental observations highlighting the importance of cytoplasm in the development of the egg. In fact, Just thought, whether non-nucleated fragments of egg developed anyway, whether changes in salinity or temperature affected cytoplasm without relevant effects on nucleus, whether ultra-violet rays provoked variation of the cytoplasm before affecting the nucleus, and whether the external substances – such as oxygen or water – interacted primarily with cytoplasm, all induced Just to conclude that: "...Nuclear (and therefore chromosomal) behaviour is secondary to that of the cytoplasm...Cytoplasm determines nuclear behaviour, the chromosomal behaviour then is an expression of a more fundamental cytoplasmic activity."¹¹⁶

Nuclear behaviour was subject to cytoplasmic reactions, and both experimental cytology and embryology demonstrated that mutations had their primary origins both in the cytoplasm and in the complex modification of cells as unit-systems.¹¹⁷ To Just, unlike Muller's opinion according which mutations were due to a localised disruption of the chromosome, mutations were due to a precedent

¹¹⁵ Just, 1932.

¹¹⁶ *Ibid.*, p. 69.

¹¹⁷ As Just specified in the same article: "The cell is a unit: the nucleus influences the plasma, the plasma the nucleus. The cell reacts as a whole" (Just, 1932, p. 73.).

reactions interesting the cell as whole which, secondarily, affected chromosome's behaviour. In short, chromosomes were not the direct source of mutations because they were controlled by factors coming from outside: "...the normal behaviour of the chromosomes is too rigidly mechanical for them to be responsible as primary agents in heredity. Such a mechanism strongly suggests some deep-seated force of which they are the expression. If we compare them to soldiers going through manoeuvres, we must then assume some source of command. Their orderly behaviour is not automatic but conditioned."¹¹⁸ However, the fact that a deeper causal level of reactions was required did not hinder the possibility to discover a chronological causal chain of respective causes and effects: "It is highly probable that the first effects of the environment manifest themselves on the cortex. It stands as the medium of exchange between the cell's inner and outer worlds. It is first impressed. The superficial reactions in protoplasm therefore come first. And these reactions certainly must affect the whole cell-system."¹¹⁹

In Just's second paper, the importance of cytoplasm for mutation phenomena, heredity and development was extended even to evolution.¹²⁰ Nobody, he stated, could doubt the fact of evolution: too many disciplines converged – taxonomy, comparative anatomy, embryology, physiology and biochemistry – toward the facts that species had changed and evolved. However, even though evolution happened, the mechanisms through which organisms change was still a matter for discussion. Furthermore, another riddle waited to be solved: how life emerged from inorganic matter. It was clear, Just admitted, that the first organic being had to be a kind of complex device separated from the environmental fluctuations; still, it had to be "responsive" to environmental changes. In fact, as he argued, paralleling Haldane's philosophy, "...we should not speak of the fitness of the environment or the fitness of the organism: rather, we should regard organism and environment as one reacting system."¹²¹ All reactions between a new organic entity and environment had to be mediated by a membrane that Just identified with cortical cytoplasm. Any viable organism, Just argued, able to survive and thrive (probably a simple proto-cell or "protoplast" as ancestor of both plants and animals) had to be divided in an inner and outer spatial differentiation. The outer part, that is, the cell's cortical cytoplasm, was the most

¹¹⁸ Just, 1932, p. 74.

¹¹⁹ *Ibid.*, p. 74.

¹²⁰ Just, 1933.

¹²¹ *Ibid.*, p. 23.

important area because all fundamental functions such as contraction, conduction, respiration and nutrition took place there. No organism, Just concluded, could thrive, reproduce and change without the fundamental contribution of the cell surface.¹²² Because of the importance of such an area for all living functions, Just believed that even organic evolution, the progressive modification of the species, was due to specific changes happening at the outer cell level. In sum, organisms change because cortical cytoplasm reacts in different ways to an ever-changing environment: “Animal evolution advanced rapidly or slowly, to a higher or lower stage, depending upon the degree of ectoplasmic behaviour exhibited as contraction and conduction. Animals to-day differ largely because of differences in these two manifestations of life.”¹²³ Just did not mention Lamarck or any neo-Lamarckian author although the mechanisms of variation he conceived shared a neo-Lamarckian approach: organisms change because there is a direct, constant, and conflicting relation between living beings (cells) and their environment.

Through these preliminary papers, Just was preparing his larger synthesis; a biological synthesis which brought together development, heredity and evolution within a neo-Kantian framework. The hypotheses he advanced on each of these issues were based on a theoretical viewpoint that was clearly organismal, anti-physicalist and anti-mechanist. Indeed, one of his repeated refrains was that neither vitalism nor materialism could be accepted, but an approach regarding living organisation as non-reducible data was required. In his words:

We have often striven to prove life as wholly mechanistic, starting with the hypothesis that organisms are machines! Thus we overlook the organo-dynamic of protoplasm – its power to organize itself. Living substance is such because it possesses this organization – something more than the sum of all its minutest parts. Our refined and particularistic physico-chemical studies, beautiful though they are, for the most part fail because they do not encompass that residuum left after electrons and atoms and molecules and compounds even have been studied as such. It is this residuum, the organization of protoplasm, which is its predominant characteristic and which places biology in a category quite apart from physics and chemistry.¹²⁴

¹²² We have seen that D’Arcy Thompson too propounded such a hypothesis. See chapter 3.

¹²³ Just, 1933, p. 26.

¹²⁴ Ibid., p. 28.

In the following and final years of his life, Just would improve his hypotheses and his synthesis; he would even develop his own original interpretation of genetical sciences and their relation with development: an interpretation strongly focused on cytoplasm's functional activities.

5.8: A Bizarre Form of "Mendelism"

Between 1936 and 1937 Just published two audacious papers.¹²⁵ The two articles addressed one of the hottest biological topics of the time: the possible connections between genetics and developmental biology. They were papers that anticipated the broad synthesis he would propose in his 1939 monograph, but they are interesting in their own right because Just offers an overview of the discussions, arguments, and common ideas circulating within the American community at that time. First of all, Just, unlike Lillie, Conklin and Morgan, was profoundly convinced that a synthesis was possible; but that such a synthesis required a new perspective in which the apparently unrelated phenomena, i.e., heredity and development, were viewed as two complementary aspects of the same phenomenon. In fact, Just argued:

Though therefore *a priori* development could be thought of as showing no hereditary characteristics and hence we cannot state categorically that the two terms, development and heredity, are identical, nevertheless, all development which we know through experience shows without exception heredity, both at the beginning and at the end as well as at every intervening stage of development. The organism does not exist which has its genesis from an egg and at the same time fails to exhibit characters, Mendelian or otherwise. Nor is it possible for Mendelian characters, especially since they are minute and inconsequential, to display themselves apart from the form of the organism. An organism, either as egg, as adult or as any intervening stage of its differentiation, is heritage, inheritor and visible tangible evidence of heredity; its closest resemblance of its progenitor lies in its grossest and essential parts on which appear the inconsequential minor differences which constitute the

¹²⁵ See Just, 1936, pp. 267–312, and Just, 1937, pp. 97–112.

Mendelian characters. Since neither process reveals itself independently of the other, we can postulate a cause common to both.”¹²⁶

I have quoted this passage extensively because it demonstrates that Just did not confuse heredity and development. He was totally aware that some of the most important biologists of his time considered heredity and development two separate things. He, however, disagreed because he regarded the whole matter from a very different viewpoint, a perspective that, as I am arguing, was profoundly organismal.

Before displaying his own proposals, Just noted that biologists of his time were divided in two opposing parties: on one side, he argued, were the embryologists, that is, biologists upholding Lillie’s theory of embryonic segregation (a theory I have described in the previous sections); on the other side there were geneticists or those Just dubbed “*Drosophila*-culturists”, who accepted the gene-theory exemplified by Morgan. However, both parties presented weaknesses and misunderstandings; Just dismissed and criticised both the theory of embryonic segregation and gene-theory as least as they were formulated by their supporters. The former was subjected to a wealth of objections, whereas the latter was useless in understanding development because, as Lillie had previously stated, if the cell contained homogenous hereditary material, then the phenomenon of cellular differentiation required other causal factors.

Just followed von Baer’s embryology (as he explicitly acknowledged). Differentiation was a process of progressive complexification and could be divided into more or less delimited stages. Any process of differentiation entailed a movement of individual cells that, in turn, were differentiated into nucleus and cytoplasm. Now, Just observed, there was firm evidence confirming the fact that during egg cleavage, and during embryonic development, nuclear substance increased: cell nuclei grew whereas cytoplasm decreased. Just felt constrained to conclude that such a phenomenon was caused by the fact that nucleic substance (chromosomes) removed specific elements from cytoplasm. Just argued against the common hypothesis of his time, according to which chromosomes affected cytoplasm in different ways;¹²⁷ indeed, he claimed the opposite, i.e., substances were transferred from the cytoplasm to the

¹²⁶ Just, 1936, p. 272.

¹²⁷ A hypothesis advocated, among others, by Morgan himself.

nucleus: “I consider that the progressive differentiation of the egg during cleavage is not the result of the pouring out of the stuffs by the chromosomes into the cytoplasm, nor that of segregation of embryonic materials, but more truly the result of a genetic restriction of potencies by the removal of stuff from the cytoplasm to the nuclei...”¹²⁸ The theory required visualisation: If the fertilized egg is represented as ABCD (where each letter represents one specific potency), then, during embryogenesis, the first two blastomeres would contain, respectively, AB and CD potencies, then, after a further cleavage, A and B and C and D severed potencies. Now, whereas Lillie’s theory of embryonic segregation stated that, at each division, the potencies were segregated, Just’s theory prescribed a mechanism of progressive “restrictions” in which, at each division, the cytoplasm lost potencies in favour of the nucleus and, conversely, the nucleus acquired more and more bounded potencies. In short, when the potencies ABCD are transferred from cytoplasm to nucleus, the egg loses its pluripotency; the blastomeres become “restricted” and cellular differentiation proceeds.¹²⁹

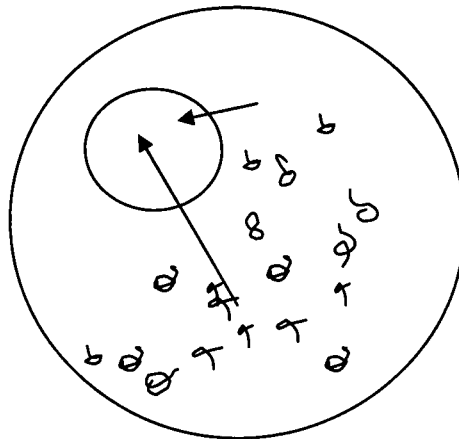


Fig 5.6, During development, hereditary material is removed from the cytoplasm and segregated in the nucleus. The cytoplasm becomes increasingly freer to express its own inherited potencies.

Just claimed that his theory was both supported by evidence and that it was able to explain many unrelated phenomena. It explained, among other things, phenomena such as polyembryony, merogony, asexual reproduction, post-generation of severed blastomeres, animal and plant regeneration as well as

¹²⁸ Just, 1936, pp. 280–281.

¹²⁹ Gilbert argues that Just’s theory sounds like an inverted Weismannism insofar as all hereditary potencies are displayed in the cytoplasm. I think that comparing Just’s theory to Weismann’s germ-plasm can be misleading. Indeed, Just never talked about hereditary particles or determinants, but vague hereditary material. Probably, the process that Just had in mind was much less mechanical/mechanistic than that described by Weismann. Just was very careful in formulating a theory of heredity that was not particulate.

tumour growth.¹³⁰ Moreover, it was a far better theory than Morgan's genetics; indeed, Just produced some of the harshest criticism ever written against gene-theory during the year of its triumph.¹³¹ "The gene theory of heredity,¹³² Just argued, "is an ultra-mechanistic rigidly bound concept,"¹³³ and this "rigidity", he added, is the reason why it is useless to explain cellular differentiation, which is a plastic and environmentally bound process. To Just, in fact, the real hereditary factors lay in the cytoplasm and were expressed only when the nucleic substance appropriated all the chemical elements hindering their expression. Just's theory – in according a very secondary and negative role to the genes – reverted genetic causation: at most, genes removed all those substances obstructing differentiation and the expression of hereditary potencies. However, such a theory was compatible, Just believed, with the Mendelian phenomena observed by the "*Drosophila* culturists": "...the hereditary factors for pink or red-eye are located in the cytoplasm and pink or red-eye results, depending upon the abstraction of red or pink respectively by the genes."¹³⁴

Just's alternative theory was an improvement on the classic one because, as he claimed, it could explain how hereditary material could affect the cytoplasm: by absorbing stuff the genes freed cytoplasm to express its hereditary potentialities during embryogeny: "...I relate the origin of the tangible embryo to tangible cytoplasmic changes. The cytoplasm builds the embryo. Then it builds all of it, including characters called Mendelian."¹³⁵ But, even though Just posited the cytoplasm as the first mover in developmental and hereditary phenomena, he, as any organismal biologist, regarded the cell as an integrated unit-system in which nucleus and cytoplasm were in constant interaction: "The protoplasmic

¹³⁰ Just believed that regeneration happened when environmental factors, such as an injury, fostered the release of material from nucleus to cytoplasm; all the potencies that had been taken off from the cytoplasm during development. Tumours were explainable according to the same line of reasoning; they were due to a sudden releasing of nuclear potencies once they were removed from cytoplasm.

¹³¹ It was Just who famously questioned Morgan's genetics saying, at the joint session of the American Society of Zoologists, the American Society of Naturalists, and the Genetics Society of America in 1936, that he was more interested in how the embryo makes its back than how it makes the bristles on the back. See Harrison, 1937. Gilbert, 1988), pp. 311-346.

¹³² Notice the language. Just, like many of his contemporaries, deemed gene-theory only one theory of heredity among others.

¹³³ Just, 1936, p. 290.

¹³⁴ Ibid., p. 298.

¹³⁵ Just, 1937, p. 108.

system, nucleus and cytoplasm, is structurally the biological unit and acts as such. Then physiological processes inhere in the interplay of the components of this unit, parts of an integrated whole.”¹³⁶

Another important piece for Just’s synthesis was thus displayed: with the physiological interpretation of all hereditary phenomena and with the clear recognition that nucleus and cytoplasm are two necessary elements of a unique interacting system, development and heredity could be regarded, Just thought, as two complementary expressions of the same life-history.

5.9: Conclusion

Why must the world have human troubles while there are salamanders and worms to engage one’s attention and elicit one’s enthusiasm? I hope that you do not stay over-long from your animals!¹³⁷

E. E. Just to E. G. Harrison

The monograph Just published in 1939, *The Biology of the Cell Surface*, was the outcome of several years of laboratory work and thinking:¹³⁸ From his first experiences as laboratory assistant under Frank Lillie at Woods Hole to his European experience at the Naples Marine Station, then at the Kaiser-Wilhelm-Institut in Berlin and finally at the Roscoff Marine Station in France.¹³⁹ The book was therefore a highly

¹³⁶ Just, 1936, p. 305.

¹³⁷ Just to Harrison, August 17th, 1938, Box 6, Folder II A 54 (Just - 1912 – 41), Lillie Papers, MBL Archive, Woods Hole.

¹³⁸ Gilbert describes Just’s book in the following terms: “*The Biology of the Cell Surface* was an attack on the mechanistic and reductionist view of development promulgated by the geneticists on the one hand and the biochemists on the other. Just’s work attempted to accomplish two tasks thought to be mutually exclusive. First, it sought to counter the genetic mechanistic view with a cellular holism. To this end, Just redefined the scientific vocabulary used to describe developmental phenomena and elevated the cytoplasm at the expense of the nucleus. Second, it tried to integrate genetics and embryology, as both the nucleus and the cytoplasm played necessary roles in cell differentiation. In this synthesis, Just posited that all the potentials for development were present in the cytoplasm, and gave the nucleus a necessary, but secondary function” (Gilbert, 1988, p. 12). I agree, but I consider the monograph even more audacious. In fact, it was an attempt to formulate a synthesis going well beyond the unification of development and genetics: it was a theoretical bio-synthesis that tied together epistemology of biology, philosophy of biology, heredity, embryology and evolution.

¹³⁹ In the same year his monograph was published, Just launched a new research project that he had described in short typescript entitled “Status of my research program in embryology and its implication for general biology” - a document that Just sent to Lillie. The central question of this project was, of course, how a single cell can form a whole organism, a question that, if answered - Just argued - could shed light not only on embryological issues, but also provide fundamental information to general biology and medicine. The project included a detailed list of all the phenomena requiring further investigation: from fertilization and cytoplasmic cleavage to the study of enucleated egg development and egg axis formation. It also provided some methodological prescriptions: “...the character of my research has wide significance: It marks a point of departure for a chemistry and physics as well as a biology of protoplasm *in vivo*...the value of a program that aims to study vital processes as such within the narrow limits where life persists is here apparent”. The project entailed a wide plan and observation of very different species of eggs.

articulate text in which philosophical speculations in biology were mingled with experiments and technical information. Just's commitment to the neo-Kantian principles, appears evident, even from the first pages¹⁴⁰ a commitment in which the influence of Yves Delage is unmistakable: living beings are material things; they are formed from inorganic particles, atoms and composed of chemical substances. No transcendent entity is required to explain biological phenomena, no mystical forces or entelechies need to be invoked; to Just, organisms were open to direct observation through the accurate and skilled practice of the experimenter. However, although life was coextensive with the laws of physics and chemistry, it was not reducible to them. Any reduction was impossible insofar as living entities exhibited behaviours that inorganic bodies did not; such behaviour was exemplified by living organisation acting as a unity transcending its physical components. Not only did living organisation transcend its compounds, it also implied a constant process of change: "life is exquisitely a time-thing, like music. And beyond the plane of life, out of infinite time may have come that harmony of motion which endowed the combination of compounds with life."¹⁴¹

Of course, with Kant, Just believed that the mechanical analysis had to be sought as far as possible. Measurements and experiments, in which parts are analysed in their own right, should never be stopped. However, the investigator in biology should never forget that analysis alone destroys life and, in so doing, frustrates any attempt to understand functional organisation: "The investigator of the living state can and must use physics and chemistry since the living state is a zone in nature and his method of investigation can parallel that of the physical scientist inasmuch as he finally comes to the unit-organization of life. Below this he cannot go, for life is the harmonious organization of events, the resultant of a communion of structures and reactions."¹⁴² In addition, organisms had to be observed in

This required performing experiments in different laboratories, where the various specimens would be available. For instance, Just planned to visit Norwegian and French Marine stations, spend a few months in Paris (where he could work on fixed eggs), then go for a few months to Plymouth (England), and finally, in 1940, return to Paris where he could conclude the research. A long list of forms to be studied followed. As Just concluded: "Since the plan calls for work at several stations in order to obtain diversity of forms, it demands support ample to render possible expert and dependable collecting". Of course, Just never received that support and his plan remained unachieved. See E. E. Just, 1912-41, Box 6, Folder II A 54, pp. 6, Lillie Papers, MBL Archive, Woods Hole.

¹⁴⁰ Lillie really appreciated Just's book, in a letter sent to Harrison he wrote: "I have just been through his new book (Just) and am quite impressed with his point of view with reference to the principles of scientific analysis in biology stated in the introduction, and with which I agree. He has stated the situation very well", Lillie to R. G. Harrison, March 20th, 1939, Box 6, Folder II A 54, MBL Archive, Woods Hole.

¹⁴¹ Just, p. 2, 1939.

¹⁴² Ibid., p. 7.

their normal state and natural environment before undertaking any artificial experimentation, because, as Just argued, in the Cuvierian mould, life was living function before structure. In order to comprehend structural organisation the biologist needs to understand how organisms live and are adapted to their contexts.¹⁴³

To summarise, Just drew on several sources in order to support his organismal philosophy: apart from Goethe and von Baer, he mentioned Whitman, Sedgwick, Child, Lillie, Woodger, Delage, Geddes and Conklin, all responsible, in different degrees and diverse contexts, for putting forward an organismal conception of biology. This conception, as we have seen, he readily applied to his theory of heredity and development; he used it against Morgan's school and employed it as a theoretical weapon against the "physico-chemical" school headed in the US by Jacques Loeb. Yet, the great synthesis proposed by Just, a synthesis which tied heredity, development and evolution, was based substantially on the idea that the cell surface was the central zone to examine. In fact, Just believed that all cell functions, from the mechanism of fertilization through to any material interaction with environment, required cytoplasmic reactions of different kinds: reactions concealing the most important problems in biology.¹⁴⁴ Ectoplasm, in particular, played a chief role so that cell multiplication, cell differentiation, cleavage and development were all narrowly related to the complex behaviour of the cell surface (ectoplasm and cytoplasm).¹⁴⁵ As we have seen in the previous sections, even hereditary potencies were contained in the cytoplasm. The nucleus and the genes had only a negative role of freeing cytoplasmic potencies from "hindrance-expression" substances. Finally, evolution: differences among species were once again reducible, in principle at least, to the actions and reactions happening at the level of the cell surface. The ectoplasm was the substance most exposed to the environment insofar as it registered and actively responded to it so that: "...species arose through changes in the structure and behaviour of the ectoplasm.

¹⁴³ Just was part of the tradition of *New Natural History* as Robert E. Kohler has defined it. As did many of his contemporaries, Just attempted to find a middle ground between results obtained in the lab, and fieldwork observations. To him, both practices had to work together. Of course, this was probably the result of his long training at Woods Hole, where both lab experiment and observations in the field were daily practices. As Kohler well described the 'spirit' of the 'new naturalist': "The ideal of the new naturalists was a synthesis of sympathy and intellect, observation and experiment, spontaneity and control, laboratory and field" (R. E. Kohler, 2002, p. 34).

¹⁴⁴ See also Just, 1940.

¹⁴⁵ The ectoplasm is defined as the outer level of cytoplasm.

In the differentiation of ectoplasm from ground-substance we thus seek the cause of evolution.”¹⁴⁶ Even though Just’s synthesis was original, it attracted no followers and, as such, it was forgotten. Certainly though, it is a splendid example of 20th century organismal philosophy as applied to modern biology.

In the next chapter I shall focus on two other forgotten American syntheses: those of W. E. Ritter and C. M. Child. We will also see that, apart from the role played by Institutions such as the University of Chicago and Wood Holes, the marine station in San Diego too played a central role in the tradition I am reconstructing.

¹⁴⁶ Just, 1939, p. 361.

6.0: Neo-Kantian Bio-Philosophy from California's shores

6.1: Introduction

The best way to introduce Ritter and Child's organismal bio-philosophies is with a German aphorism: "*Die Pflanze bildet Zellen, nicht die Zelle bildet Pflanzen*" (The plant forms cells; the cell does not form plants). At the end of the 19th century this oft-quoted sentence circulated among critics of Schleiden's cell theory and was usually attributed to the German botanist and mycologist, Anton de Bary (1831-1888).¹ Although in the beginning the aphorism was employed against the widespread practice, since Schleiden's cell theory, of starting textbooks on botany with the study of cells rather than the whole plants², its use was quickly extended. In the hands of embryologists and physiologists the aphorism acquired a polemic charge against the mechanist interpretation of organic development and indicated a holist way to conceive the process of morphogenesis. As Barlow notes, the aphorism conveyed the idea that "...the properties of the cells are fashioned, or determined, according to their context within the developing whole; it is not the cells that fashion the plant, or direct its morphogenesis, for this is a phenomenon that transcends the individual cells"³

In the previous chapter we have already seen that in the US the idea that the organism was more than its composite elements was clearly supported by one of the most influential late-nineteenth American Chicago biologists: C. O. Whitman. Indeed, in 1893, he published an article which inspired many young biologists⁴ who were critical of mechanist and "elementalist" interpretations of living phenomena. It is not surprising then, that in such a short piece, Whitman began by criticising Schleiden's cell-theory. Cells should not be seen as individual or elementary entities able to produce and form, during morphogenesis, complex organs and tissues. Rather, a higher guiding or formative principle had to be presupposed. For Whitman, in fact, organisation during development preceded cellular regulation and not vice-versa:

¹ Hoppe and Kutschera, 2010.

² According to Barlow the aphorism did not originate by De Bary but from A. Rauber in 1883 (Barlow, 1981).

³ Barlow, 1981, p. 10.

⁴ The article is "The Inadequacy of the Cell Theory of Development" and we have seen how inspiring it was for Lillie.

“Development, no less than other vital phenomena, is a function of organization”, and again, “...the formation of the embryo is not controlled by the form of cleavage. The plastic forces heed no cell-boundaries, but mould the germ-mass regardless of the way it is cut up into cells”⁵. Regenerative phenomena reinforced such an interpretation because both hydra’s and Stentor’s reproduction showed that “...the organism dominates cell-formation, using for the same purpose one, several, or many cells, massing its material and directing its movements, and shaping its organs, as if cells did not exist, or as if they existed only in complete subordination to its will...”⁶.

Whitman defined this view as the “organism-standpoint”, a stance he considered prominent among botanists but that he deemed extendable to the whole living kingdom. Indeed, at the beginning of the 20th century, organismal philosophies dominated American biology. In one of the most successful late-19th-century American textbooks, E. B. Wilson pointed out that: “...as far as the plants are concerned...it has conclusively been shown by Hofmeister, De Bary and Sachs that *the growth of the mass is the primary factor*; for the characteristic mode of growth is often shown by the growing mass before it splits up into cells, and the form of cell-division adapts itself to that of the mass: ‘die Pflanze bildet Zellen, nicht die Zelle bildet Pflanzen’(De Bary).”⁷ Paralleling Whitman, Wilson concluded: “Much of the recent work in normal and experimental embryology, as well as that of regeneration, indicates that the same is true in principle of animal growth”⁸. At the beginning of the 20th century, several promising, young biologists – people such as Wilson, Morgan, Conklin, Harrison, Lillie, Ritter and Child – endorsed diverse forms of organicism⁹. After all, they endorsed what their teachers taught them: people such as H. N. Martin and W. K. Brooks at John Hopkins¹⁰, and former Leuckart students such as C. Whitman in Chicago, C. Minot¹¹ and E. Mark in Harvard. As a result, during the very first decades of the 20th century, as we have seen, the post-Kantian tradition thrived in many leading American departments of Zoology.

⁵ Whitman, 1893, p. 655.

⁶ Ibid, p. 653.

⁷ Wilson, 1896.

⁸ Wilson, 1896, p. 393.

⁹ See Maienschein, 1991a.

¹⁰ See Maienschein, 1987.

¹¹ See Morse, 1920.

We have already seen that part of the reason why such a tradition spread in the US was that many American biologists spent a significant part of their training in Europe and especially in Germany. Then, after their stay abroad, they were able to get a job in the US and make careers in important institutions: institutions they helped to shape according to philosophies and experimental practices acquired in the old world. Both of the figures I will focus on in this chapter, W. E. Ritter and C. M. Child, represented a vivid instance of this tendency. They were the second generation of biologists who had undertaken part of their formation in Europe and, once back in the US, they made outstanding careers: Child in the University of Chicago, Ritter in the University of California, Berkley and, afterwards, in his own Institution. Although they were specialists in diverse disciplines, they shared an organismal and neo-Kantian conception of biology — a conception they discussed in several letters they exchanged and also during Child's stays at the Scripps Marine Institution in San Diego. In the next sections I shall assess the importance of such an Institution for the diffusion of American neo-Kantianism. I will then introduce the bio-philosophy of Ritter and how it was related to his theory of heredity. Finally, I will introduce Child, describe his biological agenda and explain how it was related to the Scripps Marine Association's program.¹²

¹² On the American tradition of biology see Pauly, 2000.

6.2: Scripps Foundation and its Institutional Policies

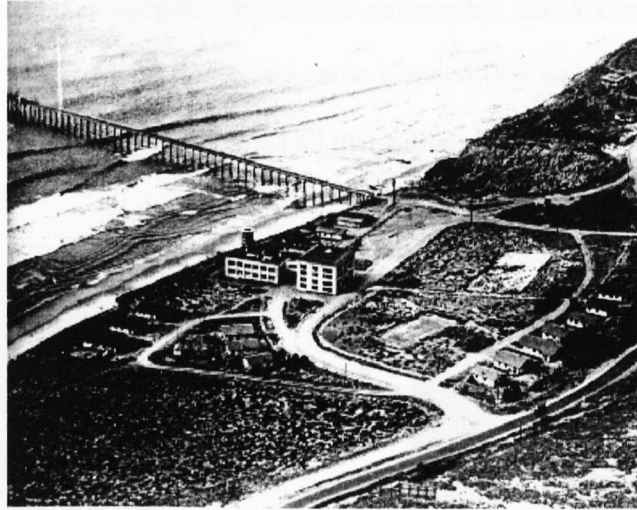


Fig. 6.1, Scripps Marine Association, ca. 1914¹³

The Scripps Marine Association was founded in 1903 by the newspaper magnate E. W. Scripps, his sister E. B. Scripps and the biologist W. E. Ritter. As we will see, together with the Zoology department at the University of Chicago, it was one of the most successful associations based on neo-Kantian biophilosophy and a/the leading institution for the diffusion of organismal philosophy on American soil. The evidence supporting such a statement is multiple and convincing. It comes from documents conserved today at both the Scripps Institution of Oceanography in San Diego and the Bancroft Library at the University of California Berkeley. Indeed, all these documents demonstrate that behind the Scripps

¹³ Source: On Scripps history and pictures see <http://explorations.ucsd.edu>

Association there were converging ideas that supported a well-defined biological agenda — an agenda tying together many different, though related issues: the nature of scientific research and the supposed irreducibility of biology to other sciences; organismal philosophy; anti-Weismannism; anti-Mendelism; anti-eugenicism, as well as the application of scientific ideas to political progressivism and democratic doctrines more generally. It probably represented all that Lillie's *Institute of Genetic Biology* would have been had it succeeded.



Fig. 6.2, E. W. Scripps, ca. 1912¹⁴



Fig. 6.3, E. B. Scripps ca. 1919¹⁵



Fig. 6.4, W. E. Ritter, ca. 1900¹⁶

Before the Scripps Association became a reality, Ritter was an instructor in Biology at Berkeley. When he

¹⁴ Source: http://media.library.ohiou.edu/cdm4/item_viewer.php?CISOROOT=/scripps&CISOPTR=6

¹⁵ Source: <http://www.sandiegohistory.org/bio/scripps/ebscripps.htm>

¹⁶ Source : D. Day, 2006, W. E. Ritter Biography, Scripps Institute of Oceanography Archives.

was appointed there he already had a very respectable CV. Born in Hampden, Wisconsin in 1856, Ritter began his career as a teacher in public school, in 1877. Although of humble origins, he gained a degree at Berkeley under Joseph Le Conte's supervision. Then, in 1891, Ritter was awarded a PhD from Harvard, as pupil of the zoologist E. Mark who, in turn, had been a student of Leuckart. In 1893, Ritter sailed for Europe, spending part of his training in Liverpool with the Scottish zoologist and oceanographer W. A. Herdman,¹⁷ and, in 1894, he occupied an Agassiz table at the Naples zoological station and completed his European tour at the University of Berlin in 1895.¹⁸ Once back in the US, Ritter became a Zoology instructor at Berkeley and, in 1899, thanks to his advanced knowledge in marine biology, he was given the opportunity to participate in the Harriman Alaska expedition, a journey organised by the American magnate Edward H. Harriman.¹⁹ During this trip, Ritter was able to gather and observe unclassified species and, even though, as B. L. Norgross remembers: "the world of marine invertebrates – sponges, crabs, sea stars, snails and worms, to name a few – went largely unnoticed in the 1899 expedition's popular accounts...", they were "surveyed most extensively..." after reports were displayed. Ritter, together with some of the naturalists embarked on a program of collecting samples, and "...collected samples of a wide variety of invertebrates, distributing them on their return to universities and museums for analysis and classification."²⁰

It was in 1892 that Ritter and his students began inspecting the coasts of California in order to find a suitable place for a permanent zoological station.²¹ However, only in the summer of 1903 was the decision made in a locality close to San Diego. Indeed, from 1891, Ritter was in contact with a San Diego local physician who, as an amateur, used to collect seashells around San Diego Bay: Fred Baker. Baker first met Ritter during Ritter's honeymoon in South California. They remained in contact and, in 1903, Ritter decided that a small hotel boathouse in La Jolla (in the bay of San Diego) could be used as a provisional marine laboratory. During the first stays in La Jolla, Ritter and his fellows got visits from

¹⁷ An old friend of Haldane and D'Arcy Thompson during their youthful years in Edinburgh.

¹⁸ See the following documents conserved at the Bancroft Library, Berkeley in the Ritter Collection, 71/3 c, Box 10, Biographical record folder: W. E. Ritter, 1935, Supplementary biographical record, for year 1935-36, requested by President Sproul, University of California. Autobiographical sketch: The manner of the Man. See also Thone and Bailey, 1927.

¹⁹ Litwin, 2005.

²⁰ Norgross 2005, p. 127. See also Lindsay 1978.

²¹ For a complete history of the first 50 years of Scripps Institution see: Raitt and Moulton, 1966.

some of the local entrepreneurs who eventually became interested in financing a Marine Laboratory. As Ritter recalled in an unpublished document written in 1915,²² he first met E. W. Scripps and his sister during one of these visits. The Scripps were extremely interested in the idea of a zoological institute on the shore of La Jolla²³ and quickly offered Ritter the necessary funding. By the end of 1903 the Marine Biological Association of San Diego became a reality.²⁴

Of course, the project that Scripps had in mind was not limited to a scientific institution in which theoretical research in zoology would be pursued. Instead, Scripps had a very precise agenda in his mind; a project embodying his progressivist, democratic and pragmatic political ideals. Scientific research was not done just for its own sake, but for the technological and economic improvement of the nation. As a newspaper publishing magnate, Scripps was not an expert in scientific research; however, as a committed philanthropist and skilled entrepreneur, he imagined a democratic scientific institution composed of original investigators working for the general wealth. As Scripps himself described it:

I wish to gather together at this institution a number of men of strong minds and force who are eager for research work, eager to penetrate the, as yet, unexplored realms of knowledge. I think of this body of men being organized into separate groups, the groups themselves being composed of different individuals, each group working in a special department, and each individual having some special work to do. In some sort of democratic fashion, I would have these men organize and cooperate, governing themselves and governing each other, but all composing one block or army.²⁵

Ritter could not agree more. In fact, as he had experienced during his trip to Alaska, scientific research had to be organised according to a very definite division of labour, a division settled in a democratic

²² See W. E. Ritter, 1915, Box 4, Folder: The philosophy of E. W. Scripps, SIO Archives, La Jolla, CA.

²³ As Ritter reminds the episode: "His interest (Scripps) in the enterprise seemed greater than that of the other visitors. My memorandum made at the time was to the effect that his "interest ought to count for much". My most vivid impression connected with the visit of this group of our financial helpers was of this unique person cruising around in the laboratory among the workers, to see for himself what was going on. This was probably his first sight of anything like a scientific laboratory. From table to table he went inspecting whatever was visible – not neglecting, I have no doubt, the students themselves, males and females"(Ritter, 1915 Box 4, Folder: The philosophy of E. W. Scripps, SIO Archives, La Jolla, CA).

²⁴ For a detailed history of the early foundations of Scripps Association see Shore, 1981.

²⁵ E.W. Scripps, "The Scripps Institute for Biological Research," September 15, 1916, W. E. Ritter Papers, Box 2, folder 95, p. 9, SIO Archives, La Jolla, CA.

framework. As Ritter wrote in 1904 on *Popular Science Monthly*:

...marine biology...must have the correlated efforts of highly trained investigators in several separated fields of science. In the first place, there must be, of course, for biological investigations proper, a considerable number of specialists in botany and zoology. Then, in addition, there must be at least the physicist or physical chemist for the physico-chemical study of the water; the geologist for bottom and shore topography and bottom deposits, and the hydrographer must be called in for currents, tides, up-welling water and meteorological conditions.”²⁶

In brief, according to Ritter, scientific research was similar to a geographical expedition with all its experts and trained specialists communicating their observations to one another.²⁷ Furthermore, as I will show later, the kind of institutional organization Ritter had in mind reflected his deep philosophical convictions about what biology was and how it should be pursued. In sum, we will see that the philosophical ideas supporting such an enterprise represented one the most important aspects of the Scripps Association.²⁸

First of all, both Ritter and Scripps aimed for the realization of what they dubbed “humanist biology”, i.e. a science fully committed to solving human issues and applied to humanist disciplines. The scientific knowledge acquired in the Scripps laboratories had to inform and clarify economic and political problems as well as social and ethical concerns. Indeed, biological research had to give decisive support to the theories and practices developed by professional politicians and sociologists as well as philosophers and educators. Letters and documents on the early years of the Scripps’ activities exhibit over and over again such a concern. Scripps himself, in 1916, pointed out:

²⁶ Ritter, 1904, pp. 49-53.

²⁷ J. Burroughs, a writer present in the Harriman Expedition, describes in detail the organization of the crew according their different specializations: “..what Professors Emerson, Palache, and Gilbert could not tell us about the geology of the country, or Brewer and Gannett about the climate and physical geography, or Coville and Trelease about the plants, or Ritter and Saunders about the life in the sea, or Merriam about the mammals, or Ridgway and Fisher about the birds, or Elliot about the game-birds, or Devereux about mines, or Grinnell and Dellenbaugh about Indians, it could hardly be worth our while to try to find out”. In Burroughs, 1901.

²⁸ As Pauly recalls: “Scripps saw in Ritter’s vision of biological research and theory some basis for understanding humans as political animals. He wanted biologists to provide Americans a naturalistic account of customs, ethics, religion, and philosophy that would increase their happiness and reinforce democracy” (Pauly, 2000, p. 206).

I take it that it is impossible to begin the study of psychology, sociology, economics, and even the most vulgar politics, at any other point than that where the physiologist begins. That there can be any adequate conception of the mentality of man without a rather complete, if not as nearly as possible, absolutely complete knowledge of the purely physical man, seems to me impossible. Biology, as a science, might be considered the parent stem of all the social sciences.²⁹

The fact that the Scripps Association was thought to be much more than just a marine station is clearly indicated from a letter Ritter sent in 1912 to a Los Angeles politician belonging to the Progressive Party, Meyer Lissner.³⁰ In the letter Ritter mentioned that any possible political and social regeneration of US could be achieved only with a new political party — a party which, furthermore, based its policies on scientific advice. The new Progressive Party, Ritter continued, could improve only if it would be able to account for “...the biological and psychological basis of individual life and social organization, and so will work out a genuine science, theoretical and practical, of society”.³¹ For Ritter, the science practiced at Scripps had to go in that direction i.e., to provide scientific underpinning for the right political decisions.³² In short, the Scripps Association had to supply progressivist politics with unbiased truths taken from objective investigations into human nature. In a small extract from a long letter he addressed to Scripps in 1921, Ritter was even more explicit:

It has become quite clear to me that economic, political, social and ethical teachings are so largely futile or even worse, because their foundations are almost wholly lacking in natural knowledge. And as for human history – it is as absurd to try to understand its meaning by merely studying the portion of it which falls within the period since man has developed a written language, as to try to understand banana plants, for example, by merely studying some ripe fruit bought from a city green grocer, or to understand the Pacific Ocean by merely studying False Bay. Professional economists, statesmen,

²⁹ E.W. Scripps, "The Scripps Institute for Biological Research," September 15, 1916, W. E. Ritter Papers, Box 2, Folder 95, p. 7, SIO Archives, La Jolla, CA.

³⁰ See Stevens, 2009.

³¹ W. E. Ritter, August 24, 1912, Meyer Lissner, W. E. Ritter papers, Box 15, Ctn. 33, Folder: Outgoing letters, 1912-1914), Bancroft Library, University of California Berkeley.

³² In a letter addressed at the President of the University of California in 1912, Ritter wrote: “Politically I am heart and head for the creed of the Progressive Party, and would like to show its leaders and others what, to me at least, its scientific meaning is...never again can political doctrine safely ignore certain basal biological principles”(Ritter to Wheeler, 1912, W. E. Ritter Papers, Box 1, Folder: Correspondence June-Aug, SIO Archives, La Jolla).

sociologists, ethicists and historians know next to nothing about the natural history elements of their respective sciences. They are simply unformed – untutored – in the foundational phenomena upon which their systems of knowledge and theory rest...now there is certainly no way to overcome this fatal defect in the humanistic sciences except to underpin the study of them by actual observation upon, and formal instruction about, lower animals of various grades and very backward races of men as they all work out their problems of securing and using nourishment, reproducing their kind, defending themselves against destructive agencies etc...I wish to use the Scripps Research Institution for demonstrating the necessity and the practicability of pre-humanistic courses of instruction somewhat comparable to the pre-medical courses now given in all colleges. Though it will probably be better to call the work “Biology for humanists”.³³

Of course, biological knowledge not only supported humanist sciences,³⁴ but it also had to underpin a positivist view of the future where technological knowledge, intellectual progress and well-founded scientific investigations went hand in hand.³⁵

In addition, the Scripps Association was thought by Ritter to be a pluralistic institution in which both experiments in the laboratory and observations in the natural environment had to be seen as

³³ Ritter to Scripps, 1921, W. E Ritter papers, 71/3 c, Ctn. 33, Folder: Scripps correspondence, Bancroft Library, Berkeley.

³⁴ Ritter stresses such a point in his letters quite often. In 1908 he even expressed his intention to tie together biology and human welfare in a letter to F. R. Lillie: “I believe that within a limited period, say of five years more or less, the Station may be made one of the most influential biological foundations in existence. Further I believe that within another limited period, the years of which I will not venture to specify, it may become as potent for general human welfare as any single institution of physical science that has hitherto existed...there is I am sure, an ill-defined though wide-spread and powerful conviction among biologists that a deep-reaching renovation of biological theory, and so of aim and method, is imperative to further great advance in the sciences of the living world. For myself I am convinced that when such renovation is effected it will turn out to be of the utmost consequence to human life and society... I believe that the San Diego Station is in position to become an institutional center for this process of regeneration. (Ritter to Lillie, March 25 1908, Ritter Papers, Box 1, Folder: correspondence-1908, SIO Archive, La Jolla).

³⁵ As Ritter specified in an unpublished document addressed to the community of San Diego: “The general policy and working program of the Scripps Institution has always been shaped in accordance with the theory that the future of California as the home of a happy, prosperous and growing population is absolutely dependent upon a knowledge of nature in this part of the world obtainable in no other way than by far reaching and long continued scientific investigation...the fact that the Scripps Institution is primarily a research institution does not mean that it is committed to a doctrine of “research for its own sake” but rather that it is convinced it can render better service to the community and the state and its generation by this course than by one of effort primarily in behalf of industrial development...The Scripps Institution is highly desirous of contributing to the prosperity and industrial development of the community. But it is more desirous of contributing to the intellectual and spiritual development of the community. (Ritter, 1910, W. E. Ritter Papers, Box 3, Folder: Descriptions of the Scripps Institute of Oceanography. SIO Archive, La Jolla).

complementary³⁶. Ritter was rather polemical on this point. Many American institutions, he declared, were committed to a very “monomethodic” approach to biology. The laboratory was considered the only appropriate place where reliable knowledge could be accumulated, and experiments were focused on a few model organisms opportunistically selected for specific theoretical outcomes. Nothing like that would happen at the Scripps Institution.³⁷ Indeed, as Ritter explained in 1922 to the Berkeley anthropologist, D. P. Barrows:

Field observation alone unquestionably encourages illy supported and more or less sentimentally colored generalizations. Unsupplemented descriptions, whether of organisms as a whole or of parts of organisms, produce results that savor more of the collector and cataloguer than of the whole-hearted student of animate nature. The laboratory too singly confided in has still greater danger because a danger more pervasive and subtle. There can be no question that laboratory biology may have much of the stamp of museum anthropology, of library sociology, of scholastic philosophy, and of cloister theology. We must undoubtedly take many, probably most biological problems, into our laboratories for study. But the idea of learning biology proper in a laboratory or a museum is as preposterous as the idea of learning navigation from a toy ship on a mill pond.³⁸

The Ritter policy was readily applied at Scripps. It is especially visible if we consider the work of F. B. Sumner³⁹ on the influences of the environment on inheritance in the field mouse, *Peromyscus*. Sumner was appointed by Ritter in 1913; he was the Scripps’s specialist in heredity studies and remained in San Diego until his death. Sumner was a key figure among the Scripps crowd and Ritter’s conception of heredity⁴⁰ surely owed a good deal to Sumner’s findings.⁴¹

³⁶ As Kohler recalls the frontier between lab and field: “The dynamics of the lab-field border began to change around the turn of the century, and in the following decades an uneasy frontier gradually evolved into a zone of interaction and mixed border practices. In the United States this change was marked initially by a spate of public pronouncements by leading biologists that the laboratory movement had gone too far and that it would be to all biologists’ advantage to combine the older natural history with the more recent experimental tradition”(Kohler, 2002, p. 24).

³⁷ The polemic against Morgan’s Columbia lab is evident.

³⁸ Ritter to Barrow, 1922, W. E. Ritter, Papers, 71/3 c, Ctn. 33, Folder: Barrows, David Prescott, Bancroft Library, Berkeley, CA.

³⁹ See Provine, 1979.

⁴⁰ In particular, for Sumner, both field and laboratory work undertaken on mice proved that small inherited variations were due to natural selection. As I will show later, even though Ritter was sceptical about the inheritance

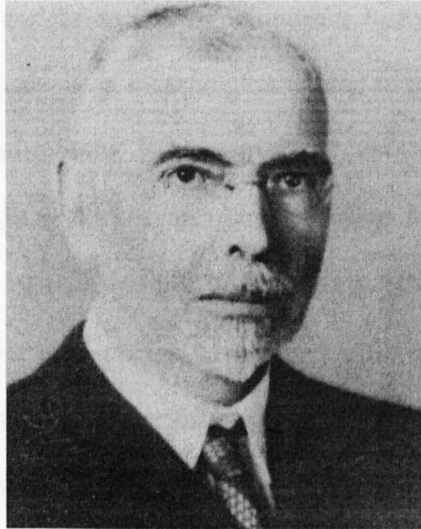


Fig. 6.5, F. B. Sumner (1874-1945)⁴²

If we look at one of the Scripps' surveys, we see the extent of the inheritance studies: investigations involving both lab experiments and field observations. Indeed, at Scripps, researches in heredity implied hybridization experiments on animal and plants, followed by animal and plants transplantations in order to assess hereditary 'tendencies'. Yet, colour analyses, the study of environmental factors on variations; and the use of birth records in order to evaluate seasonal sex relations were also made.⁴³ All these

of acquired characters, he thought that any study on heredity required both a field and laboratory work. See Ritter, 1903. As Koehler argued, the results that Sumner obtained were due to his unorthodox approach to studying genetics in the field: "...Sumner carried on experimental breeding at the Scripps mouse colony or 'murarium', crossing subspecies to see how species characters were inherited. The results agreed against mutations, he believed, despite the growing consensus among lab geneticists that 'blending' inheritance was the result of normal Mendelian segregation in multiple-factor characters. Sumner's genetic apostasy was the result of applying methods designed for standard animals to the complex traits of a wild species – the result, in other words, of bringing nature into the lab"(Kohler, 2002, p. 143).

⁴¹ As C. M. Child reminds us in the biographical memoir dedicated to Sumner: "According to Sumner, the different races appear to have arisen through accumulation of small differences, not essentially different from those between individuals of the same race. As regards color, this accumulation has probably occurred by natural selection of characteristics aiding in concealment of the animals. Many differences, for example, differences in proportions of the body and length of appendages, have no evident adaptive value but they may be morphological expressions of significant physiological differences. High humidity has been regarded by some biologists as directly favoring development of dark pigmentation in the individual. Sumner was at first inclined to accept this view but later became convinced that aerial humidity and soil moisture are chiefly effective only indirectly on the colors of the mouse races by their influence on soil color. The bare, or mostly bare, soil of arid regions is in general pale in color and the light colored animals are less visible there; in damp regions the soil is darker and dark colored animals are less visible. Also during the earlier years of the mouse studies Sumner thought that the Mendelian theory of inheritance was not adequate to account for the blending of characteristics when two races were crossed but came finally to accept the concepts of modern genetics, though, as he has admitted, somewhat reluctantly, partly because particulate theories, such as the gene theory, were repugnant to him as they are to some other biologists, and partly because he disliked what he viewed as attempts to get on the bandwagon of Mendelian theory" (Child, 1947, pp. 12-13).

⁴² Source: Child, 1947.

⁴³ See Survey of Scripps Institution for Biological Research, Box 3, Folder: Survey of SIO for Bio. Research, SIO Archives, La Jolla.

investigations were deemed relevant for social issues; indeed, Ritter encouraged Sumner to undertake studies on racial relations among man — an investigation related to the immigration issues preoccupying US public opinion in the first decades of the 20th century.⁴⁴ Of course, the same policy was also valid for other disciplines: from the biology of the ocean (which implied descriptions of organisms and their classification, migrations, studies of temperatures, salinities etc.) to climatology of the area: from the establishment of a natural museum and specialised library to the organization of explorations (which included studies on animal distribution for fishing, the study of the ocean's bottom and even anthropological research on the distribution of human races).⁴⁵

The aims that both Scripps and Ritter had pronounced were rather audacious. However, all the humanist, educative, political and methodological aspects of the Scripps enterprise comprised only one

⁴⁴ In November 1919 Ritter sent two letters to Sumner in which he advised him to consider a possible line of research; research which entailed a study of the relation of the human races. Both Ritter and Scripps considered such a topic a hot issue of the time, especially because they related it to American immigration policies. In Ritter's words: "A subject to which I have been giving considerable attention recently, and which is unquestionably one upon which it is of very great importance for the general public to be instructed, is that of the relation of races of man. The aspect of it, which is immediate and pressing for Californian and people of other Pacific states, is summed up in the phrase "The Japanese question". In talking about various phases of the question with Mr. Scripps, the other day, our old familiar topic of the relative force of race as an expression of physical heredity, and culture as an expression of social and other environmental forms of heredity, come in for consideration...If, for example, you were to read a few of the good recent works on race mixture, as this has been discussed in connection with immigration into the United States, it seems to me you would feel perhaps more keenly than you ever have before, not only the importance of the problem, but the importance of having it investigated by somebody with a more rigorously scientific training and out-look in biology than most of the writers on the subject have had". In the second letter Ritter was even more explicit about the importance of biological studies on heredity for immigration policies: "It is my strong feeling that these discussions (inheritance and race) should have in view the very practical problem of what position California and the rest of the nation ought to take relative to the legislation by the state and the nation, which is bound to be demanded by the people of this state and the other western states, at least, in the very near future...Shall the immigration laws be made still more definite and drastic than they are? If so, what form ought they to take? What should be done with the question of naturalisation of Asiatics and other non-Caucasian races? Are there good grounds for supposing that assimilation at least to a certain extent of people of other races could take place into our nation? How should the question of intermarriage and misogamiation be looked upon, especially with reference to Japanese?...in the face of this, it is out of the question to put off the decisions until such time as scientific research should have accumulated all the data that would be necessary for making the decisions completely scientific" (Ritter to Sumner, November 13 and 17, 1919, W. E. Ritter Papers, Box 3, Folder: correspondence Sept-Dec, 1919, SIO Archive, La Jolla).

⁴⁵ See also Ritter, 1905. In another report published in 1912, Ritter lists the results achieved from the Scripps institution so far; studies on many diverse forms of marine and terrestrial organisms had been made; their distribution, abundance and mode of life, their morphological and physiological aspects, their different kinds of reproduction, development and behavior, their adaptations through natural selection or other causal factors. *A propos* of the studies on animal behavior, Ritter highlighted the researches performed by H. S. Jennings on starfish behavior. In fact, observations on different aspects of these organisms led Jennings toward an organismal conception of life's phenomena. Finally, of particular importance is the emphasis on the use of mathematics in order to solve biological issues. In particular, studies on the correlation between organisms and environmental factors, measured quantitatively. Indeed, for Ritter, quantitative measures had to be an essential tool not only in the chemical and physical laboratories, but also in the biology laboratories. He mentions Karl Pearson, who furnished: "...a splendid example of how useful to biology the biologically inclined mathematician may be...mathematics called to the service of biology and kept strictly in its place as an assistant, is not only enormously important, but for many of the deepest problems absolutely indispensable." Ritter, 1912, pp. 137-248.

side of Ritter's vision. Indeed, since its beginning, the Scripps Association was committed to the diffusion of a very precise philosophy of biology: a philosophy that Ritter dubbed the "organismal conception of life". Such a philosophy of biology implied the rebuttal of other available alternatives — alternatives that Ritter identified with the biology of Weismann and its more recent successful instantiation, Mendelian genetics. These doctrines that, according to Ritter, underpinned a very dangerous and harmful ideology that, in the first decades of the 20th century, gained more and more followers in the US: positive eugenics.⁴⁶ As I will show in the next section, both Ritter and Scripps regarded their new institution as a bulwark against materialist and reductionist approaches to biology and, at the same time, as the place where a new biology had to be formulated, an organismal biology heavily based on the neo-Kantian tradition mentioned in the previous chapters.

6.3: A Progressivist Enterprise within a Neo-Kantian Institution

For the Scripps Institution had had a creed, which its members have repeated with child-like faith, following the words of their father-confessor. One of the articles of this creed had been the importance of studying the relations between the organism and its environment. Another has been a recognition of the one-sidedness of either field or laboratory study, considered by itself, and the consequent need of combining the two for a proper understanding of vital phenomena. Still another has been the necessity of employing rigidly quantitative methods, so far as these may be applicable. Finally, the organism itself has been wholeheartedly recognized as having a real existence, in its own right, and not merely allowed a provisional existence, pending its analysis into chemical, morphological or genetic elements.⁴⁷

F. E. A. Thone and E. W. Baley

⁴⁶ Ritter endorsed a physiological theory of heredity in which environment played a central role. In fact, Ritter did not believe there was a neat separation between nature and nurture and that surely reinforced his scepticism about eugenic policies. In a letter he sent to Irving Fisher in 1922 (see W. E. Ritter Papers, 71/3 c, Ctn. 33, Folder: Fisher Irving, 1867-1947, Bancroft Library, Berkeley) he harshly criticised eugenic agendas; he believed that such a social program was doomed to failure because it was based on a mistaken conception of heredity, a conception that overlooked development. He concluded that eugenics, as it was based on Weismannian biology, was undemocratic, amoral and in contradiction with a liberal state. On the other hand, he believed that race improvement depended on the betterment of the social environment. Children's education and cultural environment was central for him.

⁴⁷ Thone and Baley, 1928, pp. 259-260.

Ritter did nothing to hide his positioning of his philosophy of the organism at the base of the Scripps Institution. He explicitly connected (both in published documents and private letters) his theoretical convictions with his Scripps directorship. Indeed, behind institutional policies, there were two connected elements inspiring the Scripps enterprise as a whole: the first was the positive agenda instantiated by Ritter's bio-philosophy; the second was the negative program exemplified in Ritter's persistent critique against materialism and mechanism in biological sciences — a critique mainly addressed to Weismannism and Mendelism. However, Ritter did not believe that his organismal philosophy was totally original; indeed, he considered it as a philosophical tradition rooted in very old discussions about the nature of the living organism. The theoretical elements composing Ritter's organismal theory i.e., the prominence of function over structure, the unavoidable teleological thinking when studying biological entities, the rebuttal of vitalism and materialism, the fact that a whole living organism expresses qualities not directly reducible to its parts, were all ideas belonging to what he saw as a venerable tradition stretching back to Aristotle's philosophy. In fact, Ritter admitted:

Both Miss Scripps and Mr Scripps have become convinced, with me, that there is an idea of wide and deep importance to mankind behind this enterprise. In just what sense they conceive that idea to be mine I am not sure; but I know well that it is mine only in so far as I have picked it out from among a large number of already existent ideas and tracked it home more assiduously than has anyone else. It is my idea only by assimilation and elaboration.⁴⁸

This heterogeneous corpus of old ideas formed a doctrine that Ritter dubbed the "organismal conception of life": a conception which entailed both ontological theses on the nature of the organism and epistemic theses about the way biologists tackle their investigations.⁴⁹ Indeed, the Scripps Association, Ritter argued, is "...an instrument for working out this idea...that is why I have made so much from the beginning of organically correlated continuous researches".⁵⁰ According to Ritter, the endorsement of such an idea entailed a very definite commitment toward the organization of the institution he directed. In

⁴⁸ Letter to B. I. Wheeler, August, 24th, 1912, Box 1, Folder Correspondence, June-Aug, SIO Archive, La Jolla.

⁴⁹ I will treat such a philosophical conception further on in detail.

⁵⁰ Ritter to B. I. Wheeler, August, 24th, 1912, Ritter Papers, Box 1, Folder Correspondence, June-Aug, SIO Archive, La Jolla.

1914, writing to R. P. Merritt, an administrator of the University of California, Ritter made the direct connection between his bio-philosophy, his inspirations and the way all these elements would impact on the Scripps institutional organization:

...I look upon the development of the Institution in all its aspects, physical as well as intellectual, as much as part of the working out of my general theory or philosophy of biology as I do the planning for and carrying out any particular piece of research. The fundamental conception that underlies the whole, as all my biological contemporaries know, who have taken any interest in the Institution is that of the “organism as a whole”, or as I prefer to express it of the organismal integrity.⁵¹

Some of the main naturalists behind such a conception were, Ritter added, Cuvier and Goethe. In particular Cuvier: “...who found expression in the statement that every organism presents a fundamental ‘balance of parts’.”⁵² Of course, such a philosophy of biology, which began with Kant and Goethe and continued through the French school, had to shape the Scripps Institution and the way it worked. First of all, the institution had to pursue comparative work going well beyond the marine organism; as long as funding permitted, the lines of enquiry had to be extended to the whole of living nature. Secondly, a very close cooperation among naturalists working in the Institution had to be fostered; a cooperation aiming for a unified knowledge requiring “...the obligation which every professional man or specialist in any field of activity ought to feel himself under to subordinate to a certain extent his own ambitions as touching his specialty to the interests and needs of the larger whole of which his particular province is part.”⁵³ In short, in order to satisfy the requirements demanded by an organismal theory, an institution was set up in which a wide and diversified range of research was done and, at the same time, a strong cooperation among different disciplines was achieved.

Of course, although the Scripps Association was committed to the working out and diffusion of organismal philosophy, it was also oriented, as I have mentioned, against any form of materialism and mechanism in biological sciences and, for Ritter, that meant neo-Darwinian biologies. There is no letter

⁵¹ Ritter to Merritt, August 1 1914, Box 2, Folder correspondence-Apr-Sept, SIO archive, La Jolla, p. 1.

⁵² Ibid, p. 2.

⁵³ Ibid, p. 3.

more indicative of and explicit about these aims than that sent to Miss Harriman in 1910. Ritter compared his enterprise to that of Miss Harriman's father, E. H. Harriman, a leading entrepreneur and director of the Union Pacific Railroad.⁵⁴ Just as Harriman's father rebuilt the Central Pacific rail-roads, Ritter claimed, the Scripps institution was formulating a new philosophy of biology founded on the ashes of neo-Darwinian-Weismannian bio-philosophy.⁵⁵ Such a reconstruction was seen by Ritter as necessary; as long as Weismannian biology, together with its derivations, had significant social and political consequences. Firstly, to Ritter, mechanistic and materialist philosophies undermined social progress: "Professional students of living nature" – Ritter wrote to Scripps – "have been so absorbed, particularly since Chas. Darwin, with the vast and fascinating problems of the purely mechanical aspects of life that they have failed to notice that a serious attempt to 'reduce' the phenomena of life 'to the terms' of mechanics must inevitably tend to turn civilised man back, literally, toward the brute ancestry from whence he came."⁵⁶ However, he added, there were even more worrying threats: for materialist philosophies had deeply informed and influenced mechanistic theories of heredity which, in turn, underpinned social and political doctrines extremely dangerous for liberal and democratic societies. One of them was, as we have seen, eugenics: "Eugenics", Ritter wrote to Scripps in 1914, "carried out in accordance with the general biological theories held by the men who are foremost in the eugenics movement in this country at the present time, would establish an aristocracy more heartless and insolent than anything the world has ever seen."⁵⁷

Very probably Ritter's deep interest in heredity studies derived in part from his profound concerns about eugenic policies. He had already widely discussed such an issue with one of his colleagues at Berkeley, C. A. Kafoid.⁵⁸ Ritter's reflections and hypotheses on heredity will be presented in detail later on. However, it is important to briefly outline Ritter's concerns on eugenics because they

⁵⁴ E. H. Harriman financed the Alaska exploration; an exploration in which Ritter, as I have already mentioned, participated as zoologist.

⁵⁵ "For one I am satisfied the time has come to rebuild the whole theory of living things, man included, as thoroughly as your father and his associates rebuilt the rail-road systems which came into their hands. I further believe that we here at the San Diego Station are in position to play a large part in this reconstruction" (Letter to Harriman, February 8, 1910, Ritter Papers, Ctn. 1, Folder: Harriman outgoing letters, 1910-1911, Bancroft Library, Berkeley).

⁵⁶ Ritter to Scripps, October 24th 1921, Box 1, Folder 10, SIO Archive, La Jolla.

⁵⁷ Ritter to Scripps, May 4th 1914, Ritter Papers, Box 2, Folder: correspondence Apr-Sept, 1914, SIO Archive, La Jolla.

⁵⁸ See Pierce, 1973.

were strictly related to the Scripps institutional aims. Ritter lamented that, insofar as eugenics was based on a false biology, it could never achieve what the Eugenics movement aimed at i.e., the improvement of the race. Instead, in the best conditions, the eugenic policies would have no effects at all: "... I would suggest the Eugenics movement if continuing to rest as largely on defective and fallacious biological theory as it now does, were to carry out fully its desire of preventing the propagation of the unfit and of securing the 'mating of the fit', the result would be without appreciable effect in checking the supposed race deterioration."⁵⁹ Still, such a defective biology — on which eugenics depended — could also have negative social consequences because, as Ritter explained to Kafoid in 1913: "...the mode of interpreting organic nature prevalent in our generation and applied more consistently by Weismann than anyone else, is largely responsible for the habit now so common of trying to shunt all responsibility for foolish and evil acts off from the individual upon ancestry, or the race, or society."⁶⁰

The supposed ideological threats hidden in the Weismannian discourse on heredity was a staple topic in Ritter's general thinking. In 1919, in his large monograph *The Unity of the Organism*, a book in which he developed his own conception of heredity, he returned to the ideological risks of *Germplasm* speculations: Weismann's theory, Ritter thought, drawing on an idea dear to the American palaeontologist H. F. Osborn,⁶¹ is a fatalist doctrine similar to many theistic philosophies of fatalism insofar as the individual is conceived as totally impotent in respect to his unchangeable hereditary substance:

The germ-plasmic eugenicist virtually says: 'yes, indeed is man a reasoning, willing, aspiring animal, but all his activities in these ways are futile so far as the race as a whole is concerned, except as they are brought to bear, extrinsically and operatively rather than organically, on the germ-plasm'. This form of Eugenic idea corresponds in spirit to the propitiative offerings of primitive religion. It aims to mollify by human

⁵⁹ Ritter to Kafoid, Oct, 1912, Ritter Papers, Ctn. 1, Folder: Outgoing letters, 1912-1914, Bancroft Library, Berkeley

⁶⁰ Ritter to Kafoid, Dec 1914, Ritter Papers, Ctn. 1, Folder: Outgoing letters, 1912-1914, Bancroft Library, Berkeley.

⁶¹"If the Weismann idea triumphs, it will be in a sense a triumph of fatalism; for, according to it, while we may indefinitely improve the forces of our education and surroundings, and this civilizing nurture will improve the individuals of each generation, its actual effects will not be cumulative as regards the race itself, but only as regards the environment of the race; each new generation must start de novo, receiving no increment of the moral and intellectual advance made during the lifetime of its predecessors. It would follow that one deep, almost instinctive motive for a higher life would be removed if the race were only superficially benefited by its nurture, and the only possible channel of actual improvement were in the selection of the fittest chains of race plasma", Osborn, 1891, p. 363.

agency powers that act upon men's lives, but which are in themselves largely extraneous, largely evil, and wholly irresponsible."⁶²

Of course, the Scripps Association, together with the researches undertaken by Sumner there, had to be at the forefront in order to provide the right biological insights that might underpin a sound eugenics — a positive eugenical ideology compatible with democratic and liberal principles.⁶³ At the end, Ritter regarded the mechanist and reductionist conceptions of heredity⁶⁴ — as expressed by some Weismann's advocates and Mendelian's prophets — not as unsupported scientific hypotheses but as ideological doctrines with pessimistic social outcomes. Ritter discussed his ideas on heredity with many relevant figures of the time — with Whitman, with E. B. Wilson, with T. H. Morgan and others — but he remained attached to the idea that genetical thinking was so paradoxical, speculative and unscientific that it concealed strong ideological elements. After all, Ritter's position was very akin to that of the French cultural historian Jacques Barzun who, in 1937 concisely argued: "The philosophical implication of race-thinking is that by offering us the mystery of heredity as an explanation, it diverts our attention from the social and intellectual factors that make up personality."⁶⁵

To sum up, the Scripps Association was committed in a series of important battles: it aimed to work out and disseminate an organismal and neo-Kantian philosophy representing a viable alternative to neo-Darwinian bio-philosophies. Still, as a consequence, the Scripps Association hoped to give important scientific advice and support to progressivist social, political and economic doctrines. Finally, it was

⁶² Ritter, 1919, Vol. II, pp. 89-90.

⁶³ As Ritter pointed out to Kafoid, in 1912: "The part I have thought the Scripps Institution might play in all this is not to work at Eugenics proper, but to take up a few problems of both general and human biology and deal with them in such fashion as to show that biology, if scientifically and logically sound, is not only not hostile to humanitarian and religious sentiments of the loftiest type, but really accepts them as necessary to supplement, to round out, to complete whatever it may undertake in the way of the application of biology to human welfare". Ritter to Kafoid, October 12, 1912, Ritter Papers, Ctn. 1, Folder: Outgoing letter 1912-1914, Bancroft Library, Berkeley.

⁶⁴ Orthodox Eugenics would never achieve its goals if it kept environmental forces out. To Ritter, heredity was unthinkable without development and environment: "What eugenists of this school have failed to see, evidently, is that even were unit-factors as differentiate from one another in heredity as the extremest Mendelist conceives them to be, and that even were the germ-plasm improved up to the level of his highest hopes, his results in terms of actual human lives and social conditions would be distressingly meager. They would be so, because whether unit-factors exist independently in heredity or not, they certainly do not exist thus independently in development and function. In these ways they interact upon one another in the most vital manner, as physiology, especially of the internal secretions and nervous system, and as physiological and social psychology are rapidly and conclusively demonstrating"(Ritter, 1919, p. 90, VOL.II).

⁶⁵ Barzun, 1937.

engaged in a strenuous critique against orthodox eugenical policy accused of having dangerous social implications. Therefore, in supplying positive eugenics with a sound bio-philosophy, the Scripps Association wished to give important contributions to the future of both California and the whole nation.

Given Ritter's background, we should not be surprised at Scripps's institutional endorsement of organismal approaches to biology. Ritter, as we have seen, was a pupil of Mark in Harvard, he studied and worked in European institutions where he had had close contacts with continental bio-philosophies. His lifelong profound interests in European philosophers and naturalists made him an indirect scholar of Kant, von Baer, Goethe and Cuvier.⁶⁶ Furthermore, his constant relations with organismic American figures such as Whitman, Lillie and Child, his regular contacts with European biologists (among others Ludwig von Bertalanffy), his acquaintance with the theoretical biology of E. S. Haldane, E. E. S. Russell and H. Woodger,⁶⁷ had to reinforce his organismal conception of biology. Finally, Ritter's close friendship with Scripps added a significant political and ideological dimension to his institutional enterprise. In Ritter's opinion, European organicist philosophy was a perfect match for American political progressivism: A liberal and democratic creed which deeply shaped the Scripps institutional organization.

In the following sections we will see in what Ritter's organismal theory precisely consisted and also how such a doctrine required a conception of heredity in neat contrast with Weismann's germ-plasm and Mendelian inheritance. I will also introduce C. M. Child and his adjunct lifelong commitment with Ritter in formulating a coherent theoretical biology: a biological synthesis in which heredity and evolution were regarded as two aspects of the same developmental phenomenon.

⁶⁶ We have seen that in a letter addressed to Merritt in 1914, Ritter mentioned Cuvier and Goethe as some of the inspirers of his organismal philosophy, in another letter addressed to the French biologist Maurice Caullery in 1917, Ritter wrote: "...I am constantly led to the writings of Jussieu, Cuvier and Geoffrey Saint-Hilaire, and their discussions on organic correlation and the unity of the organism. Many of the details of their teaching are now antiquated, but the general conceptions they held had much of vital truth in them. Indeed, I get the impression that French botanists and zoologists have all along been more inclined to synthetic thinking than have the biologists of any other country" (Ritter to Caullery, February 27th, 1917, Ritter Papers, Ctn. 1, Folder: Outgoing letters 1917, Bancroft Library, Berkeley). Still, in the Ritter collection at the Bancroft Library are conserved many hand written notes in which Ritter discusses Aristotle, Kant's Critique of Judgment, the bio-philosophies of Blumenbach, Goethe, von Baer, Cuvier, and Owen's morphology.

⁶⁷ In 1931 Ritter attended the 2nd Congress for the History of Science held in London. On that occasion he was directly confronted with the bio-philosophies of Russell, and the young Needham and Woodger. In the Bancroft Library are conserved the Ritter's annotated papers that all three British scholars addressed at that congress. All treated the same topic: the relations between physical and biological sciences. Still, Ritter knew very well Russell's book *Interpretation of Heredity and Development*. Indeed he warmly recommended reading it in a letter addressed to von Bertalanffy in 1933. See chapter 4.

6.4: Ritter's Organismal Doctrine

...in all parts of nature and in nature itself as one gigantic whole, wholes are so related to their parts that not only does the existence of the whole depend on the orderly cooperation and interdependence of its parts, but the whole exercises a measure of determinative control over its parts. This idea of wholeness involves the recognition that a unit exists and is possible only through the existence of parts, or elements. The conception of a unit as something uncomposed, ultimately simple, is at odds with all our best known facts.⁶⁸

W. E. Ritter and E. W. Bailey

Ritter's organismal doctrine required that organisms be considered the fundamental entities any biologist should start with, just as physicists started their investigations with atoms, and chemists with substances. Furthermore, like Just after him, Ritter thought that any scientific enquiry in biology had to begin with a direct observation of organisms in their environment, because, as he argued in an article published in *Popular Science Monthly* in 1909: "The data of biology are living plants and animals. These are what nature presents. To these we must always go in order to a beginning at any investigation."⁶⁹ In sum, as we have seen with the Scripps epistemic policies, Ritter prescribed observation before experiment: therefore broad knowledge of the organisms in relation with their environment before any planned investigation was performed in artificial settings or laboratory. As many neo-Kantian figures before and after him, Ritter believed that organism and environment could never be neatly separated except from an abstract point of view.

Moreover, as would any neo-Kantian biologist, Ritter believed that biology certainly depended on other sciences such as physics and chemistry, but yet held that living things transcended mere physico-chemical organization. For after all, he contended, were the evidences – even taken from different sciences than biology – in speaking against a complete equivalence between physico-chemistry and life in organisms: "The presumption that biological phenomena may be adequately treated in terms of chemistry

⁶⁸ Ritter & Bailey, 1928, p. 307.

⁶⁹ Ritter, 1909, pp. 174-190.

and physics...leads inevitably to a forcing of evidence..."⁷⁰ Ritter used many scientific examples taken from various disciplines in order to support his philosophical arguments. The atoms in modern chemistry and chemical substances (atomic combinations) have different properties; the former "...are small bodies imagined to constitute visible substances..."⁷¹ whereas the latter are the visible result of the dynamic interactions of atoms. Now, what Ritter aimed to argue is that our minds are made in such a way that "...every object in the world must be treated *on its own merits*..."⁷² This implied that we are forced, given our epistemic limitations and the external constitution of the world, to consider atoms and substances as ontologically different objects (even if related); in short, substances are not mere epiphenomena of atomic interactions and atoms are not "more real" than substances. They are two complementary expressions of the same reality which deserve separate investigations and treatment. To sum up, the physical sciences cannot, in any sense "...raise the question of absolute reality..."⁷³ and, as a consequence, just as substances are not less real than atoms, so organisms are not less real than their composing parts: "...in whatever sense you predicate reality, or fundamentality, or ultimateness to the germ or any part of an organism, in exactly the same sense you must predicate reality, or fundamentality, or ultimateness to the completed and whole organism."⁷⁴

Yet, according to Ritter, organismal doctrine did not entail the acceptance of vitalism. Indeed, as Child similarly put it, presupposing the existence of transcendent powers acting on organic matter was not a better option than pure reductionism. After all, vitalism was open to objections similar to those advanced against Weismannian reductionism:⁷⁵ with all its metaphysical presuppositions, it prevented any possible factual investigation and experimental confirmation. Organismal doctrine appeared as a viable third way between vitalism and mechanistic reductionism. But such a way required the acceptance of a dogma: living organization is an irreducible reality and any biologist had to deal with this fact. As Ritter argued: "...life...is the sum total of the phenomena exhibited by myriads of natural objects called living because they present these phenomena. To understand any organism it must be studied as a whole and in

⁷⁰ Ibid., p. 178.

⁷¹ Ibid., p. 180.

⁷² Ibid., p. 180.

⁷³ Ibid., p. 181.

⁷⁴ Ibid., p. 181.

⁷⁵ Ritter defined vitalism as: "...a walled city with the gates locked and the keys lost beyond recovery", in Ritter, 1909, p. 184.

all its relations.”⁷⁶ In other words, morphological parts *function* for the whole and those parts are only comprehensible, by the biologist, as parts of a functional whole. In the end, Ritter’s arguments satisfied all the tenets of neo-Kantian tradition: the importance of the environment, the inadequacy of a reductionist and mechanist approach to biology, the repudiation of vitalism, the primacy of function over structure and, therefore, the pre-eminence of teleological explanation over efficient causes.

Apart from philosophical and scientific debates, Ritter’s doctrinal system was supported from a wide and interesting historical interpretation of biological sciences. In the 1919 monograph, which was a result of several lectures he had given both in Berkeley and at Scripps during the previous decade, he gave flesh to his philosophical ideas by reconstructing two antagonistic historical traditions exemplified by those who thought, in the one side, that: “...the organism is explained by the substances or elements of which it is composed”, and on the other side, those who believed that: “...the substances or elements are explained by the organism.”⁷⁷ The former belonged to the “Lucretian school” whereas the latter fitted into the “Aristotelian school.”⁷⁸ Ritter analyzed the Lucretians first. As “elementalists” (reductionists), they found their 19th and early 20th century champions in Bichat, Schwann and Weismann. Schwann, in particular, stressed a molecularistic epistemic approach to all living phenomena offering a mere *knowledge of organisms* rather than a *theory of the organism*: “To explain organisms is, according to this theory of knowledge (elementalism), to reduce them to their elements, and it is nothing else.”⁷⁹

Although Ritter deemed the history of elementalism important and the methods upheld by its members significant in retrospect, the organismical standpoint was certainly more fruitful and historically successful. Since Aristotelian zoology, passing through biologists like Cuvier, Geoffroy Saint-Hilaire and the French school of comparative anatomy, until the more recent developments of American embryology, the organismal standpoint had never declined. Even though “Aristotelians” had known a brief crisis at the end of the 19th century, due to the influence and appeal of Schwann’s school, a new organismical theory was emerging. The organismal research program continued through US embryologists; figures such as C. O. Whitman, F. R. Lillie, E. B. Wilson and C. M. Child had fostered a new direction in biology. In

⁷⁶ Ibid., p.190.

⁷⁷ Ritter, 1919, Vol. I, p. 1.

⁷⁸ Ritter considered himself a disciple of Aristotle. In the first pages of *The Unity of the Organism* he praises Aristotelian biology and he deemed it one of the most important sources of his philosophy of biology.

⁷⁹ Ibid., p. 10.

particular, the “physiological” outlook put forward by Child, with his stress on the “physiological correlations” among parts, introduced a new theory of the organism which highlighted functional, rather than structural, interpretation of living phenomena. In sum, Ritter considered himself, the institution he directed, and Child’s biology, as defining the forefront of organismal doctrine.

6.5: The Evidential Support for Ritter’s Organismal Doctrine

Of course, organismal theory, as thought of by Ritter, was not only the outcome of philosophical reflections and historical assessment; it was also supported by a huge mass of scientific evidence taken from various fields of study. But, before passing to a long list of facts and disciplines that, according to Ritter, backed his organismal view, he insisted that his doctrine, unlike other holist philosophies, did not exclude reductionism. In fact, as he claimed: “The organism in its totality is as essential to an explanation of its elements as its elements are to an explanation of the organism.”⁸⁰ Ritter’s theory of the organism required a double epistemic strategy because, on one hand, we have the organism as integrated individual, and on the other, we have interacting parts. Now, for Ritter, in order to obtain a comprehensive knowledge of biological things, one needed to travel in both directions through the levels of complexity — from the organism to the parts and vice versa: “I hope to be able to clear the conception of the ‘organism’ taken alive and whole...and make it as clear, as serviceable, and as indispensable to science as are ‘foot’ or ‘head’ or ‘brain’, or ‘eye’ or ‘muscle’ or “cell” or ‘ovum’ or ‘nucleus’ or ‘chromosome’ or ‘nucleo-proteid’ or ‘Ptyalin’ or any other fully accredited and inescapable biological entity.”⁸¹

Ritter’s idea that organisms were dynamic integrated systems requiring an “up and down” investigation was motivated by some peculiar phenomena that life itself exhibited. Firstly, there was animal regeneration:⁸² “No biologists, and especially no organismal biologist” – wrote Ritter – “would

⁸⁰ Ibid., p. 24.

⁸¹ Ibid., p. 25.

⁸² Ritter repeatedly asked Child about regeneration issues. Since 1908 he had corresponded with him asking for detailed clarification on Child’s own experiments; things like the difference between animals and plants with respect to regenerative characteristics, the role of nervous systems in vertebrates and also about instances of abnormal or teratological regenerations. (see Ritter Papers, Ctn. 1, Folder: Outgoing Child’s letters 1907-1909, Bancroft Library, Berkeley). Yet, Ritter was interested in Child’s general views on organic forms and their development and, in 1909, Child sent a letter in which he reported a synthetic version of his gradient theory and organic correlation. Through

minimize the significance of the fact that the severed parts of many organisms possess such a remarkable reconstitutive power. The organismal biologist, I assert, is especially interested in the phenomena because they are to him unique and unanticipated evidence favourable to his general standpoint.”⁸³ The fact that many organisms are endowed with regenerative powers offered the most important evidence supporting organismal philosophy insofar as it showed the strict interdependence of the parts within the whole. Quoting Matthias Schleiden,⁸⁴ Ritter illustrated the difficulties that an “elementalist” met when he pretended to explain the development and regeneration of plants through reductionist approaches alone. Any reductionist attempt to explain the complex behaviour of the plant’s regeneration as a mere sum of cells was a failure because, at the very end of the investigations, the fundamentality of the individual as an integrated system was undeniable. Indeed, Ritter claimed “...regenerative processes so frequently involve considerable masses of more or less differentiated tissues rather than individual cells.”⁸⁵ In sum, animal regeneration involved “mass actions” transcending any defined element, being “...cells, nuclei, centrosomes, chromosomes etc.,”⁸⁶ and even though it would have been possible to track cell migrations in different tissues or organs, it was still missing the general plan according to which any single cell was moving.

Yet observation and experiments on animal regeneration showed that organisms were able to adjust themselves in unpredictable ways and, therefore, these phenomena encouraged a functional and teleological viewpoint because the widely recognised capacity of the organisms: “...to press into service some of their parts to replace other parts that have been lost, even though the parts implicated are normally quite different, structurally, functionally and developmentally, is undoubtedly one of the most important result on the researches on animal regeneration...”⁸⁷. Insofar as elementalist approaches were focused only on cells and structures, they could never give a proper account of these phenomena.

Animal regeneration was not the only evidence in favour of an organismal philosophy. There were other important facts – more or less related to regenerative phenomena – supporting Ritter’s ideas.

such correspondence, Ritter was able to know and assess new theories that were at the forefront of Biology. On Child’s theory see next sections.

⁸³ Ibid., p. 33.

⁸⁴ A botanist co-founder with Schwann of the cell-theory.

⁸⁵ Ibid., p. 180.

⁸⁶ Ibid., p. 180.

⁸⁷ Ibid., p. 190.

Reproduction by budding was an important example. Indeed, that mode of reproduction was quite widespread in nature, among plants, and the mechanisms involved required an organismal explanation. In the case of the Coast Redwood of California, the reproduction of new buds from stumps which have received severe injuries, may lead to the blossom of thousands of new shoots. This demonstrated, for Ritter, that a part of the tree normally not concerned with reproduction may be “diverted” to reproduce other trees by budding. Therefore, if the Cambium (lateral meristem) — which is a tissue mainly responsible for secondary growth — may only in specifically determined circumstances, gain a reproductive function, then: “...the redwood tree as a whole is essential to a causal explanation of the capacity of its cambium tissue. Efforts to escape such a recognition by resorting to conceptions like those of germ-plasm...is unmitigated sophistry.”⁸⁸

Biochemistry offered further support. Indeed organisms are chemical laboratories; they produce hundreds of different substances from the beginning of their development: substances which are the result of a truly epigenetic process - new chemical substances unpredictable, in principle and in practice, at beginning of embryogenesis, “...the number of substances remaining exactly the same from the earliest to the latest stages of development is very small in comparison with the number wholly or partly new in the later stages.”⁸⁹ Cell biochemistry too sustained organismal theory. In fact, looking at the cell’s organization from a biochemical point of view, we would realise how “...a living cell is...a highly differentiated system...Corresponding to the difference in their constitution, different chemical events may go on contemporaneously in the different phases, though every change in any phase affects the chemical and physico-chemical equilibrium of the whole system.”⁹⁰ According to Ritter, organisms control cells just as cells constitute organisms.

Ritter considered microbiology (bacteriology) a further element in favour of his organismal philosophy. Microbes, he claimed, as any other organism, reproduce, feed and respire. Indeed, the fact that they are both morphologically and physiologically different from animals and plants — that they are not composed from cells or that they appear simple and extremely minute did not imply that they could not be classified as proper organisms. However, the significant plasticity these living entities exhibit, the

⁸⁸ Ibid., p. 39.

⁸⁹ Ibid., p. 80.

⁹⁰ Ibid., p. 117.

difficulty of classifying them according to well-defined structural criteria, the “pleomorphism” with which microbes and bacteria seem to be endowed render the elemental approach powerless in understanding their behaviour, organization, and diversification. As long as an elemental approach prioritised structural investigations over functional analysis, the elemental investigator would be lost in describing the infinite morphological differences that all microbes exhibit. In sum, biological observation and explanation of organic function, as Cuvier had also taught, must precede structural study, and microbes represented a perfect example of such a principle: “...the concept of organism being primarily one of function and only secondarily one of structure, is quite as applicable to invisible as to the visible beings if, as in the case of disease-producing microbes, we have observational evidence on the functional side of their nature.”⁹¹ Because Ritter identified functional biology with organismal biology and because the study of microbes required a functional approach, the organismal theory had necessarily to be sustained from the bacteriological investigations.

To synthesise Ritter’s bio-philosophy: biology begins with organisms, presupposes living organisation, requires environment. It demands the study of interactions before substances, processes rather than static models, functions before structures. It is not surprising then, following the implications of this system, that Ritter considered heredity not as transmission but as organic self-transformation.

6.6: Heredity as Developmental Expression

Biological elementalism of to-day undoubtedly has its chief stronghold in the realm of heredity. The germ-plasm theory, accepted by probably a majority of biologists as an absolute monarch in the empire of biological thought, was elaborated for the sole purpose of explaining heredity⁹²

W. E. Ritter

Ritter was extremely concerned about heredity and its different interpretations. He not only discussed the topic in published articles and books but also in private letters addressed to important scholars of his time. Of course, Sumner was one of them, but also Whitman, Wilson, Morgan, Pearl, and Metcalf were

⁹¹ Ibid., p. 267.

⁹² Ritter, 1919, Vol. I, p. 305

included in Ritter's constant requests for clarification. As we have seen, the Scripps institution was committed to a crusade against neo-Darwinian tradition and any hypothesis of heredity supporting such a tradition was scrutinised and rejected by Ritter. However, his rebuttal of Weismannism and Mendelism was an informed one. For example, among Ritter's papers at both the Bancroft Library and Scripps Institution, there are countless notes and comments written on the theories formulated by the most outspoken 19th and 20th century figures in heredity and genetics: people such as Galton, Spencer, Haeckel, MacBride, De Vries, Davenport, Crew, Pearl, Pearson, Conklin, Castle, Morgan, Punnett, Klebs, Correns and many other names. In sum, we should bear in mind that Ritter was not an amateur, but a very well-informed spectator of what these new disciplines related to the science of heredity had to offer.

In approaching Ritter's positive agenda on heredity and development, we can begin with an early document Ritter published in 1900 in the *University Chronicle* issued from the University of Berkeley. In the article Ritter suggested the following definition of heredity: "Heredity is that in the nature of organisms by virtue of which they tend to reproduce their kind, and by virtue of which, also, they are never produced, either as wholes or in part, in any other way than by their kind."⁹³ The fact that organisms always reproduce their kind was not so obvious because, Ritter argued, it was a truth only established in the 19th century. Indeed, before that, beliefs in spontaneous generation dominated the minds of naturalists; from Harvey to Redi and Spallanzani, from Muller to Lamarck there was not reproduction but generation.⁹⁴ Once the idea that organisms always beget their kind was established, the laws of heredity could be properly investigated. Yet studies on heredity showed that any organism is subjected to two opposite universal laws: the first was clearly shown by Darwin in stressing the fact that organisms always differ from one another. Therefore, variation represented the dynamic side of the living world. The other law instead characterised the persistent tendency of the organisms to maintain a fixed form, generation over generation; this was seen by Ritter as the static law of the living realm. Such a static property of the biological realm was heredity: "the force of heredity is a negative force, if indeed it may be called a force at all. What in reality we mean by the force of heredity is the persistence of the type-form that has been engendered by the limitation to the play of forces on the dynamic side of life, through

⁹³ Ritter, 1903.

⁹⁴ Strikingly, a similar point was advanced by F. Jacob in his *The Logic of Life*, first published in 1970. Jacob argued that the concept of reproduction only appeared during the late 18th century.

the sum total of conditions under which life exists”⁹⁵.

This presumptive hereditary force was expressed through different kinds of more or less definite characters and Ritter furnished a quite complex taxonomy for them: individual, specific, generic, and class characters. Furthermore, he distinguished between ancestral characters and extra-ancestral characters. The former were characters inherited from the species, the latter were acquired during individual lifetimes. Ritter argued that all specific, generic and class characters were ancestral whereas individual characters could be extra-ancestral. Now, the question of the inheritance of acquired characters was only applicable to individual extra-ancestral characters. Ritter, in common with some neo-Kantian thinkers, was quite sceptical about neo-Lamarckian mechanisms of inheritance. He conceded that probably, in lower organisms, acquired characters could be transmitted; however, he believed that there was not enough evidence to argue that in higher organisms acquired habits could be transmitted. Ritter suggested that during the evolution of higher forms (such as *Homo sapiens*), a sort of immunity from somatic influences was gradually acquired, but, he added, that did not depend on a Weismannian fundamental distinction between soma and germ plasm.

The issue of characters and their possible transmission was further discussed in 1907 with Whitman. Indeed, Ritter explained to the Chicago professor that the specific characters of any organism should not only be found only in the egg (as Weismann and his followers asserted) but also in the adults as well as at any developmental stage. Both Whitman and Ritter concluded then that hereditary units as assumed by De Vries and Weismann, i.e., as representative characters sequestered in the first developmental stages, were of no help in explaining the expression of hereditary characters,⁹⁶ even as a working hypothesis. This debate about “representative characters”⁹⁷ and their presence in the egg was also the subject of a short article Ritter published in 1909 on *Science*.⁹⁸ In that paper, Ritter applied his objections to the explanatory philosophy behind Mendelism⁹⁹ and its supposed unit-characters:

⁹⁵ Ritter, 1903, p. 7

⁹⁶ See letter sent by Ritter to Whitman, November, 29th, 1907, Ritter Papers, Ctn 1, Folder: correspondence 1907, Bancroft Library, Berkeley.

⁹⁷ Ritter ascribed to Yves Delage the use of that terminology.

⁹⁸ Ritter, 1909, pp. 367-368.

⁹⁹ It is important to remember that Ritter considered genetical theory a direct outcome of Weismann’s germ-plasm theory; the supposed strong evidences geneticists put forward “...have affected a rejuvenation of the germ-plasm theory of Weismann. Rejuvenation, I say, because that theory was approaching death and decay when the

The characters of a frog are undoubtedly latent in the frog's tadpole. What is to hinder, therefore, expressing or explaining the frog in terms of the tadpole by saying the tadpole carries the characters of the frog? The logic is sound in the statement that the tadpole contains "frog factors" or "frogness". The question is merely as the helpfulness of sound logic used that way. This seems like the method of reasoning that, as somewhere remarked by Prof. William James, would enable Hegel; and his followers to successfully support the hypothesis that men are always naked – under their clothes.¹⁰⁰

The logic behind "representative characters" was for Ritter ridiculous and the Mendelian language was compared to Hegel's doctrine of essence.

One year later, Ritter returned again to the same issue. He asked E. B. Wilson for clarification, in particular about a well-defined problem: "When the egg of a white mouse is fertilised by a spermatozoon of a grey mouse, is not the spermatozoon a determinant or determiner of greyness in the resulting hybrid?"¹⁰¹

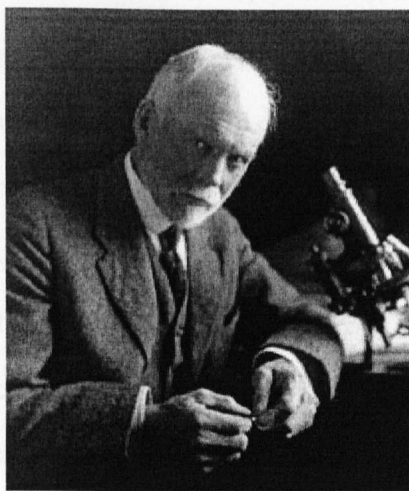


Fig., 6.6, E. B. Wilson (1856-1939)¹⁰²

Ritter in fact, assumed that a sharp distinction between "determinant" and "determiner" was required; the former, understood in Weismannian terms, only *represented* the greyness potential quality contained in

rediscovery of the Mendelian mode of inheritance occurred" (Ritter, 1919, p. 306, Vol. I). Ritter believed there was a direct historical line among Weismannism, neo-Mendelism and Morganism, all tied together from an elemental view of living phenomena. In fact, following the Ritter's historical scheme, "elementalists" supported Weismannian or Morganian theory of heredity whereas organismal scientists had to sustain alternative theories and methods as that of Ritter.

¹⁰⁰ Ritter, 1909, p. 367

¹⁰¹ Ritter to H. B. Wilson, June 1, 1910, Ritter Papers, Ctn 1, Folder: Outgoing Letters 1910-1911, Bancroft Library, Berkeley.

¹⁰² <http://www.columbia.edu/cu/alumni/Magazine/Fall2002/Wilson.html>

the germ-cell, whereas the latter indicated a causal-chain relation between a specific region of sperm and the development of grey hairs.¹⁰³ First, Ritter claimed, we are not sure that chromatin alone was sufficient in carrying all morphological potentialities expressed in the adult stage. Other factors could play an important role.

Second, the fact that there is a representative relation between chromatin and adult characters does not add anything to our knowledge. Indeed, in Ritter's terms: "...hundreds, yes probably thousands of other things than the spermatozoon between the sperm and the gray hair of the adult are determiners of greyness. The hair papillae of the ectoderm, the ectoderm itself, the blood coming to the ectoderm etc, etc, are surely determiners more close at hand, so to speak, than is the germ cell."¹⁰⁴ Here Ritter introduces his *principle of standardization*, which was one of the pivotal tenets of his organismal philosophy as applied to heredity: any part of the organism during development is 'determiner' of something, and in the chain of possible visible effects, more causes must be invoked: causes lying at different levels of complexity. In other words, to say that x (chromatin or part of it) represents y (greyness) is only a figurative language that should never be reified¹⁰⁵ because our experience teaches that it is an incorrect oversimplification: "...if I examine and describe ever so carefully the spermatozoon of a grey mouse I do not find any grey colour — any 'greyness'. It is only by a long developmental process in which a great many stages occur describable in terms among which neither 'greyness' nor 'spermness' can be used except with the hardest kind of forcing."¹⁰⁶

However, Ritter did not confuse heredity and development; he simply rejected the theoretical presuppositions hidden behind such a distinction. When, in 1911, he discussed the matter with another

¹⁰³ In other words, determiners were not the direct cause for greyness but represented only a chemical element triggering a cascade of causes-effects bringing toward the final result: greyness.

¹⁰⁴ Ritter to H. B. Wilson, June 1, 1910, Ritter Papers, Ctn. 1, Folder: Outgoing Letters 1910-1911, Bancroft Library, Berkeley.

¹⁰⁵ In the same letter, Ritter harshly criticised De Vries and his ultimate units of heredity. Not only had Ritter compared Mendelian genetics to Hegel's philosophy, he compared De Vries' science to dogmatic theology. As Ritter puts it: "...De Vries falls into the practice so almost inevitably disastrous, scientifically viewed, of making an hypothesis then using it as basis of a second and even a third, without having first proved the first? Note this is an instance: 'If every unit, that is, every inner character or every material bearer of an external peculiarity, forms an entity in each pronucleus, and if the two like units lie opposite each other at any given moment, we may assume a simple exchange of them'. Hypothesis No. 1: every unit, that is, every inner character (what is an 'inner character?') is an entity — surely not proved. Hypothesis No. 2: units lying opposite one another undergo a simple exchange. But since 2 is based on 1 of what value is it until one had been proved?"(Ritter to Wilson, 1910).

¹⁰⁶ Ritter to H. B. Wilson, June 1, 1910, Ritter Papers, Ctn. 1, Folder: Outgoing Letters 1910-1911, Bancroft Library, Berkeley.

eminent Columbia scientist, T. H. Morgan, Ritter had in mind precisely such a distinction. From 1908, Morgan had been engaged in a successful research program in heredity with some of his pupils, mainly based on the study of chromosomal behaviour of the fruit fly *Drosophila melanogaster* - the program would lay the foundations of modern genetics.¹⁰⁷ Ritter knew well the embryological work of Morgan before his enthusiastic commitment to Mendelian genetics, and reproached him for the fact that his own previous embryological work was in contradiction with his genetical results. In fact, such a supposed contrast between the way that experimental embryologists worked and “Weismann-Mendelian” advocates thought was not seen by Ritter as two different though legitimate disciplinary interests, but, he objected to Morgan, as alternative hypotheses: if heredity as seen by embryologists was true, Mendelian genetics had to be necessarily wrong and vice versa.¹⁰⁸

Ritter discussed similar issues with another well-known figure of the time, a scientist he particularly admired, Raymond Pearl.



Fig. 6.7, R. Pearl (1879-1940)¹⁰⁹

In his underestimated book *Modes of Research in Genetics*¹¹⁰ Pearl contended that embryological observations and experiments had not been properly used in genetical researches, although embryology could offer important insights for an understanding of the hereditary mechanisms. Ritter agreed with Pearl and criticised the unilateral tendency of the geneticists to focus their observations only on adult

¹⁰⁷ See Allen, 1978.

¹⁰⁸ See Ritter to Morgan, September, 15th, 1911, Ritter Papers, Ctn. 1, Folder: Outgoing letters, 1910-1911, Bancroft Library, Berkeley.

¹⁰⁹ Source: <http://www.medicalarchives.jhmi.edu/sgml/pearl.html>

¹¹⁰ Pearl, 1916.

characters, totally overlooking the embryonic resemblances emerging at different stages of development. After all, Ritter asked, why should the observable characters (we could translate ‘phenotypes’) of an adult organism be more important than “phenotypes” we could observe in other developmental stages? Pearl thought that whereas it was true that the geneticists overstressed the importance of the adult characters, it was nonetheless also true that embryologists concentrated only on the first stages of development, considering post-embryonic development less interesting. The result was an unbridgeable gap between embryology (with its methods and observations) and genetics (with its methods and observations). Ritter intended to fill this gap by proposing an alternative view of heredity: an option which implied the dismissal of the “transmissive” conception. In other words, Ritter suggested changing the notion of heredity: from transmission of things to a conception of heredity as epigenetic transformation.¹¹¹

After all, Ritter claimed, drawing on E.G. Conklin and W. Johannsen,¹¹² the orthodox conception of heredity took its meaning from other contexts than biology: “Another weak spot in much thinking about heredity...is due to the fiction of “transmitting” characters from parents to offspring. This appears to have come from the original meaning of the terms *inheritance* and *heredity*, which have to do with heirship to property.”¹¹³ To Ritter, economic analogy dominated genetics. However, it was a bad analogy simply because, whereas hereditary characters are the outcome of a complex series of organic transformations, the properties and goods inherited dealt with something fixed by law.

Of course, such an analogy did not work because as he had clearly mentioned to Kafoid, any supposed visible “character” was the result of an unbreakable developmental chain: each ontogenetic stage, with all its unique characteristics, is caused by its precedent state so that:

...we can no more describe, or express, or explain the adult stage of a given individual in terms of the egg or germ cell of that individual than we can describe or express or explain one individual man, for example, in terms of another individual man...the upshot of all this for the logic of the student of

¹¹¹ In the 1919 monograph, Ritter defined heredity in the following way: “...‘heredity’ is the term applied to the universal truth that as the organism unfolds itself from the relatively minute and simple stage known as the germ into the relatively large and complex stage known as the adult, it does this in accordance with a scheme or pattern characteristic of the species to which the organism belongs, so that any particular individual in the series resembles those which have gone before it...this unfolding...consists essentially of a great intricacy and succession of transformations”(Ritter, 1919, p. 322, Vol. 1).

¹¹² See Conklin, 1908, pp. 89 – 99 and Johannsen, 1911.

¹¹³ Ritter, 1919, Vol. I, p. 312.

biological genesis is that he has to deploy or expand the familiar, unbreakable cycle hen-egg, egg-hen, hen-egg etc. and recognize that a stage chosen at random from any part of the cycle or concatenation is at the same time explained by all stages before it and explanatory of all stages in front of it...¹¹⁴

A similar argument was restated in letters that Ritter sent to many of his interlocutors. All these discussions though never supposed or showed any confusion between heredity and development; they rather highlighted the impossibility of talking about heredity without development. Indeed, we should not be led astray by anachronistic interpretations according to which there would be a neat separation between transmission and expression that early opponents to genetics failed to see. In fact, according to Ritter's and other organismic discourses, there were not things transmitted, but only indefinite potentialities expressed at different ontogenetic stages. From a theoretical viewpoint, as long as particulate theories of heredity were rejected, no distinction between transmission and expression could have been drawn. Therefore, the reason why Ritter could not endorse a particulate theory of heredity of any kind lay with his organismal theory. As Ritter explained in 1916, to Maynard Metcalf, a zoologist at the John Hopkins University,¹¹⁵ determinants or genes could never be the only cause for morphological characters. In fact, genes do not determine anything if not in cooperation with many other causal elements.¹¹⁶ For Ritter, the only way we could still continue to talk about "determiners" is to conceive them as "starters" or "initiators" of ontogenetic transformations: "on this view" – Ritter concluded – "all other factors that enter into the production of the result, no matter where situated, in the cytoplasm or anywhere else, have as much right to be called determiners as the particular factors that initiated the series of changes".¹¹⁷

If genes or determiners were seen as mere "starters" or "initiators" of developmental processes, they could not be invested with formative powers, insofar as the final outcome resulted from a

¹¹⁴ Ritter to Kafoid, October 12, 1912, Ritter Papers, Box 1, Folder: Correspondence Sept-Oct 1912, SIO Archive, La Jolla.

¹¹⁵ In 1925, Metcalf actively participated to the Scopes trial as expert in evolutionary biology. See Larson, 1997.

¹¹⁶ In this Metcalf totally agreed. In fact, he had responded to Ritter arguing that: "I do not for a minute believe that determiners do it all. I suspect the whole organism reacts in everything". See Metcalf to Ritter, January 13, 1916, Ritter Papers, Ctn. 1, Folder: Outgoing letters, 1915-1916, Bancroft Library, Berkeley.

¹¹⁷ Ritter to Metcalf, February 8th, 1916, Ctn. 1, Ritter Paper, Ctn. 1, Folder: Outgoing letters, 1915-1916, Bancroft Library, Berkeley.

long chain of causes,¹¹⁸ all with their own irreducible importance. Hair pigment, for example, could not be “caused” from that pigment’s gene because a pigment’s gene, say red, would have been only a starter of a long causal chain that, during development, produced red pigment. In sum, what was transmitted were not discrete things, but, as Child clearly argued, reaction systems. Now, if a science of heredity dealt with reaction systems expressing themselves during development, a separation between transmission and expression was simply unconceivable.

However, if such a distinction was conceived as misleading, Ritter had his own alternative. Indeed, he argued, a scholar of hereditary phenomena should investigate “the real study of biotic genesis”. This meant that a proper study of hereditary mechanisms implied not only the direct investigation of the germ-cell structure and substance, but also of how the formation of hereditary parts is achieved; it needed observation, comparatively, of how organs or parts of them develop from preceding stages. In sum, any biologist interested in heredity had to follow what Ritter dubbed a “descriptive ontogenesis”. It is worthwhile to quote the example he gives:

...the lens of the vertebrate eye originates from the patch of ectoderm exterior to the optic globe. The optic globe itself arises by an outpocketing of the primitive brain. Since both lens and globe resemble the corresponding parts of the eye of ancestors near and remote, their development comes under the principle of heredity; and the ectodermal patch giving rise to the lens, and the part of the primitive brain giving rise to the optic globe are mechanisms of heredity; and the whole observable series of embryonic parts which culminate in the completed eye are the only direct evidence for the mechanism of heredity for the eye. So is it with all biotic ontogenesis whatever.¹¹⁹

In light of all this, it is not surprising that many of those biologists who were sceptical about genetics and

¹¹⁸ As Ritter explicitly argued in his 1919 monograph, his proposal would reunify heredity and development under a unique framework, insofar as it: “...would surely correct the tendency of genetic research under the guidance of the determiner hypothesis, to restrict its attention to attributes of adults at one end of the ontogenic series and to the chromosomes of the germ-cells at the other end...This correction results because the new standpoint would bring the whole series of continuities and transformations alike into proper perspective, revealing thus that the members of the series intervening between germ and adult must be investigated in exactly the same way and with the same objects in view as the end members, if complete understanding of the hereditary process be the goal of research (Ritter, 1919, p. 83, Vol. II).

¹¹⁹Ritter, 1919, Vol. II p.323.

the chromosome theory of inheritance, considered organisms with regenerative powers to be the best candidate to understand how heredity worked: they could observe the developmental processes in which heredity was, so to speak, “exhibited”, over and over again. The similarities between Ritter and Child on these issues are striking.

There were two other important issues at stake in Ritter’s discussion. First, the specific roles of the cell nucleus and cytoplasm and, second, the importance of agamic reproduction. Sapp¹²⁰ vividly reconstructs the debate between Mendelians and supporters of cytoplasmatic inheritance since the late 19th century. Many prominent biologists took sides in the controversy and their goal was to establish whether hereditary materials were located inside or outside the nucleus of the cell. There were a number of biologists who attempted to find a middle way between the two extremes; scientists like Loeb, Wilson, Conklin and Johannsen maintained that both nucleic material and cytoplasmic substance could have important roles. The quarrel was now concentrated on the relative importance of the nucleus and cytoplasm in heredity. It is a shame we cannot find Ritter’s remarks on this debate in Sapp’s book, because he dedicated massive efforts in clearing up the controversy. He pondered the two opposite stances using observations, collecting data and speculating. Ritter’s conclusions were quite clear and in accordance with his organismal philosophy: the chromatinic material inside the nucleus of the cell is responsible for many hereditary phenomena but it is not enough.¹²¹ Of course, careful observation of protozoan development showed that there was a direct causal relation between chromatin and the formation of specific structures such as flagella and pigment cells; therefore chromatin was involved, Ritter concluded, as hereditary substance. However, when we extend our observations to other organisms,

¹²⁰ Sapp, 1987; 2003.

¹²¹ In 1916 Ritter sent a letter to E. W. Cowdry. Cowdry was a zoologist who had gained a PhD at the University of Chicago in 1913, and was associate professor at the Johns Hopkins University at the time he was in contact with Ritter. In this letter, Ritter expressed his concerns about the general underestimation of the cytoplasm in heredity: “I want to...congratulate you on having recognized that the great interest taken by students of cytology and heredity of late years in the nucleus had diverted attention from the study of the cytoplasm, thought as a matter of fact cytoplasmic studies are of great importance. I should like to raise the question with you, who have done so much good work in histogenesis, how it is possible to refuse to consider such portions of the cytoplasm as the ‘physical basis of heredity’ that are observed to transform directly into structures which are surely hereditary. Since the production of hereditary structures, like the production of all structures, is a process of transformation, does it not seem, logically at any rate, that there is something wrong in a general theory that would explain these transformations by referring them to portions of the cell which do not transform – as is the case with chromosomes?”(Ritter to Cowdry, December 4th, 1916, Ritter Papers, Ctn. 1, Folder: Outgoing letters 1915-1916, Bancroft Library, Berkeley).

we find deviant cases. For example Ritter investigated many specific cases in which extra-nucleic substance played an important role.¹²²

The difference between nuclear and cytoplasmic inheritance had for Ritter also an evolutionary significance. These remarks are important to remember because they were of paramount importance for a Ritterian comprehensive theory of heredity. Ritter argued that, whereas nuclear inheritance was a relatively new mechanism of heredity, cytoplasmic inheritance was the most primitive and universal instrument of reproduction: “Heredity is far *older*, phylogenetically, and far *broader* taxonomically than is the chromatin mechanism by which it now in part manifests itself. Under this interpretation the acquisition by chromosomes of the function of carrying heredity would belong to the same evolutionary type as for example the acquisition by certain cells of the function of muscular contraction, of by certain other cells of conducting nervous stimuli”.¹²³ In other terms, whereas cytoplasmic inheritance was a universal phenomenon in the organic realm, nuclear heredity had a rather restricted occurrence within the overall economy of nature.

Second, Ritter warned that any theory of heredity had to include phenomena of agamic reproduction.¹²⁴ A theory which did not include “...the growth of a tiger lily from a bulb, of a sponge from a gemmule, and if an ascidiozoid from an ascidian bud, is so obviously forced that it ought to raise a suspicion that consciously or otherwise it is framed with some other motive in view than that of telling

¹²² Ritter dedicated a whole chapter of his 1919 large monograph to demonstrating that there were other substances than chromatin as physical basis of heredity: investigations taken on *Stentor*, the ontogeny of *Diplodinium*, the formation of *Paramecium* and *Stylonychia* organs, the skeleton of *Radiolaria*, the shells of *Foraminifera*, the clinging organs of *Sporozoa*, the division centre of *Noctiluca*, and, in general, the centrosphere of *Protozoa*. And again, germ cells: both the development of sperm than the ovum – Ritter undertook a comparative study of the gametes among different species - depended on other materials than chromatin. Finally, Ritter tackled a quite broad investigation on multicellular organisms. He examined the mitochondrial theory of heredity, looked at the origin of the cell-wall in “higher plants” and inspected the source of the striated muscle fibres: all factual evidences, Ritter believed, of cytoplasmic inheritance. At the end of his wide scientific literature overview he concludes: “...overwhelming observational evidence has been secured that the cytoplasm of cells participates directly in the formation of organic parts which have hereditary attributes.” However, there were also compelling evidences that chromosomes – both in plants and animals – have a fundamental role in the formation of parts having “hereditary attributes.” Ritter reached his organismal conclusion: “Any substance which plays such parts in development may be named a physical basis of heredity...” (Ritter, 1919, Vol. II, p. 65).

¹²³ Ritter, 1919, p. 69, Vol. II.

¹²⁴ Although Ritter ranked Mendel’s discovery of the segregation of characters as a milestone in the history of biology, he also contended that such a progress was limited to the sexual species. Mendelian supporters who redefined, extended and even improved the Mendelian theory of inheritance were prone to exclude all the cases that did not fit within a Mendelian framework: for example, all the cases of agamic reproduction and “propagation by other means”.

what heredity is".¹²⁵ As Child had already asserted, asexual organisms and alternative ways of propagation are phenomena of too much importance to be overlooked: "...if a complete census were made at this hour of the individual organisms composing the living world, the enumeration taking note of all individuals produced sexually and all those produce asexually, the asexually produced would probably exceed in numbers those produced by the other process"¹²⁶.

To conclude, what Ritter aimed for was a theory of heredity devoid of transmitted stuff (genes or determinants) but that, at the same time, highlighted the dynamic side of hereditary expression. It was a theory that gave equal importance to nuclear substance and cytoplasm and it was a theory that took as main reference the phenomena related to agamic reproduction. Although not totally denying genetics and the chromosome theory of heredity, Ritter denied their supposed universality and fundamentality.¹²⁷ His organismal theory indeed, excluded the existence of any fundamental stuff behind the organic phenomena *a-priori*; as R.C. Lewontin once said: "It is not that the whole is more than the sum of its parts. It is that the properties of the parts cannot be understood except in their context in the whole."¹²⁸ It is precisely such a kind of philosophy that Ritter defended. Therefore, for Ritter, heredity was much more than chromosomes, genes or determinants; it involved dynamic processes, complex transformations and development according to inherited system reactions.

6.7: A Forgotten Research Agenda: Ritter's Modern Synthesis

Nine years after the great biological synthesis that Ritter had formulated in his 1919 two volume monograph, he published a long article with Edna Watson Bailey,¹²⁹ "The Organismal Conception, its

¹²⁵ Ritter, 1919, p. 309, Vol. I.

¹²⁶ Ibid, p. 310.

¹²⁷ In Ritter's words: "...the real though usually unperceived ground of dissatisfaction is not with all-sufficiency of the nuclear theory of heredity, but with the all-sufficiency of any theory that attempts to localize the function of carrying heredity in some small, specific fraction of the germ-cells". (Ritter, 1919, p. 34, VOL. II).

¹²⁸ Lewontin, 1992, p. 122.

¹²⁹ Bailey was a zoologist who had studied in Berkeley and became an expert in child education. She collaborated with Ritter for many years on several publications and after Ritter's death, she became his literary executor. As a publication of the University of California reports: "Professor Bailey's principal method of study was to observe the individual child in a natural setting, an approach which has gained increasing acceptance in recent years. For Edna Bailey, the technique was a logical outgrowth of her early interest in the life-sciences, an interest which she pursued

Place in Science and Its Bearing on Philosophy” (1928). Here, they proposed a large research agenda aimed at unifying several disciplines, both scientific and humanist. Cytology, physiology, genetical biology, respiratory biology, neurology, endocrinology, psychology, physics (in their terminology, sciences of inanimate nature) were all to be unified under an organismal conception of biology — a conception that had much to say to philosophy and epistemology.¹³⁰ This paper is particularly interesting for two reasons at least. First of all, the organismal research program appears as a collective international commitment. The philosophy of Whitehead¹³¹ towered behind all individual scientific fields, and each discipline had its own organismal and neo-Kantian representative figure: people such as Whitman, Lillie and Child were, of course, at the forefront, but other more or less known figures were enlisted too, including, E. Rohde, L. W. Sharp, J. C. Smuts, C. A. Kafoid, J. S. Haldane, C. S. Sherrington, G. H. Parker, G. N. Lewis, C. J. Herrick and C. L. Morgan. Second, the paper introduced a synthesis between heredity, development and evolution in an original way.

Ritter in fact endorsed Morgan’s *Emergent evolution*; he believed that: “Emergent evolution and the organismal conception applied to living nature are the same thing looked at from different directions. ‘Emergent evolution’ is what that ‘same thing’ is called when the origin and development of living beings are the central interest, while the ‘organismal conception’ is what it is called when their morphology and physiological functioning are considered.”¹³² However, in common with many biologists at that time, Ritter’s views about evolution were quite anti-Darwinian. As he had explained to Scripps more than fifteen years before, organic evolution was far more complex than expected and natural selection alone could never explain evolutionary modifications to which organisms were subjected.¹³³

to her doctorate.” University of California (System) Academic Senate, 1976, University of California: In Memoriam.

¹³⁰ In particular, epistemology. Both authors argued for a “naturalized epistemology” well before Quine. Indeed, they believed that epistemology was part of the scientific enterprise and had to be an empirical and experimental discipline. Both philosophy *tout court* and epistemology had to study the way in which the brain organises and processes information coming from the environment. For this reason, they discussed the relation between reality and mind and, at the same time, the nature of abstract concepts and their functions.

¹³¹ Henry Bergson too was another figure admired by Ritter. Indeed, he had a very occasional correspondence with him. At the Bancroft Library is conserved a small visiting card on which Bergson wrote: “trouve’ chez lui, en rentrant à Paris, le travail que Prof. W. E. Ritter a bien voulu lui adresser (Ritter’s Life from the Biologist’s Standpoint) et le remercie de cette très intéressant étude, qui met si bien en lumière l’impossibilité d’isoler complètement quelque chose dans le domaine de la vie” (H. Bergson to Ritter, no date, Ritter Papers, Box 6, 71\3 Folder: Correspondence and paper, ca. 1879-1944. Incoming letters B, Bancroft Library, Berkeley.

¹³² Ritter & Baley, 1928, p. 334.

¹³³ Ritter to Scripps, June 14, 1911, Ritter Papers, Folder: Correspondence Jan-Jun, 1911, SIO Archive, La Jolla.

Still, in an unpublished paper titled "Biology greater than evolution", Ritter analysed the issue in a broader context: "Evolution...is the central, the really great idea of the modern world, and hence is the mainspring of modern motive and action. Yet we have seen that the doctrine of evolution is proving unsatisfactory."¹³⁴ Even though no-one could doubt the fact of evolution, the causes behind such a phenomenon are unknown. Arguably, Ritter claimed, many causes should be invoked: natural selection, hybridization, mutation, isolation, orthogenesis, and environmental forces;¹³⁵ although the acceptance of evolution was in no way dependent on a full knowledge of its causes. Furthermore, any evolutionary account had to include individual development in all its complexity. Ritter complained that the dominating philosophies of evolution pretended to explain morphological differences only through a modification of the whole race or species, overlooking individual processes of growth. He compared such a mistake to the genetical theory of heredity which pretended to explain adult organisms supposing the existence of definite particles within germ-cells.¹³⁶

However, even though evolution was central in biology and even though the study of its causes was a fundamental task to undertake, biology still remained more than evolution. To Ritter indeed, organismal bio-philosophy included evolution and not vice-versa, and the reason supporting such a position was epistemological. The recognition that an organism or part of it evolved from precedent states presupposed observation, identification, and classification; a bone or a land fossil did not speak itself, without an empirical inference, made on the basis of detailed descriptions and comparisons. In sum, any evidence for evolution was seen by Ritter as theory-laden, and such a theory could only be given from a specific bio-philosophy.

¹³⁴ W. E. Ritter, Unknown date, Ritter papers, Ctn. 1, Folder: Biology greater than evolution, Bancroft Library, Berkeley.

¹³⁵ In Ritter's words: "We are at last coming to see quite clearly that there can be no one all-sufficient cause of evolution; that there are, of necessity must be, a very large number of such causes. It seems pretty clear that we shall soon recognize that, taking evolution as a whole, of all sorts, part, present and future, the number of causes or 'factors' must be infinite, and the business of biology on this side must be to investigate as many of these as nearly a complete fashion is possible; without, however, supposing that the task will ever be finished". (W. E. Ritter, Unknown date, Ritter papers, Ctn. 1, Folder: Biology greater than evolution, Bancroft Library, Berkeley, p. 5). Nevertheless, although evolution may have several causes, Ritter excluded any supernatural force behind it.

¹³⁶ As Ritter argued: "The philosophy of life that makes evolution the 'master key' practically excludes from its purview the evolution of the individual. This exclusively processive biological philosophy is so dominating and many-faced, and has overflowed into so many other departments of thought, that we must run it home relentlessly. When this is done its breeding ground is found to be in exactly the same country as that of the erroneous notions about the competency of a few elements in the germ-cells to explain the adult organism which arises there from" (Ibid, p. 7).

We have seen that, according to Ritter, no real separation between heredity and development could be proposed and in 1928 he updated his ideas on this. In fact, he now accepted as hypothesis the existence of genes but considered them as entities formed by organisms during ontogeny, as any other organic product such as tissues or organs.¹³⁷ In other words, genes neither explained nor controlled development, but they were effects of it. Then, as the authors explain: “On the basis of our conception of organic activity as implying reaction systems, to which chemical transformation as well as surface interchanges are fundamental, we can make reasonable guesses about the nature and origin of genes.”¹³⁸ First of all, for Ritter and Bailey, there were not individual genes but systems of genes¹³⁹ and these consisted in the: “...smallest masses into which a portion of the substance of a living organism can be resolved, and still preserve (in the latent state) attributes of the organism.”¹⁴⁰ Second, gene systems were produced during the first developmental stages, when the individual was undergoing its first chemical differentiation. During these earlier phases, germ cells were affected from parental “impressment”, conceived as a chemical process that, in turn, produced a system of genes. In short, gene systems were nothing other than a chemical form of the species “impressing” on potential offspring. Once these early processes were achieved, embryological development followed, as Lillie had showed with his theory of embryonic segregation. According to Ritter and Bailey, such a hypothesis was not only in agreement with a wealth of embryological evidence but it also avoided treating genes as “entelechies” or “psychods”.

To summarise, while both ontogeny and phylogeny characterised evolution, heredity and development were unified under a single hypothesis which regarded gene systems as effects of development and not as causes of it. Insofar as development preceded heredity, the only way to study the mechanisms of inheritance was through embryological observations. As both Ritter and Bailey concluded, drawing on Lillie:¹⁴¹ “Investigation of the total ontogenic career of the individual would

¹³⁷ As they explicitly argued: “...chromosomes are elements of cells which have arisen by differentiation for the special function of hereditary transmission, just as the characteristic elements of striated muscles cells have arisen by differentiation for the special function of motion production by contraction ...the contribution of hereditary units to the production of the characters of an organism is no more incredible than is the contribution of the nutritial units consumed by the developing organism” (Ritter & Bailey, 1928, pp. 321-322).

¹³⁸ Ritter & Bailey, 1928, p. 322.

¹³⁹ Probably today we would call it “genome”.

¹⁴⁰ Ritter & Bailey, 1928, p. 322.

¹⁴¹ Lillie had published his paper in which he expounded his theory of embryonic segregation in 1927, one year before Ritter and Bailey’s paper.

include not only the primordial of that portion of the ontogenic career which begins with fertilization, but also of that portion of the career represented by the incipient and maturing stages of the germ cells themselves. These stages would be the ones in which the primordia are called genes."¹⁴² Yet embryology remained the fundamental science behind evolutionary studies insofar as the knowledge of individual development gave central pointers in understanding phylogenetic modifications.

6.8: C. M. Child's Lifelong Organismal Commitment

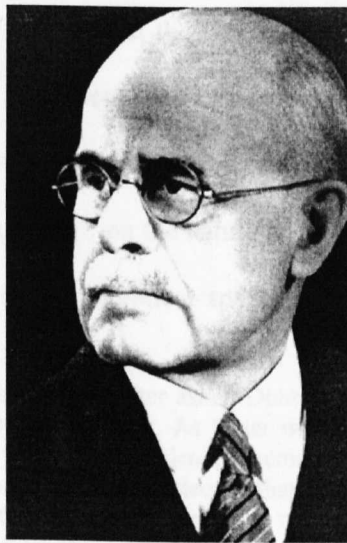


Fig. 6.8, C. M. Child, 1869-1954¹⁴³

The development of zoology along predominantly morphological lines has led to structural rather than dynamic conceptions of the animal organism, and the zoologist has not always found it easy to attain any idea of 'the organism as a whole'. It is evident, that the orderly behavior of the organism in development and function must be determined either by an effective physiological dominance or leadership of some sort, or by some metaphysical principle such as Driesch's entelechy, and the evidence points us to the first alternative.¹⁴⁴

C. M. Child

As we have seen, Ritter and Child worked in two different institutions. However, they were often in

¹⁴² Ritter & Bailey, 1928, p. 323.

¹⁴³ Source: L. H. Hyman, 1957.

¹⁴⁴ Child, 1924, pp. 282-283.

contact and, as letters in the archives demonstrate, they were close friends. They first met in 1894 at the Naples zoological station; Child was spending his last months in Europe after having attained a PhD, in Leipzig whereas Ritter arrived from Liverpool where he had worked with Herdman. Ritter, after a short period of travelling in Belgium, Germany, Switzerland and northern Italy (all places in which he visited laboratories, universities and natural history collections) arrived in Naples on 13th October 1894. Ritter's private diaries for the period spent in Naples are dense with information confirming his close friendship with Child. They worked together and explored together southern Italy and both became enthusiasts for Dohrn's¹⁴⁵ hospitality and his institution. As we have seen, once back in the US, Child got a job at Chicago whereas Ritter, after a brief interlude at the University of Berlin, was hired at Berkeley. Their friendship involved also a profound agreement on bio-philosophical issues: the organismal theory they developed was very similar, though from two different perspectives. Whereas Ritter was much more involved in a deep philosophical discussion¹⁴⁶ on the nature of the organism and the different epistemic of biological investigations, Child based his theoretical speculations on his physiological experiments —

¹⁴⁵ During the first years of the Scripps activities, Ritter asked Dohrn for some advice about the development of a Marine station; its possible aims and methods of work. As Ritter wrote: "...how much I would appreciate even a brief statement from you of what, after your rich experience, seems to you should be the central aims, (one or a few), of a marine station, and the worst pitfalls to be avoided! ...that the possibilities are unlimited both as to things to be done and good to be accomplished for science and humanity, no one would deny. In what order should they be taken hold of? What are the best means instrumentally, organisationally, and philosophically, to be employed? On these large questions I have thought much and experienced some. You have thought and experienced ten times more than I. How I should like and could profit by the results of your thinking and your experience". (Ritter to Dohrn, July 12th, 1909, Box 1, Folder: Correspondence 1909, SIO Archive, La Jolla). To Ritter indeed, the Naples zoological station remained a model to follow. Dohrn's fame abroad was enormous among young and old American biologists. In an unpublished document written in 1893, Ritter praises the importance of zoological stations for biological research in general; he first estimated the pioneer effort of Agassiz at the Penikese Island, then he mentioned Plymouth station in England, Woods Hole and Johns Hopkins laboratory in US and added: "...today there is hardly a civilized nation whose territory borders upon the sea that does not possess one or more marine biological stations in some form or other". However, Ritter observed, German science still led the way, and, in particular, Dohrn's station in Naples: "...the greatest of all such foundations, that at Naples, having been conceived and made a reality almost exclusively by the energy and devotion to science of a single German citizen, Dr. Anton Dohrn. The influence that this magnificent institution has had in the advancement of biological science during the twenty years of its existence is simply inestimable. About six hundred trained specialists have carried on work at its tables since it was opened, and the published results of their investigations would in themselves form a goodly library, all of the most valuable kind of scientific literature". (W. E. Ritter, Berkeley, Cal., Feb, 10th, 1893, Ritter Papers, Ctn. 1, 71/3, Folder: Outgoing letters 1879-1904, Bancroft Library, Berkeley). Already at that time, Ritter was convinced that marine stations provided the best tools and equipment for advanced biological research; he endorsed and quoted W. R. Brooks who had said that: "Nearly every one of the great generalizations of morphology is based upon the study of marine animals, and most of the problems which are now awaiting a solution must be answered in the same way"(Ritter quoting Brooks, 1893).

¹⁴⁶ Sumner described Ritter in the following way: "His stature as a biological philosopher can probably be fairly measured only by another philosopher. His writings reveal extensive acquaintance both with the literature of philosophy and of the history of science, such as an acquaintance as I believe few living zoologist possess. And they reveal preoccupation with certain philosophical problems throughout much of his life" in Sumner, 1944, pp. 335-338.

experiments often focused on animal regeneration and physiological regulation. The intellectual connections between Child and Ritter are also explicit in Ritter's publications; indeed, as Ritter wrote in his 1919 monograph: "...Child formulates views of the nature of organisms that agree very well with the organismal standpoint upheld in this volume."¹⁴⁷ In sum, at the end, even though there were important differences of method between Child¹⁴⁸ and Ritter, they shared a very similar conception of biology as science, namely a science generally studying the irreducible interactions among parts without losing the integrity of the whole.

As the letters exchanged with Ritter, Scripps institutional reports and Hyman's *Biographical Memoir* demonstrate, Child preferred spending his summer researches in San Diego rather than in Woods Hole. In fact, apart from research facilities that Ritter enthusiastically provided (and the rich fauna present in La Jolla), he had his own community of friends and colleagues who met regularly every summer he was there.¹⁴⁹ Yet, as I will show later on, Child's ideas and theories were constantly discussed with Ritter and Scripps' staff. In short, the organismal philosophy Child endorsed and developed was not only a result of his training in Germany and the strong influence of Whitman or Wheeler on Chicago's young crowd,¹⁵⁰ but it was also the outcome of Ritter's friendship and the frequent visits to Scripps.

In fact, looking at the letters exchanged with Ritter, we see how relevant the reciprocal influences were. Ritter considered Child the expert on animal regeneration and physiological regulation

¹⁴⁷ Ritter, 1919, Vol. II p. 111.

¹⁴⁸ In 1915 Ritter received a letter from the University of Chicago Press. Indeed, they asked an opinion about Child's new book *Individuality in Organisms*. Ritter responded that he totally agreed with Child's conclusions and methods. As Ritter put it: "The great amount of unimpeachable evidence he marshals (Child) in support of the claim that "nothing can be more certain than that it (the organism) acts as a unit in inheritance": and that "it is the fundamental reaction system which is inherited, not a multitude of distinct substances or other entities with definite spatial location", is the main feature of his work, so it seems to me, presents such a mass of evidence of just this sort that it must, one may suppose, take effect in time. The younger generation of biologists at any rate, will not brush it aside as insignificant or answer it on purely a priori grounds". W. E. Ritter, The University of Chicago Press, 15 Dec. 1915, Ritter Papers, Ctn. 3, Folder: Outgoing letters 1915-1916, Bancroft Library, Berkeley.

¹⁴⁹ Usually, all the letters Child sent to Ritter concluded in the following way: "Please remember me to my friends there (La Jolla). Mrs. Child joins me in kindest regards to yourself and Mrs. Ritter" (Child to Ritter, July 21th, 1908, Ritter papers, Ctn. 8, Folder: Child 1868-1954, Bancroft Library, Berkeley). Yet, Ritter was always glad to offer Child all the research facilities he would require. As Ritter wrote: "If you will come to La Jolla next summer to work up the flat-worms (Turbellarias), I will furnish an artist to do such drawings and colour works you might need and also give you such assistance as may be necessary for collecting. Of course, you would be expected to handle the work entirely in your own way. The Station would either pay you on the basis on which other members of the staff are paid, that is duplicate your university salary while you are thus occupied in La Jolla, or perhaps on some other basis if more satisfactory to you (Ritter to Child, March 10th, 1907, Ritter Papers, Ctn. 1, Folder: Outgoing letters 1907-1909, Bancroft Library, Berkeley).

¹⁵⁰ As Maienschein puts it: "Such concentration on the organization of the whole, approached in a variety of ways, characterizes the work of many Chicago biologists" (J. Maienschein, 1991).

and he often asked for clarification not only on these topics, but also about the theoretical consequences such phenomena entailed.¹⁵¹ Child, for his part, discussed both experimental and philosophical issues with Ritter; for instance, the relation between nucleus and cytoplasm, individuality in organism and organic correlations, the conceptual differences between abnormal, usual and normal growth, and development, and many other problems. In sum, they critically and actively negotiated their ideas, experimental results and consequent philosophical implications and interpretations. Furthermore, the Child-Ritter letters offer an interesting window on the development of Child's organismal philosophy and gradient theory. One of Child's pupils, L. Hyman,¹⁵² recalled that from 1910, Child: "... began to perceive that the unity of the organism is a matter of correlation...". Plastic organisms like *Planaria* showed, during their processes of regeneration, an organic tension and correlation among parts: a complex set of partial activities aimed to re-establish the whole reshaping and reconstructing of the parts. "His search for the mechanisms of correlation", suggested Hyman, led Child – "to the gradient theory which emerged about 1911 and with which his name will always be associated."¹⁵³ What Hyman does not say is that Child regarded his conception of organic correlation as related to other investigations undertaken in Germany some decades before. As Child explained to Ritter in 1909: "It would not be correct for you to credit me with originating the idea that division of organic systems may occur in consequence of weakening of correlation or its elimination. That idea has been suggested repeatedly by the botanists: Goebel, especially has expressed himself to this effect in some papers. Among the zoologists Roux has repeatedly asserted that as the organism is weakened its parts become more independent."¹⁵⁴ Child indeed, considered his hypothesis of physiological correlation as an extension of these pioneer investigations undertaken in Germany¹⁵⁵ during the second half or the 19th century.¹⁵⁶ Once again, organismal traditions were not

¹⁵¹ For example, in 1908, Ritter asked Child about animal regeneration and development: "I have to appeal to you again as I gave you fair warning I should, on regeneration matter. I have recently been looking into the question of the influence of the central nervous system in regeneration. The results as you know, seem to be so conflicting that Driesch in his late review of the whole subject for Merkel and Bonnet, concludes that the proof for the general influence of the nervous system on development and regeneration is wanting"(Ritter to Child, March 26th, 1908, Ritter Papers, Ctn. 1, Folder: Outgoing letters 1907-1909, Bancroft Library, Berkeley).

¹⁵² See Ronald, 2004.

¹⁵³ Ibid., p. 79.

¹⁵⁴ Child to Ritter, July, 12th, 1909, Ritter Papers, Ctn. 8, Folder: Child 1868-1954, Bancroft Library, Berkeley.

¹⁵⁵ Not coincidentally, one of the first formulations of Child's gradient theory and organic correlations was well into a typical German discussion of "Anlagen" and their expression during development. In a letter Child sent to Ritter in 1908 it is possible to see how much Child owed to Continental discussions. As Child explained to Ritter: "In plants, i.e., the higher plants, the actual form of the individual is determined as a whole very largely by nutritive conditions.

distinguished from the emergence of a new paradigm in developmental biology, as Haraway and Beckner have claimed.¹⁵⁷ These traditions were instead the continuance of older investigations, conceptions, research programs and theories on organic development.¹⁵⁸

However, as I have mentioned before, Child's organismal philosophy, unlike Ritter's, was closely related to his experiments and results on animal regeneration and developmental regulation; in other words, his neo-Kantianism ran in parallel with the formulation of his theory of metabolic gradients. As we will see later on, Child's recognition of the importance of organic physiological correlations during ontogeny fostered and reinforced a new and articulate definition of the organism which, in turn, supported his synthesis of heredity, development and evolution. Child indeed, like Ritter, never underestimated heredity. As he clearly stated in 1911, if we define heredity as "...the capacity of a physiologically or physically isolated part for regulation", then, "the only way in which we can discover anything concerning this capacity is by allowing the *regulation* to occur under the most various and carefully controlled conditions, i.e., we can investigate and analyze the problem of heredity only with the aid of development."¹⁵⁹

In sum, Child, like Ritter, Lillie and then Just, did not confuse heredity and development but considered them inseparable, because he painstakingly denied any particulate theory of heredity. For Child, any theory of heredity made sense only within an organismal framework insofar as the organism was considered the real unit of inheritance. Every new reproduction was indeed a new epigenesis, a new formation never reducible to any supposed germinal substance carried from organisms generation over

Many parts begin their development but cannot complete it because they cannot obtain sufficient food. If we remove some of the fully developed parts certain of the "anlagen" may then receive sufficient energy to complete their development, or new "anlagen" may be formed, according to conditions in the individual case. The replacement of lost parts in plants seems to me to be in considerable part of this character, though other than nutritive correlations are undoubtedly involved in many cases. The case of the operculum in *Serpula* resembles restitution in plants in so far as an anlage, which was prevented from developing so long as the fully developed organ was present, does develop and replace functionally the other organ when that is absent. I do not at present see any reason for regarding the case in which a single differentiated organ is concerned as different from that involving a complex totipotent system, or rather the two cases seem to me to be different only in degree not in kind. In planaria the part which takes the place of the part removed is just as capable of forming a new whole under proper conditions as is the bud or anlage of the plant which takes the place of the part removed". Child to Ritter, July, 21th, 1908, Ritter Papers, Ctn. 1, Folder: Outgoing letters 1907-1909, Bancroft Library, Berkeley.

¹⁵⁶ As Haraway reminds us, drawing on Harrison, it was Boveri who first introduced the term "gradient" in biology.

¹⁵⁷ Beckner 1967, and Haraway, 1976.

¹⁵⁸ None of the American figures I am considering in this work regarded themselves as initiators of a new "paradigm" in science, rather they perceived their work as an innovation building on a venerable and respected old tradition.

¹⁵⁹ Child, 1911, p.268.

generation: "...wherever a new whole, a new 'individual' arises in the organic world, there we have before us the problem of heredity."¹⁶⁰ As a consequence of his organismal theory, what was transmitted or inherited were not factors, elements, ids, genes or anything we can define as discrete molecules, but, as Child put forward, "possibilities". Possibilities that, for any specific generation, were "actualized" in dynamic relations between internal and external environment: "Heredity is the sum total of the inherent capacities or 'potences' with which a reproductive element of any kind, natural or artificial, sexual or asexual, giving rise to a whole or to a part, enters upon the developmental process."¹⁶¹

Child first formulated, in a broad and accessible way, his organismal conception in two books published in 1915: *Senescence and Rejuvenescence*, and *Individuality in Organism*. Both works were, as he explained, a record of his researches and results during the previous fifteen years; investigations which aimed to understand the most simple reproductive processes which implied "...the whole problem of the organic individual, its origin, development, physiological character and limiting factors..."¹⁶² Although both books tackled similar problems from slightly different perspectives, the rhetorical order Child imposed on his arguments is the same: a general definition of what is an organism, b) investigation and assessment of all experimental and theoretical implications such a definition implied — a strategy that he frequently used in his articles too.

In the following pages it is not my intention to provide a comprehensive description of Child's biological thought overall. Instead, what I will show is how Child connected his scientific conception of the organism (including both epistemic and ontological issues) and his large synthesis of development, heredity and evolution. Furthermore, I will also show that Child, with Ritter, Lillie and Just, was rather sceptical about neo-Lamarckian hypotheses on inheritance; he argued only that the transmission of acquired characters, although very partially supported from evidence, was compatible with his theory of heredity and development. This demonstrates, I think, that Child's view on heredity was not based on a previous commitment to neo-Lamarckism and its political agenda. In other words, according to Child's viewpoint, neo-Lamarckian mechanisms of heredity could only be a consequence of his results. Finally, I will suggest that Child's scientific program was not based on a single model organism, i.e. *Planaria*, quite

¹⁶⁰ Ibid, p.267.

¹⁶¹ Ibid, p. 268.

¹⁶² Child, 1915, p. V.

unlike Mitman and Fausto-Sterling's beliefs, according to which Child's physiological conception of heredity was based on his investigations on *Planaria*.¹⁶³ Indeed, we will see that Child's theory of inheritance was based on a very broad comparative approach; a method which included many different organisms with diverse characteristics.

6.9: Life, Organisms and Colloids

Like Ritter, Child was a strenuous enemy of Weismann's germ-plasm and the Mendelian theory of heredity. He used large parts of his books and articles to criticise both theories, considering them a direct result of vitalist traditions and mystical speculations. However, once he had established the total inadequacy of these doctrines, Child tried to build up a consistent physico-chemical organismal theory able to meet the requirements of a proper scientific investigation. However, before undertaking the hard job of defining what an organism is, Child was concerned with the definition of what life is. Indeed, for him, if life did not consist in any process based on or dependent on particular vital molecules, it was: "...the result of many processes occurring under conditions of a certain kind and influencing each other."¹⁶⁴ Child conceived life as a dynamic process involving different levels of organization and, as a consequence, regarded organisms not as material things but as physico-chemical systems in constant change. Furthermore, for Child the organism was not an individual self-contained static unity, but it was a dynamic unity that: "...itself determines, constructs, and harmonizes...it channels and develops a characteristic morphological structure and mutual dynamic activity in mutual relation to each other."¹⁶⁵ One of the most interesting outcomes of Child's bio-philosophy was that his conception of organism did not require denying a mechanistic view of life, because organisms were deemed mechanisms of a very particular kind. Organisms work and function according to different modes of physiological "correlations" which involve mechanical contiguities, transportation of substances through different parts and conduction of chemical signals.

For Child however, as a proper physico-chemical system, the organism was composed in a quite

¹⁶³ See Mitman and Fausto-Sterling, 1992.

¹⁶⁴ Child, 1915, p. 19.

¹⁶⁵ Child, 1915b, p. 4

particular substratum that many chemists of the first decades of the 20th century identified with colloidal systems.¹⁶⁶ Drawing on Heinrich Bechhold's *Colloids in Biology and Medicine*, Child concluded that organisms were made of colloids and therefore, as a provisional definition of the organism he proposed that: "A living organism is a specific complex of dynamic changes occurring in a specific colloid substratum which is itself a product of such changes and which influences their course and character and is altered by them."¹⁶⁷ Therefore, if a colloidal substratum was both cause and effect of the organism's changes, this implied that organic structure was strictly related to organic function so that: "...function produces structure and structure modifies and determines the character of function."¹⁶⁸ In order to explain this point, Child used effectively the analogy of a stream channel: as long as a stream current changed in relation to the channel's size, that size was shaped and modified from water currents. Therefore, if the relation between function and structure was valid for the normal physiological processes happening in adult organisms, the importance of function on structure gained strength when theories of development were considered. In fact, unlike some orthodox theories formulated in his time, Child argued that, during development, functions were not superimposed on a developing structure; rather, the organism built itself from its own functional activity.¹⁶⁹ Unlike a man-made machine, which does not work until its structure is accomplished, a living mechanism "functions" from its first formation: "...organism is always functioning while it is alive: life is function...in no case does the organism begin to function only after its construction is completed...it constructs itself by functioning, and the character of its functional activity changes as its structural development progresses."¹⁷⁰ Development for Child was a functional process characterised from a highly complex set of ordered mechanisms, implying both growth (increasing amount of organic substance) and reduction (constant elimination of substances accumulated previously).

¹⁶⁶ During the first three decades of the 20th century colloid science, as Andrew Ede showed in his book *The Rise and Decline of Colloid Science in North America, 1900-1935: The Neglected Dimension*, was a hot topic which gained progressive recognition among American scientists. Particular in biology, it was held that the science of colloids could provide an answer to the fundamental basis of life; i.e., the protoplasm in cells possessed a kind of colloidal organization.

¹⁶⁷ Child, 1915, p. 26.

¹⁶⁸ Child, 1915b, p.16.

¹⁶⁹ Child argued against orthodox conception of development as expressed by Roux, who had distinguished between two different phases happening during development; structural formation and functional development. According to Child instead: "The activities of the organism are considered as two-fold, one group being concerned with the construction of a complex machine, the other with the functions of that machine when completed" in Child, 1906, p. 180.

¹⁷⁰ *Ibid.*, p. 16.

Such dialectic between growths and reductions of organic materials constituting organism's body was, for Child, the direct or indirect outcome of the physico-chemical activity of metabolism.

However, growth usually implied another related process; differentiation. This process was, for Child, characterized by a "...structural complication...different regions of the cell, different cells or cell groups, become different from each other and from the original undifferentiated or so-called embryonic condition."¹⁷¹ Differentiation followed a given, if not necessary, plan; a plan directing the countless cells in undergoing diversification and specialisation.¹⁷² In general, just as growth was often associated with cell-differentiation, organic reduction could be associated with dedifferentiation (even if not necessarily). The phenomenon of dedifferentiation was totally rejected by Weismann and his followers because Weismann's theory of development was conceived as a one-direction process, i.e., only differentiation occurred. However, Child added, dedifferentiation was a very common phenomenon occurring in lower organisms with great capacities for regeneration and resulted from: "...the breakdown and elimination of the differentiated substratum or certain components of it, and the synthesis of new undifferentiated substances from nutritive material, as well as by the reversal of the reactions which occurred in the differentiation."¹⁷³ Regeneration showed that development could be a reversible process involving some regressions as much as progressions. In short, Child considered the processes of growth and reduction – both characterised as differentiation and dedifferentiation — associated with a dynamic change of metabolic activities. The fact that metabolic rates were involved in all developmental processes opened the door to a broad scientific investigation, a very large comparative study on many lower and higher organisms.

¹⁷¹ Child, 1915b, p. 6.

¹⁷² Child thoroughly denied that the origin of such an order exhibited during development could be explained with Weismann's determinants or Morgan's genes: the idea that the adult organism was a result of distinct preformed germs: "...succeed[ed] merely in placing the problem beyond the reach of investigation". Furthermore, even the most recent experimental investigations put forward by Morgan's students do: "...not afford any real support to the view that the morphological characters of the adult are represented in some way by distinct entities in the germ...and the attempts to connect particular factors with particular chromosomes or part of chromosomes are not at present, properly speaking, scientific hypotheses". Child, 1915, pp. 46 – 47.

¹⁷³ Child, 1915, p. 56.

6.10: Poisoning, Cutting, Comparing; Framing an Organismal Method of Investigation

The gradient, to my mind, is primarily a means of getting things going in an orderly manner. It does not necessarily persist throughout life and in any case undergoes modification and complication. Every region of local growth, for example, gives rise to a gradient which may be temporary or permanent. In the adult body of mammal or man there must be millions of these gradients, ranging from those in individual cells, e.g., in epithelial cells, to whatever traces remain of the primary body gradients. In the simpler organisms the primary gradients undergo less modification than in the higher forms and in many cases the gradients persist from the beginning of development throughout life...undoubtedly gradients determine relations of dominance and subordination in function as well as in development.¹⁷⁴

Child explored two possible ways to prove the existence of metabolic-rates involved in the processes of growth and reduction: the direct and indirect method of susceptibility. Child observed that every organism had a certain degree of susceptibility to specific chemical substances, and this degree was related to the organism's metabolic conditions. In fact, Child aimed to show how different parts of the organism responded differently to varying quantities of chemical substances (such as ethyl alcohol, chloroform, cyanides and other kind of narcotics) administered to diverse organisms. If a narcotic was administered with the intention of killing the organism (direct method), differences in susceptibility along the body axis were established. In particular, equal concentrations of lethal substances administered to planarians of different ages showed that there was a quantitative relation between the time planarians required to disintegrate and their age: i.e., older planarians lived longer than younger ones, given an equal concentration of narcotic. When the narcotic was administered with the intention to harm but not kill organisms (indirect method), an inverse quantitative relation was observed: i.e., younger specimens lived longer than older ones. Child interpreted these data by supposing that younger specimens, with their specific metabolic rates, had a higher susceptibility when exposed to lethal narcotics and, for the same reason, were less susceptible when exposed to non-lethal quantities: "...the animals which have the higher rate of metabolism and die earlier in the concentrations of the direct method live longer than those

¹⁷⁴ Child to Ritter, February 15th, 1927, Ritter papers, Ctn. 8, Folder: Child 1868-1954, Bancroft Library, Berkeley.

with the lower rate in the low concentrations used for the acclimation method.”¹⁷⁵ In other words, the experiments seemed to demonstrate that metabolic rate: “...is highest in the young animals and decreases with advancing age.”¹⁷⁶

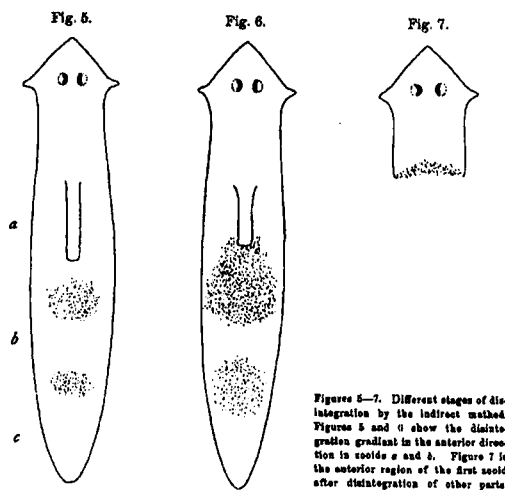


Fig. 6.9, Child's experiments showing different stages of *Planaria*'s gradual disintegration¹⁷⁷

Child performed other experiments in order to assess the relation between metabolic-rates and susceptibility. In cutting small pieces from *Planaria*, he was able to show that regenerative processes were related to higher rates of metabolism's activities because, as in the previous cases, *Planaria*'s pieces exhibited the same behaviour as the whole specimens: “The pieces with the higher rate of reaction disintegrate earlier than those with lower rate.”¹⁷⁸ In other words, pieces manifested higher susceptibility to the direct method, but again lower susceptibility to the indirect method. The existence of these differential susceptibility-rates were interpreted by Child as proof that the whole organism, as well as its isolated pieces, had to be seen as an individual dynamic entity composed of “metabolic gradients”; gradients that in *Planaria*: “...appear, not only in the susceptibility of different regions, but also in the differences in the capacity of reconstitution of pieces from different levels.”¹⁷⁹ Yet, metabolic gradients present along the axis of these specimens were, as Child claimed, of quantitative nature. The experiments he performed in order to change the developmental paths both in *Planaria* and sea urchin embryos –

¹⁷⁵ Child, 1915, p. 99.

¹⁷⁶ Ibid., p. 102.

¹⁷⁷ Source: Child, 1912, p. 615.

¹⁷⁸ Ibid, p. 607.

¹⁷⁹ Child, 1915, p. 122.

experiments aiming to inhibit or delay gradients — demonstrated the existence of specific quantitative rates along the main axes. In particular, in exposing designated regions of frog embryos to narcotics, Child showed that it was possible to retard or inhibit “...developmental processes in the posterior region of the body while in the anterior region development proceeds more or less normally.”¹⁸⁰ In sum, Child believed that the production of monsters or abnormal organisms through manipulation of gradients demonstrated that metabolic-rates could be studied in a quantitative way insofar as they developed in a quantitative way. Child based his findings on a highly comparative method involving experimental analyses of different forms.¹⁸¹ In fact, he always questioned himself: did other organisms behave similarly? Are there relations between invertebrates and vertebrates? What differences? What similarities?

To Child, what seemed to relate all the organic forms was the fact that every organism develops according to an: “...ordering, controlling principle.”¹⁸² This order, which represented one of the most important characteristics of life, characterised what Child dubbed “organic individuation.” Individuation involved two different morphological types: the radiate type, in which the process of individuation begins from a central region; and the axiate type, in which individuation starts from different areas. In general, the process of individuation follows an axial polarised gradient which was inherited during sexual or agamic reproduction. The existence of these axial gradients was easily observable in many different organisms: ciliate infusorians, hydra and other species of hydroids, turbellaria, sea-urchin, starfish, fishes, salamanders and frogs. Furthermore, the existence of these polarised axes along the body of all these forms indicated that there was a relation between metabolic gradients and axes, i.e., a definite polarity arising from a metabolic gradient along a definite axis. In fact, according to Child’s conception of the organism: “...the axial gradients are the basis of polarity and symmetry.”¹⁸³ In particular, embryology

¹⁸⁰ Child, 1915b, p. 59.

¹⁸¹ In the papers Child published between 1911 and 1913 *Planaria* was effectively the model-organism he based his results. See “Studies On the Dynamic of Morphogenesis and Inheritance in Experimental Reproduction. I. The Axial Gradient in *Planaria dorotocephala* as a Limiting Factor in Regulation” (1911), then, “Certain Dynamic Factors in Experimental Reproduction and their significance for the Problem of Reproduction and Development” (1912), finally, (1913) “Studies On the Dynamic of Morphogenesis and Inheritance in Experimental Reproduction. VI. The Nature of the Axial Gradients in *Planaria* and their Relation to Antero-Posterior Dominance, Polarity and Symmetry”. However, when Child reiterated all this data in his 1915 books, he attempted to extend such results to other model-organisms.

¹⁸² Child, 1915, p. 199.

¹⁸³ Child, 1913, p. 145.

showed that relationship clearly. The gradients are visible from the first stages of development: "...that region of the egg or early embryo which had the highest rate or metabolism gives rise to the apical or head-region, which, in consequence of the higher rate, becomes differentiated in advance of other parts, and these follow in sequence along the axis,"¹⁸⁴ Child suggested that, during morphogenesis, the origin of organization and regulation could be observed during early axial formation because each stage of embryonic development followed these polarised axes.

Even though comparative observations and experiments performed on *Planaria*, tubularia, corymorpha, strawberry, fish embryo, and chick embryo proved the existence of these axes, they also demonstrated the existence of dominant and subordinate regions as related to metabolic gradients. As we have seen, the possibility of inhibiting or delaying the development of specific parts through controlled experimentation — therefore inhibiting or triggering the emergence of new axes and new gradients — suggested to Child that organisms were shaped from definite tensions:¹⁸⁵ "...the region of highest rate becomes the chief factor in determining the rate of other regions, and since the rate thus determined is higher in regions nearer to it and lower in those farther away, a gradient in rate results."¹⁸⁶ Child's hypothesis of metabolic gradients and tensions between dominant and subordinate areas explained different phenomena — facts otherwise unintelligible. For example, the fact that in *Tubularia* the apical region was independent from other body parts whereas the behaviour of basal ends depended on what happened to the superior regions. In *Planaria*, such a phenomenon was even more evident: "An isolated piece of the planarian body is not capable of producing at its anterior end any parts characteristic of levels anterior to that from which it came, unless a head forms or begins to form first," Child noted, continuing: "...any piece ...is capable of giving rise to parts posterior to the level from which it came. In short, anterior regions are dominant over posterior regions in regulatory morphogenesis."¹⁸⁷ Although the general development of the roots and rhizoids in plants also showed similar patterns, that is "They are...subordinate to the individual as a whole,"¹⁸⁸ they depended primarily on the dominant upper regions

¹⁸⁴ Child, 1915, p. 204.

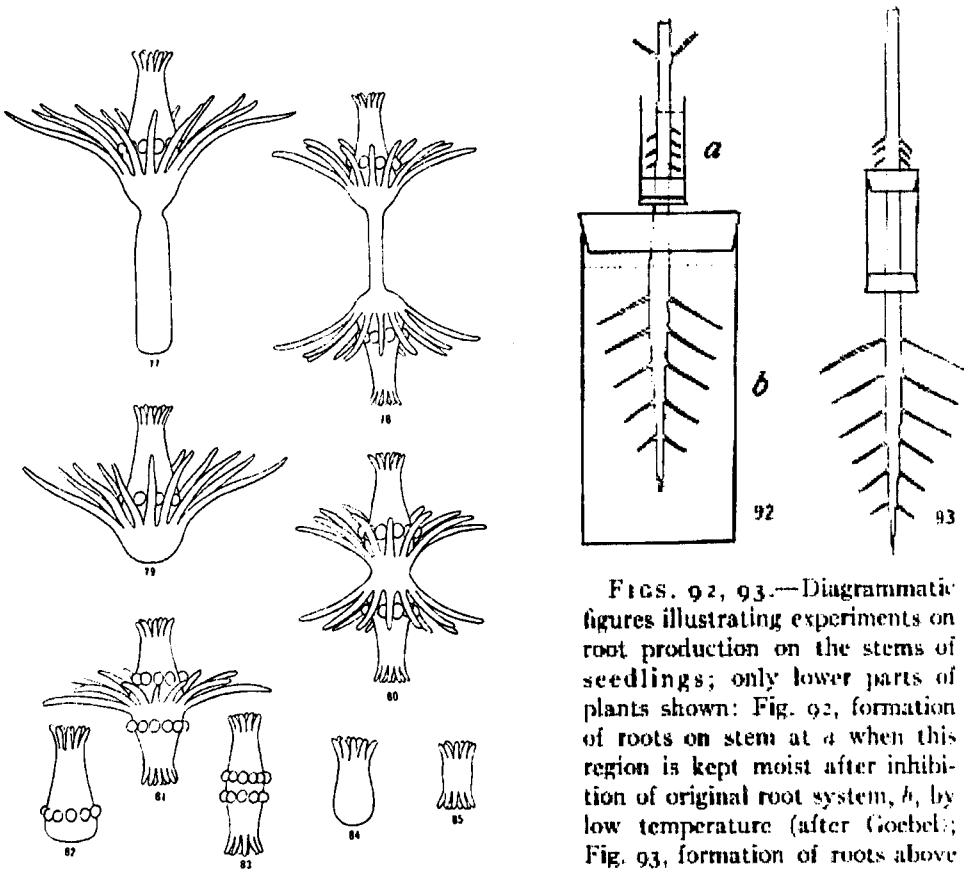
¹⁸⁵ In Morgan's book *Regeneration*, published in 1901, a similar hypothesis was proposed. Regulation during regeneration was due to some specific tensions among organism's parts.

¹⁸⁶ *Ibid.*, p. 209.

¹⁸⁷ Child, 1912, p. 604.

¹⁸⁸ Child, 1915b, p. 105.

where the gradient had been first established.



Figs. 77-85.—Different results of reconstitution in short pieces of the stem of *Tubularia*, showing that the formation of the apical region is independent of other parts.

Figs. 92, 93.—Diagrammatic figures illustrating experiments on root production on the stems of seedlings; only lower parts of plants shown: Fig. 92, formation of roots on stem at *a* when this region is kept moist after inhibition of original root system, *b*, by low temperature (after Goebel); Fig. 93, formation of roots above a region of stem included in narcotic atmosphere (after McCallum's description).

Fig. 6.10, Child's illustrations representing his experiments on plant formation according to subordinate and dominant regions. These experiments aimed, essentially, to understand the phenomena related to organic regulation during regeneration or reproduction¹⁸⁹.

Child used all his evidence and subsequent interpretations to display his general hypothesis about development and regeneration. During development, the region with the highest metabolic rate establishes a gradient axis which, in turn, guides the development of all subordinate parts of the organism's body. Animal and plant regeneration follow the same path: cutting a small piece from the body of a hydra or *Planaria* established a new metabolic gradient – therefore a new dominant region – which would progressively reduce its metabolic rate as the whole body was reconstituted. As a consequence, reproduction could be interpreted, both in lower and higher forms, as re-establishment of a new metabolic gradient driving the development of a new individual: “the degree of individuation is

¹⁸⁹ Source: Child, 1915b, p. 97.

dependent upon the rate of metabolism. At any given time of development the higher the rate of metabolism, the higher the degree of individuation.”¹⁹⁰

In *Individuality in Organism*, Child offered a more schematic representation of his metabolic gradients theory. Imagining a “...spherical mass of living protoplasm”¹⁹¹ whenever an external stimulus triggered a physico-chemical reaction in a specific area (let’s say in *a*, fig.) a metabolic reaction was established.

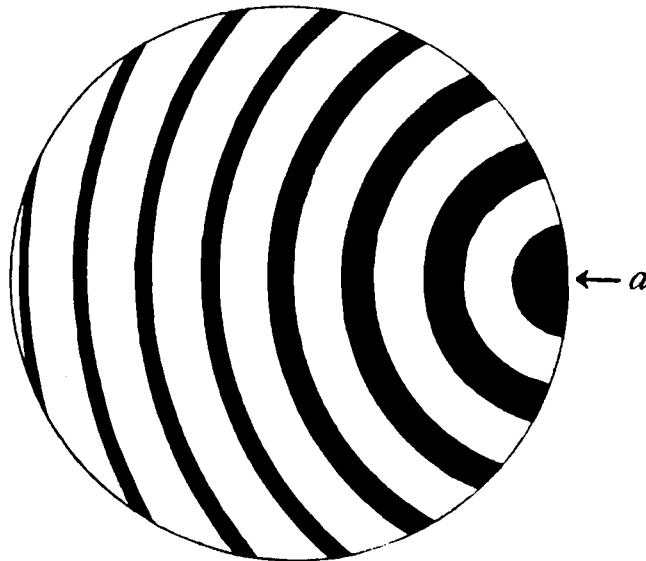


Fig. 6.12, Child’s schematic representation of gradient.¹⁹²

As in the case of spreading waves in a pond, such a reaction spread along the spherical surface while a metabolic gradient was taking form. The establishment of these gradients followed, as we have seen, from the formation of a polarised axis which represented “...the starting point of the “mysterious” organization.”¹⁹³ Yet, the physico-chemical transmission of these “waves” established regions where the metabolic rate was higher and regions where it was lower, leading to regions of dominance and subordination. Once an axis was established along a metabolic gradient, it could fully or partially persist through different generations so that such an order was transmitted during the processes of reproduction.¹⁹⁴ All correlations among parts, translated from an organismal viewpoint as tensions

¹⁹⁰ Child, 1915, p. 228.

¹⁹¹ See Child, 1915b, fig. at p. 30

¹⁹² Source: Child, 1915b.

¹⁹³ Ibid., p. 35.

¹⁹⁴ “The basis of individuality is inherited from the parents” said Child. See Child, 1915b, p. 41.

between dominant and subordinate regions, were considered by Child as: "...the foundation of unity and order in the organic individual" and therefore: "...the starting point of physiological individuation."¹⁹⁵

6.11: Child's Anti-Weismannian Synthesis: Heredity, Agamic Reproduction and Developmental Evolution

The phenomena related to animal regeneration certainly were the most inspiring to Child. As T. H. Morgan had shown with his comprehensive studies of these phenomena,¹⁹⁶ regeneration offered a great deal of material that could be used to understand development. However, for Child, regeneration also opened a large window on reproduction. As he claimed in 1911:

In the reconstitution of the whole from a part all the essential features of the reproduction of an organism of specific character from a reproductive element of a certain constitution are as truly present as in the development of the egg, though in different form because of the difference in conditions. Whether we call the process regeneration, restitution or reconstitution, whether it involves extensive redifferentiation in the isolated part or is chiefly limited to localized outgrowth and differentiation of new tissue, it is development, morphogenesis, just as certainly as is the formation of an organism from the egg¹⁹⁷

Comparative observations on the reproduction of lower forms, as for example, hydroids and plants, demonstrated that agamic (asexual) reproduction through fragmentation was rather frequent in nature. Such an extended kind of reproduction was seen by Child as a process entailing fragmentation following physiological isolation. In other words, the organism's progressive growth caused some regions to be progressively segregated from dominant regions, so that physiological isolation only depended on the distance separating subordinate and dominant districts. In short, isolation triggered cellular dedifferentiation which, in turn, caused the emergence of a new metabolic gradient and, finally, a new

¹⁹⁵ *Ibid.*, p. 40.

¹⁹⁶ Sunderland, 2010.

¹⁹⁷ Child, 1911, p. 266.

trend of cellular differentiation and individuation. In the same way as regeneration followed from the emergence of a new axis and establishment of a new metabolic gradient in severed pieces of tubularia, *Planaria* or hydra; equally, agamic reproduction consisted in cellular dedifferentiation (implying rejuvenescence) and establishment of a new metabolic gradient.

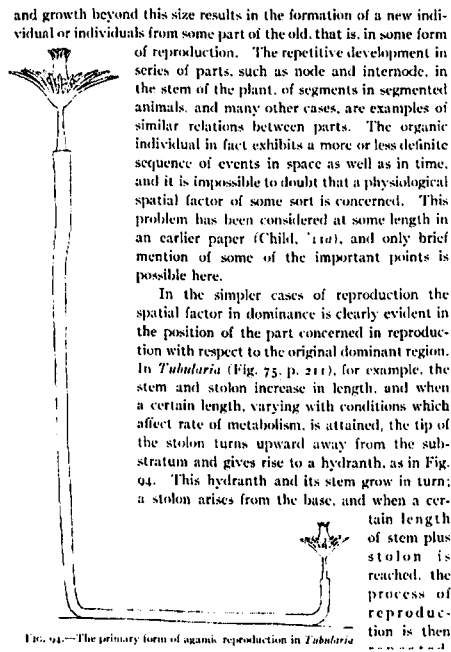


Fig. 6.12, To Child, reproduction meant establishing a new dominant region representing a new metabolic gradient, as the image of a young tubularian in the picture above shows¹⁹⁸.

Although Child suggested that there were similarities in sexual reproduction, he also recognised that organisms reproducing sexually reached a higher stage of individuality which prevented any reproduction by budding. In other words, high degrees of cellular specialisation and differentiation prevented any process of dedifferentiation and rejuvenation. As Child explained: "...the specialized structure has become so firmly fixed that physical or physiological isolation does not constitute a sufficient stimulus to initiate dedifferentiation."¹⁹⁹ However, even though the existence of specialised germ cells permitted sexual reproduction, these cells were neither simple nor sequestered at very beginning of development, as Weismann had suggested. In fact, as Child specified: "The gametes arise in the course of development like other specialized parts, and like these also possess a definite history of

¹⁹⁸ Source: Child, 1915b, p. 90.

¹⁹⁹ Child, 1912, p. 19.

differentiation.”²⁰⁰ Weismann’s hypothesis about the early sequestration of germ-cells lacked evidence, Child contended, and therefore the supposed separation between somatic and germ cells needed revising. Looking at the whole of the plant and animal kingdoms, invertebrates and vertebrates, Child could find only a few controversial cases fitting the germ-plasm theory (the parasitic worm *Ascaris megalocephala* observed by Boveri, fly *Miastor*, the gnat *Chironomus* and the worm *Sagitta*); in short, early segregation of the germ-cells during embryogenesis was observable in only a very few organisms. Child’s attack on the germ-plasm theory is withering and it is worth quoting in its entirety:

...it appears that the facts afford no adequate grounds for regarding the germ cells as anything else than an integral part of the organism specialized in a certain direction like other parts. But in spite of the complete absence of any trace of early segregation of germ cells in many organisms, in spite of the fact that the egg cytoplasm, not the nucleus, is apparently responsible in most if not in all cases of early segregation, in spite of our ignorance in many cases whether the so-called primitive germ cells really give rise only to gametes, and, finally, in spite of the remarkable conception of the organic world to which the germ-plasm theory leads us – in spite of all these difficulties – the view that these processes of early specialization in the egg constitute a spatial morphological segregation of the independent germ-plasm from the body or soma still finds supporters...²⁰¹

After an extended morphological description of different kinds of gametes, Child concluded that: “...the gametes are physiologically integral parts of the organism, that they are, like other parts of the organism, more or less highly differentiated cells, and that, like other parts, they undergo differentiation because of the conditions to which they are subjected in the organism and not because of peculiar, inherent properties.”²⁰² Moreover, germ cells were highly complex and did not contain undifferentiated substance that, during development underwent differentiation. With most organismal biologists argued, Child observed that germ-cells, both from a morphological and physiological viewpoint, were among the most

²⁰⁰ Child, 1915, p. 323.

²⁰¹ Ibid., p. 333.

²⁰² Ibid., p. 347.

differentiated cells of the entire organism.²⁰³ Unlike Weismann and his advocates, Child and Ritter did not ascribe to germ-cells' particular importance concerning the phenomena of reproduction, heredity and development.

Child's denial of Weismann's germ plasm theory had important theoretical implications. If germ plasm was nothing other than "...any protoplasm capable under the proper conditions of undergoing differentiation and reconstitution of a new individual of the species,"²⁰⁴ heredity had to be found elsewhere in the organism. Indeed, heredity, as a broad notion comprising "...the inherent capacities or "potencies" with which a reproductive element of any kind, natural or artificial, agamic or gametic, giving rise to a whole or part enters upon the developmental process"²⁰⁵, could not be associated with and reduced to some particular substance carried by organisms generation to generation: the whole pantheon of different posited particles — factors, characters, germs, gemmules, pangenes etc. — had nothing to do with what really happened with the phenomena of inheritance. Heredity dealt with potentialities and activities triggering ordered processes aimed at reconstituting new individuals from isolated parts: whether a piece of *Planaria*, a part of a plant or a gamete; instead, Child argued: "...a logical theory of heredity must concern itself primarily with the dominant or fundamental reaction system."²⁰⁶ If organisms emerged from dynamic systems of reactions, in which differentiation and dedifferentiation, growth and reduction caused defined tensions between dominant and subordinate regions²⁰⁷; the unit of inheritance had to be the organism itself²⁰⁸: "...the original specific reaction system in which the gradient arises is the fundamental reaction system of the species, the basis of inheritance and development."²⁰⁹

As we have seen with Ritter, for Child, if a science of heredity was to deal with individual development, then experiments and observations had to be addressed to the mechanisms causing ontogeny. Animal regeneration, as an appropriate instance paralleling normal development, offered the

²⁰³ See Child, 1912, p. 30.

²⁰⁴ Child, 1915, p. 427.

²⁰⁵ Ibid., p. 462.

²⁰⁶ Child, 1912a, p. 637.

²⁰⁷ As Child argued: "...even in the case of organs of such definite form and localization in the body as are the eyes, the position, form and number of the organs may be dependent upon dynamic conditions in the system as a whole, rather than upon any specific or localized hereditary element", in Child, 1911, p. 216.

²⁰⁸ As Child specified, developmental phenomena did not consist in: "...a distribution of the different qualities to different regions, but simply the realization of possibilities, of capacities of the reaction system", Child, 1915b, p. 202.

²⁰⁹ Child, 1913, p. 152.

best materials for solving the riddles of heredity because it permitted infinite experimental manipulations; treatments far more advanced than breeding strains: "...in the experimental reproductions, i.e., the processes of reconstititional regulation following the physiological or physical isolation of parts of the organism, there exist still further possibilities of control and analysis, which are not present in either asexual or sexual reproduction in nature. I believe there is much to be learned from these simpler forms of reproduction that the breeding and crossing of sexual forms can never teach us."²¹⁰ In fact, as experiments performed on *Planaria* and other regenerating forms demonstrated, hereditary potencies of different body parts could be "awakened" by changing their position with other parts.²¹¹ In sum, through cut and paste, through poisoning and diverting normal developmental processes, hereditary potencies emerged in all their possibilities.

However, if Weismann's hypothesis of a neat separation between soma and germ-plasm was rejected, evolutionary change could be explained by invoking neo-Lamarckian mechanisms of inheritance. As Child reported: "...biologists have been slow to admit the possibility of such inheritance (acquired characters), largely because it conflicts with the Weismann theory", but if: "...gametes are integral parts of the organism, there is no theoretical difficulty in the way of such inheritance."²¹² Even though Child left open the possibility of the transmission of acquired characters in evolution, he was not a neo-Lamarckian. With Ritter, he believed that many causes behind evolutionary change had to be considered or assumed. In any case, if Child's physiological theory of heredity was accepted, evolutionary change could not be caused by a dialectic between structural modification of the germ-plasm and natural selection, but as physico-chemical changes of reaction systems during individual development. Organic evolution was therefore characterised by a "...change from a less stable to a more stable condition in the dynamic reaction system which constitutes the organism."²¹³ At the same time, genetic characters assumed by geneticists could be equally explained as result of physiological correlations between parts of a dominating whole.²¹⁴

To summarise, we have seen that, unlike Ritter's philosophically oriented biology, Child based

²¹⁰ Ibid., p. 269.

²¹¹ Child, 1912b, p. 35.

²¹² Child, 1915, pp. 462-463.

²¹³ Child, 1915b, p. 205.

²¹⁴ Child, 1911, p. 216.

his own organismal theory on his experiments and observations on animal regeneration and related phenomena.²¹⁵ His hypothesis of metabolic gradients, through which system reactions emerged, unified heredity, development and evolution under one unique framework; and, with Ritter, he formulated a conception of heredity that was in opposition with that put forward by mainstream geneticists. In fact, to Child, heredity did not consist either in resemblance among parents or in transmission but reconstitution: “we have that — he claimed — in the reconstitution of a part into a new whole...all the essential features of true reproduction and inheritance.”²¹⁶ Child believed that his physiological theory of heredity was a far better alternative than genetics:

The apparent independent variation of the characters, the Mendelian phenomena, the association or coupling of characters, sex limited inheritance and in fact all the known phenomena of inheritance can be far more readily accounted for on the basis of different dynamic equilibria. If the organism is a dynamic system, changes in its constitution or in the conditions of the environment may alter its equilibrium and such changes may become evident, now in this character now in that or in a group of characters, according to the nature of the organism and the condition concerned²¹⁷.

Finally, even though Child based many of his results on repeated experiments performed on *Planaria*; his “physiology of inheritance” was the outcome of various investigations undertaken on a wide array of different organisms. Mitman and Fausto-Sterling argue that: “...*Planaria* and *Drosophila* became symbols of differing views regarding the nature of inheritance and reproduction.”²¹⁸ *Planaria*, according to the authors, was a symbol representing the Chicago school led by Child whereas *Drosophila* represented Morgan’s Columbia School. In sum, both organisms, in supporting two alternative schools,

²¹⁵ In 1921, in a book titled *The Origin and Development of the Nervous System from a Physiological Viewpoint*, Child proposed a more articulate and sophisticated version of organicism. He first defined the organism in terms of “organismic behavior pattern”. Then, any living entity was conceived as “...molar, not a molecular or atomic pattern, for it involves regions consisting of many molecules usually of many different kinds... Since these different regions are dynamically active and yet the organism is and orderly whole, physicochemical relations of some sort must exist between the different regions” (Child, 1921, p. 5). Such an organismal conception implied the absence of any preformistic hypothesis of heredity; although it did not require the acceptance of neo-Lamarckian mechanisms of inheritance.

²¹⁶ Child, 1921, p. 5.

²¹⁷ *Ibid.*, p. 36.

²¹⁸ Mitman and Fausto-Sterling, 1992, p. 173.

conveyed different and opposite hypotheses, experimental practices and conceptions of heredity. As the authors concluded: “Organisms...are co-opted and deployed by scientists in the support and defense of particular amalgamations of theories, beliefs, and practices. And, in the process, organisms are themselves transformed into symbols, embodying the theories and traditions that first put them on the map.”²¹⁹ As we have seen, however, with Child and Ritter, things were far more complicated.²²⁰ In fact, although *Planaria* was used extensively by Child and his followers in testing a vast assortment of hypotheses, the essence of Child and Ritter’s scientific method was *comparison*. We have seen that Child himself tested his theory of metabolic gradients on different kinds of organisms²²¹ and, furthermore, when he tackled problems concerning heredity, he suggested that any enquiry should begin by observing simple processes of reproduction on diverse asexually reproducing forms:

...our theories of heredity and inheritance, instead of being based solely or primarily on the phenomena of sexual reproduction, must find their basis for analysis and interpretation of these phenomena in the simpler forms of asexual and experimental reproduction. Sexual reproduction is in many respects the most unfavorable form of reproduction for investigation and analysis of the process of inheritance, for here we find the greatest number of complications...²²²

For Child *Planaria* certainly was one of his best tools in assessing the various hypotheses he advanced in heredity and development; but *Planaria* was nevertheless part of a rich catalogue of organism containing many forms, each worthy of investigation. Hence, I think, the real difference between Child’s and Morgan’s schools did not consist in their preferences about model-organisms, but between a comparative method (plural model organisms) and a method entirely based on one unique model organism.²²³

²¹⁹ Ibid., p. 176.

²²⁰ In the same way as Lillie and Just.

²²¹ Ciliate infusorians, hydra and other species of hydroids, different kinds of turbellaria (among which planarias), sea-urchin, starfish, fishes, salamanders and frogs.

²²² Child, 1912b, p. 31.

²²³ Unlike Mitman and Fausto-Sterling, Fantini (1985) argues that the embryological tradition was dominated by another model organism: the sea urchin. The sea urchin would be the equivalent of the fruit fly for geneticists. I think rather that no single organism could fairly represent the embryological and physiological traditions of which Child was part. Indeed, what really characterised these traditions was comparison. See Fantini, 1985.

6.12: Conclusion: The Biological and Social Agenda of Child and Ritter

In the espousal of a developmental view both goal oriented and progressive, Chicago biologists had humans as the end stage ever in mind. Their science was not just about the biology of leeches or Planaria; it was also about humans, about the place of humans in nature, and the laws of nature that have guided the past and direct the future course of social evolution. A morality could be discerned in nature. Even the succession of plant and animal communities offered prescriptive lessons to human society. This scheme of nature as normative has been implied – in Whitman’s appeal to specialization and organization as companion principles of progress; in Child’s search for unifying theory of development, heredity and behavior...”²²⁴

G. Mitman

Fausto Sterling and Mitman have nicely highlighted some of the social implications of Child’s physiological theory of heredity. Indeed, along with many of his colleagues at the University of Chicago, Child was a progressivist endorsing social reform policies. With Ritter, he was convinced that the social environment played a central role in shaping human development. Inspired by his own experiments and observations on animal regeneration, he believed that all organisms (including humans) were much more flexible than eugenicists would admit. As he pointed out in 1927: “We have the best reasons for believing that, within the limits of the hereditary potentialities of the individual, environment and its educational effects are potent factors in determining human character and personality. The fact that it appears at present to be difficult to alter the hereditary potentialities through the action of environment does not justify us in ignoring, or minimizing, the importance of environment for the individual²²⁵. Ritter could not have agreed more.

Indeed, as we have seen, the Scripps Institution was committed to providing the ‘right’ biological knowledge for solving social and political issues: in particular a sound biology for eugenics — a biology focused on human development. Year after year, Ritter formulated viable education projects for the “Foundation of Human Biology”. At Scripps, students had to follow lectures and laboratory courses

²²⁴ Mitman, 1992, p. 47.

²²⁵ Child, quoted in Mitman and Faust Sterling, 1992, p. 15.

on “Stages in the cycle of individual life of all higher organisms”; therefore, a thorough study of all developmental phases happening in Man and his near related species: from germ cell to senescence. Furthermore, probably sometime between 1920s and 1930s, Ritter even proposed a project for the experimental research on child development, involving the selection of twelve children who would be supervised from six months to three years. Special teachers, nurses, dieticians, paediatricians and psychiatrists would be enlisted to carry out didactic experiments. The problems that such a project would address involved both physical and mental child improvement; in Ritter words: “The development of physical, sensory and motor traits; the growth of manual habits, language habits and intelligence in a superior environment. Data should be obtained from matched individuals in control groups developing under different environmental conditions. The experiment would throw light on the problem of possibilities in nurtural modification of basic traits.”²²⁶ Learning processes had to be studied and improved, childrens’ sleeping habits controlled, their appetites corrected, their “maladaptive emotional traits” erased, their social skills reinforced and their play habits observed. Both Child and Ritter maintained that improvement of the race lay not in reproduction, but in social environment; such a position was perfectly in agreement with their scientific views on heredity and development.

Child went even further than Ritter. In 1924 he published *Physiological Foundations of Behavior*, probably the wildest and most political of his books. After a general reassessment and recapitulation of his gradient theory, in the last chapters he readily applied his notion of dominance and subordination to society and its modes of organization. As he had previously argued in 1921, the organism was not a well-defined thing or a complex entity; it was a process, a timely thing, a behaviour pattern: “...the behaviour of a specific protoplasm in a certain environment.”²²⁷ To Child, such a conception of organism could effectively represent and be extended to the “social organism” itself:

The sociologist is accustomed to call the relatively fixed and permanent social patterns institutions.

Are there not patterns or orders within the organism fundamentally similar to social institutions in that

²²⁶ See the project for eugenics based on education in W. E. Ritter, unknown date, A Project for Experimental Study of Development, Ritter Papers, Ctn. 11, 71/3 c, Folder: Children Education development, Bancroft Library, Berkeley. See also W. E. Ritter, no date, Foundation of Human Biology, Fundamentals of the Nature of Man? Ctn. 10, 71/3, Folder: Lectures and Seminars Notes, Bancroft Library, Berkeley.

²²⁷ Child, 1924, p. 267.

they represent integrations of living units? Is not the organism itself and institution of some sort in the living protoplasm of one or more cells? If the physiological conception of axiate pattern developed in earlier chapters and elsewhere is correct the axiate organism is an institution resembling the state. It represents fundamentally a relation of dominance and subordination, i.e., of government and governed.²²⁸

If the ‘animal’ organism and ‘social’ organism were subject to the same dynamics and laws – gradients, integration, dominance and subordination — then, as Ritter and Scripps had argued years before, biology had to be seen as the true foundation of sociology. In other words, sociological disciplines had to be based on what Child dubbed “sociological biology”.²²⁹ Child used the work of his younger colleague in Chicago, the ecologist and activist W. C. Allee (1885-1955) to prove the consistency of the analogy between organism and society. Allee had studied diverse phenomena of animal aggregations and, with Espinas and Kropotkin, had concluded that cooperation, not competition, dominated the evolution and behaviour of animal communities (including humans) — a belief that that eventually brought him to support some pacifist and socialist options during and between the two world wars.²³⁰

²²⁸ Ibid., p. 270.

²²⁹ As Child effectively said: “It appears to the biologist that the attempts so often made by sociologists to define and consider social problems in terms of man alone are responsible for at least certain features of the vagueness, uncertainty and difference of opinion, particularly as regards social origins...If man is a product of evolution, the foundations of human society lie, not in the human race, but in other organisms. It is certain that human society represents the highest order or plane of integration on our planet. If man is a part of organic nature it appears a difficult and uncertain task to attempt to interpret this highest order of integration without attempting to determine the relation between it and the lower and simpler orders of integration on which it must be in part based”(Child, 1924, pp. 267-268).

²³⁰ The Frenchman, Alfred Espinas (1844-1922), a pupil of Comte and scholar of Spencer, had published in 1878, *Des Société Animales*. The more famous Peter Kropotkin (1842-1921), a Russian thinker and anarchist, had published the celebrated *Mutual Aid: A Factor in Evolution in 1902*. In stressing the importance of cooperation in evolution, both books had an important influence on the Chicago crowd (see Mitman, 1992). For a biographical sketch of Allee see Schmidt, 1957.



Fig. 6.13, W. C. Allee (1885-1955)²³¹

Although Child did not share Allee's optimism about animal and human cooperation, he embraced Allee's understanding of the relations between biology, ecology and its bearings on human society. In particular, he embraced the idea that the behaviour of an individual organism could depend on its dynamic relation with the whole group. Furthermore, the reciprocal adjustment, instinctive or intelligent, of each member to the needs of the community made social integration possible. Just as single cells were united and integrated in a unique whole (what Child called "organismic integration"), the single animals were integrated in social wholes (namely, "social integration"). However, to Child, social integration was not something given or primordial, it was something built according to specific rules and laws; it was a product of organic and social evolution. Just as in the simplest forms organismic integration is partial and limited, the social integration in primitive societies – tribes or clans – is very unstable and variable.²³² Now, higher organic forms demonstrated a progress, advancement, an evolution toward integration: the dominant region better controlled subordinate regions so that cellular order followed an axiate pattern. Likewise, from primitive societies to modern states, better forms of social organization developed – forms assuring better types of integration; namely, better types of dominance and power upon the behaviour of subordinated individuals. From anarchy to monarchy, from oligarchy to democracy, dominance progressively changed. In modern democratic societies, Child explained: "...the state possesses social

²³¹ Source :Mitman, 1992.

²³² In other words, just as in Hydra or *Planaria*, each part or cell can reproduce the whole, in clan or tribe each member could establish new groups. To Child indeed, integration meant a hierarchical order where the subordinated parts (governed) are tied to the dominant part (governors).

polarity and may be termed an axiate social pattern, with government representing the dominant region and the various classes and differentiations of its members in relation to the government the subordinate regions of various levels of the axis.”²³³

In fact, with Ritter, Child’s organicism was not supporting a totalitarian regime. He believed that communism or any totalitarian form of organization was only a primitive phase toward better stages of social integration:

The progress of evolution then has apparently not been toward a socialistic or communistic form of integration. On the contrary, those types of integration which approach communism most closely, *e.g.*, the colonial animals such as the sponges, hydroids, etc. and the multiaxial plants have been left far behind in the course of evolutionary progress and such success as they have attained appears to be due to the fact that they are not strictly communistic but possess some degree of autocratic or oligarchic dominance.²³⁴

Organic evolution proved that the best type of physiological integration relied on a certain kind of democratic organization, *i.e.*, “...to the progress of the organism toward a democracy with representative government vested in deliberative organ connected through various centers with all parts of the body and in touch with the external world through the sense organs.”²³⁵ To Child indeed, the vertebrate body was not an autocracy of cells, but a democracy of organs conspiring for the welfare of the whole. In other words, the doctrine of the organism as a whole supported democracy because it represented the fittest and most successful form of organic and social integration so far developed. In sum, with Ritter and Scripps, Child concluded that after billions of years the whole evolutionary process proved, both in the organic and social world, that democracy represented the best type of organization – an organization based on American values.

A state based on social hierarchies was therefore not interpreted as a despotic organisation run by absolute power and dominance, but as a form of harmonic order run by a representative government.

²³³ Child, 1924, p. 288.

²³⁴ *Ibid.*, p. 297.

²³⁵ *Ibid.*, p. 297.

The subordinated classes were dominated because they wanted to be. Indeed, in a democratic state, dominance (power) comes not from a particular person or privileged group, but from an idea: the idea of nation or state. In other words, the individual is subordinated to an idea guiding the whole community. He is profoundly influenced by the community's values and ideas; all his actions, needs, and activities are essentially shaped by it because, what really makes a person is not his heredity, his germ plasm or genes, but his social relations: "...it is sufficiently obvious that the human individual is not simply the product of heredity. His social relations, or more specifically, his subordination in some way and in some degree to more or less definite ideas play a fundamental part in determining the course of his thought, his sentiments and his behavior."²³⁶ This is precisely what Ritter was trying to demonstrate at Scripps with his project on child development, i.e., the individual was essentially the product of his social environment and not merely a biological outcome of his parents.

Although belonging to two different institutions, Ritter and Child shared the same goals and projects. They were both against Weismann's doctrine and Mendelian biology, believing that these doctrines supported a wrong and dangerous social and political program, eugenics. Furthermore, they both endorsed organismal research programs — programs that guided their observations, drove their experimental interpretations, and inspired their alternative views on heredity. In sum, they were both innovative neo-Kantians who strived against neo-Darwinian philosophies and supported a bio-synthesis aiming to reconstruct biological sciences on new foundations — a synthesis having important social and political consequences. And while Ritter deemed Child part of his Scripps' enterprise, using and incorporating his findings and ideas within his bold project, Child benefited hugely from the philosophical and scientific discussions he had with Ritter.²³⁷ In the light of all that, it is not surprising that they were very good friends.

²³⁶ Ibid., p. 287. And yet: "According to the biological viewpoint, each human being is what he is because of present and past relations to environment of his protoplasm and the protoplasm from which it has arisen" (Child, 1924, p. 286).

²³⁷ Notwithstanding all the research facilities that Ritter provided to Child at Scripps association.

7.0: Whatever Happened to Organismic Philosophies?

First there is a speck which moves about, a thread growing and taking colour, flesh being formed, a beak, wing-tips, eyes, feet, coming into view, a yellowish substance which unwinds and turns into intestines—and you have a living creature. This creature stirs, moves about, makes a noise—I can hear it cheeping through the shell—it takes on a downy covering, it can see. The weight of its wagging head keeps on banging the beak against the inner wall of its prison. Now the wall is breached and the bird emerges, walks, flies, feels pain, runs away, comes back again, complains, suffers, loves, desires, enjoys, it experiences all your affections and does all the things you do. And will you maintain with Descartes, that it is an imitating machine pure and simple?¹

D. Diderot

Is an organism a mechanism? If organisms are just assembles of the molecular product of their genes, then there is a good case to be made that, despite their extreme complexity, they are basically molecular machines. This tends to be the view of organisms from the molecular perspective, which sees organisms as the result of a genetic program that specifies where, when and what genes are active in a developing organism and so determines all of its properties. However, we have seen that molecular composition is not sufficient to specify either properties such as the dynamic patterns of excitable media or the forms of organisms which emerge from these patterns. This requires that we understand also the relational order between molecular constituents, the way they are organized in space and interact with one another in time, which requires a description in terms of fields and their properties.²

B. Goodwin

¹ Diderot, 1976, p. 158. *Le Rêve de d'Alembert*, written in 1769, but published for the first time in 1830, nearly 40 years after Diderot's death. See P. N Furbank, 1992, *Diderot: A Critical Biography*, A. A. Knopf, New York.

² Goodwin, 1994, p. 182.

Through all these chapters we have seen that a small international community of scientists were committed to formulating an anti-mechanist, anti-reductionist, holist biology.³ We have learned that their approach and ideas were not a result of a new paradigm emerging in the 20th century, but of a complex reformulation or re-appropriation of an old tradition: a tradition having its original source in Kant and the subsequent Romantic tradition. We have also found that this tradition, as transplanted and translated in England and the US, acquired a specific and contingent political meaning and force. The notion of the organism, as an irreducible system of interdependent causes and effects, worked as a powerful political metaphor which could inspire a more equitable, harmonious, and efficient society. At the same time, mechanist and reductionist approaches, exemplified in Mendelism and Weismannism, came to be associated with capitalist ideology, and a conception of society as composed of an aggregate of selfish individuals in constant competition.

At its height, the neo-Kantian bio-philosophical tradition reconstructed here commanded the allegiances of some outstanding scientists working at prestigious institutions. But it is a tradition in need of reconstruction precisely because it subsequently went into decline, experiencing only partial and periodic revivals thereafter. By way of conclusion, I want first of all to sketch this later history of the decline and re-emergence of organismal biologies. Then I shall offer some meta-historical remarks aiming to make a general case for the kind of historical generalisations that have informed my own attempt at reconstructive narrative. Finally I will end with a few comments on the notions of reductionism, mechanism, materialism, and organicism as they emerge from this narrative, and the lessons for present-day philosophical debates on these 'isms'.

³ Although, as we have seen, there were diverse meanings of mechanism. Woodger himself distinguished between two kinds of mechanist conceptions: ontological mechanism, i.e. biologists stating that organisms are actually machines; and methodological mechanism: biologists who think that, whatever organisms may be, they can be investigated *as if* they were machines. These differences reflected real positions expressed by several scholars analysed by Woodger. Accordingly, there are several meanings of reductionism, materialism and holism. See Woodger, 1929, *BP*, p. 229.

7.1: The Organism is Dead, Long Live the Organism!

Probably one of the most interesting and eloquent examples of the tradition's decline is the Scripps Biology Association. Already from 1912, when the Scripps Institute officially became part of the University of California, Berkeley, things began to change. From that time, the unconventional agenda of the Institution – its emphasis on the organism as a whole, its social and political program based on scientific advice, its eccentric educational plans – came under fire from the University of California faculty. B. Kovarik describes how Scripps himself reacted against academic obstructions and criticism, accusing the academics of destroying his creation. In writing to Ritter in 1915 he complained that "...a bunch of wooden-headed visionless university men...burned down our temple to roast a little pig."⁴ Even though Ritter was able to maintain a certain 'unconventionality' during his directorship, after his retirement in 1923, the Scripps Oceanography Institution became a more 'conventional' place; the strong emphasis on organismal biology which had characterised the Institution during its early years faded away.

Things went similarly in Chicago. Gregg Mitman has shown how, after the retirements of Lillie, Child and all the old guard, and especially after the World War II, organismic biology, with its emphasis on cooperation, self-organisation and openness to Lamarckism, became politically uncomfortable, and therefore lost popularity among younger biologists. Regarding ecological sciences, Mitman noted that "...the organicist, cooperative renditions of nature that were the hallmark of Chicago ecology became increasingly difficult to sustain in the political climate of the cold war period in which group conflict and competition were seen as essential to a pluralistic, democratic society. A new ideological foundation for biological humanism was in order."⁵

Furthermore, the disturbing similarities between organismic philosophical views about heredity and Lysenko's theory of environmentally acquired characters did not help the Kantian cause. In fact, the harsh critiques that had been moved against Mendelian genetics before the Second World War could no longer be reiterated: they were dangerously similar to what Lysenko was saying.⁶ In the UK, as in the US,

⁴ Quoted in B. Kovarik, 2001, p. 78.

⁵ Mitman, 1992, p. 144.

⁶ The stunning similarities between Lysenko's and Child's, Ritter's or Haldane's conception of heredity and the organism appear evident while reading Lysenko's *Heredity and its Variability*: "We, on studying heredity, ascertain

the decline of organismic biology was certainly related the political threat raised by Lysenko, even though some British biologists did not take a definite position against Lysenkoism.⁷ But probably there were other important threats coming from within science itself. Morgan's chromosome theory of heredity had been extremely successful and, after the 1930s, it was widely accepted in the scientific community. With the decisive contributions of Morgan's ambitious students at Columbia University – figures such as A. Sturtevant, C. Bridges, and H. J. Muller, and then T. Dobzhansky – their views on the way that heredity should be studied overshadowed other approaches and methods. Heredity was now successfully defined in terms of genetics. In addition, the triumph of genetics opened the door wide for research on the physical basis of heredity, culminating with Watson and Crick's discovery of DNA's double-helical structure in 1953. The trend toward the molecularisation of the gene was unfavourable to organismic ideas. As the developmental biologist Brian Goodwin, quoted at the outset, observed in 1994: 'Organisms, those familiar plants and animals, including ourselves, that we see all about us, as well as the many invisible forms such as bacteria and other microbes, have disappeared as the fundamental units of life. In their place we now have genes, which have taken over all the basic properties that used to characterize living organisms'.⁸ The triumph of molecular biology after the Second World War left little space for the organismal conception of biology.⁹

A further reason for the decline must be mentioned: the influential and persuasive views of the advocates and followers of the modern evolutionary synthesis. After the 1930s, the claim that evolutionary novelties could be linked to small, chance genetic mutations, adaptively and gradually accumulated by natural selection, acquired extraordinary force. To some, Mendelian genetics combined with Darwinian evolution seemed to explain all that biology had to explain. Although the modern

the conditions of life, the conditions of development, required by the organism or by separate processes, and also the relation of the organism or separate processes of it to various environmental conditions. We thus arrive at a comprehension of the essence of heredity. The geneticists, on the other hand, do not study the essence of heredity. All they find out is how many offspring resemble the one parent with regard to a particular character and home many the other"(Lysenko, 1951, p. 11). And yet: " The development of an organism, like its growth, proceeds by means of conversion, of metabolism. The sex cells, buds or eyes from which usually entire organisms develop are, as a rule, the product of the development of the whole organism which gave rise to the particular initial basis for the new organisms. They arise and build themselves out of molecules, granules of substances – transformed many times (Lysenko, 1951, p. 21). As should be evident after reading this dissertation, Lysenko was not original in what he was arguing.

⁷ Woodger, Waddington and J. B. S. Haldane for example.

⁸ Goodwin, 1994, p. 1.

⁹ See Morange, 2000.

synthesis was just one element within a much wider, complex, articulated and interesting context,¹⁰ it cannot be denied that Darwinian evolutionary thought, with its gradualist and populationist emphasis, was at home with the emerging paradigm of molecular biology. In other words, a certain popular narrative of the modern synthesis, as had been diffused by Huxley or Dobzhansky for example, was quite consistent with newly emerging and successful disciplines such as molecular biology and biochemistry.¹¹ Most of the organismal biologists would never have accepted the philosophical basis of these disciplines, just as they had never accepted Weismann's neo-Darwinism, but everything was against their principles. After the Second World War, the metaphor of the organism as applied to society was tainted with the flavour of socialist or fascist totalitarianism; the West's campaign against Lysenko's biology and all the political suspects that Lamarckian doctrines inspired largely prevented any sympathy for organismic conceptions. The triumph of new disciplines (especially genetics, biochemistry and molecular biology) based on epistemic attitudes in total contradiction with holistic views undermined the foundations of organismal biology.

Nevertheless, organismic biology survived, and the neo-Kantian bio-philosophy is still among us, albeit in new guises. Indeed, a few individuals continued to support forms of organismic biology after the Second World War. Woodger lived until 1981, but he died quite unknown and with no influential pupils or school. Others tried to adapt more-or-less holistic views to Mendelian genetics. In the 1950s and 60s figures such as C. H. Waddington or L. von Bertalanffy, with their epigenetic and systemic thinking, revived some of the ideas that had characterised the old neo-Kantian school. However, and notwithstanding their authority and influence, they had no relevant impact, and stimulated no change within the scientific world. Arguably, it was only during the late 1970s that there gradually emerged a new sympathy towards organismic themes. A former pupil of Dobzhansky's, the evolutionary geneticist Richard Lewontin, began publishing articles and books challenging, and then arguing vociferously against, gene-centric views and approaches to biology and evolution.¹² During the 1980s and 1990s, biologists such as E. F. Keller, J. Sapp, S. F. Gilbert, B. Goodwin and others began to re-introduce

¹⁰ As J. Cain has recently shown. See Cain, 2009.

¹¹ Of course, there are exceptions.

¹² See Lewontin, 1983; Lewontin, S. Rose, L. J. Kamin, 1984; R. Lewontin and R. Levinas, 1985; Lewontin, 1991; 2000.

organismic discourses.¹³ Cumulatively, these have had an impact. At the end of the 1990s, even so orthodox a molecular biologist as W. Gelbart could write in *Science* that:

For biological research, the 20th century has arguably been the century of the gene. The central importance of the gene as a unit of inheritance and function has been crucial to our present understanding of many biological phenomena. Nonetheless, we may well have come to the point where the use of the term 'gene' is of limited value and might in fact be a hindrance to our understanding of the genome. Although this may sound heretical, especially coming from a card-carrying geneticist, it reflects the fact that, unlike chromosomes, genes are not physical objects but are merely concepts that have acquired a great deal of historic baggage over the past decades.¹⁴

Might the protagonists of the story told in this dissertation turn out to be pioneers, precursors and originators of a new 'way of seeing' emerging in biology today? Or will they remain seen as mere exponents of a deceased, outmoded tradition, having only historical interest? As ever with biology, one awaits developments with the greatest interest.

7.2: Meta-Historical Reflections

Turning now from the present and future more squarely to the past: History seems always to teach us that for any generalisation there are exceptions, contradictions and peculiarities. Finding a 'coherent' narrative can sometimes be problematic and challenging, even when, as here, the focus is on only eight individuals – in this case, a small sample of biologists sharing some ideas, notwithstanding different periods, contexts and disciplines. For my part, however, I do not consider 'deviant' cases or possible exceptions as counter-arguments to my narrative because I concerned myself with a well-defined historical trend, not a logical or necessary system of beliefs. Being neo-Kantian did not necessarily imply the questioning of Weismann's biology or Mendelian genetics; it represented only a sufficient motive for that questioning. Yes, organismal biologists could indeed, sometimes, accept Weismann's biology; they could endorse, in

¹³ Keller, 2000; 2002; 2010.

¹⁴ Gelbart, 1998, 659-661.

some respects, Mendelian genetics (as did figures such as C.H. Waddington, R. Goldschmidt and A. Kuhn, though with their own reservations). Even so, assertions about what the neo-Kantian bio-philosophical tradition generally stood for are worth making. To do otherwise is to surrender to what might be called the rhetoric of complexity ('it is always more complicated than that'), and so to be overcome by the irreducible proliferation of particulars and unique cases.

But let me, for argument's sake, briefly consider an ungenerous response. Does not the label 'neo-Kantian tradition' — a hypothetical critic might suggest — hide essential differences, veil conflicting perspectives, and conceal individual disagreements? Warming to her theme, my imagined critic might go on to argue that there was never any such thing as a neo-Kantian tradition. There were only ever some overlapping similarities and individual stories. And anyway, any attempt to propose historical 'categories' of this kind means going back to the outmoded, superficial and, in historiographic terms, palaeolithic 'history of ideas'.

My perspective is rather different. As I understand them, historical categories, labels and generalisations should not be regarded as static ontological types, but as heuristic tools, methodological instruments, provisional devices helping the historian to understand or interpret some apparently confused happenings, to order and classify facts, to comprehend specific actions and choices taken by diverse actors in different contexts. E. H. Carr used to say that history "... thrives on generalizations".¹⁵ My position is more modest: if we deny the possibility of making some meaningful generalisations, history risks becoming a collection of anecdotes and facts interesting only to a few academics and niche experts — a box of disconnected and confused tales in which stories of the most insignificant individuals assume an undeserved relevance. This dissertation, for better or worse, has attempted to tackle big issues, to investigate large questions through a coherent narrative, examining the arguments, opinions and lives of a handful of first-rank 20th-century biologists who denied some of the most widely accepted scientific beliefs of their time. My intention has been to provide the intellectual framework and historical scaffolding through which old and forgotten discussions, disputes and discourses can emerge and find significance for the contemporary reader; in other words, my principal aim was to give voice to forgotten

¹⁵ Carr, 1961, p. 58.

protagonists of the last century who proposed very controversial arguments about the nature of living phenomena — arguments still controversial today.

A final observation under this heading. In his 2005 paper “Other Histories, Other Biologies,” Gregory Radick posed two important questions about biological science. “Would quite different histories have produced roughly the same science? Or, on the contrary, would different histories have produced other, quite different biologies?”¹⁶ In the light of the history of the neo-Kantian bio-philosophical tradition, I would incline to answer yes to the second question. In all probability, if the organismal biologists of the late 19th and early 20th centuries had succeeded, a different biology would have been developed – a biology where the heroes would have been neither Weismann and Mendel, nor Bateson and Morgan but Wolff, Kant, Blumenbach, von Baer, Goethe, Cuvier, Barry, and Owen, followed by such 20th-century figures as Whitman, Child, Russell, D’Arcy Thompson and many other I have mentioned throughout this dissertation.

7.3: Philosophical Reflections (Against ‘Isms’)

For all that historical generalisation sometimes does not go far enough, philosophical generalisation sometimes goes too far. A striking feature of the story of the neo-Kantian bio-philosophical tradition in the late 19th and early 20th centuries is the extent to which a number of familiar ‘isms’ – notably reductionism, mechanism, materialism and organicism – emerge as highly context dependent. They belong not to a transcendent realm of abstract reflection (once memorably parodied as ‘the great seminar room in the sky’), but to discursive or scientific practices that particular biologists and other thinkers negotiate during specific times. One might even say that the meanings of each of these notions always involved and included disciplinary as well as institutional interests: political and philosophical assumptions; scientific practices; experimental results; organisms employed or deployed to support various stances. A question that needs asking, then, is: does it make any sense to analyse such notions outside of what scientists actually do and think – apart, that is, from contingent practices and specific

¹⁶ Radick, 2005, p. 21. On counterfactuals history see the ‘Focus’ section in *ISIS*, vol. 9, n. 3, 2008.

intellectual scientific traditions? I suspect the answer is no, and that there can be no definition of mechanism, reductionism, materialism or organicism outside of their historical formulation.

This conclusion in favour of historical specificity gains strength from a look at the handling of these concepts within contemporary analytic philosophy. To take an entirely typical example, R. H. Jones argues in his *Reductionism: Analysis and the Fullness of Reality* (2000) that there are five types of reductionism – in his terms, Substantive, Structural, Theoretical, Conceptual and Methodological – and four types of antireductionism – Substantive, Structural, Theoretical and Conceptual. Obviously, to Jones, these are not convictions maintained by flesh-and-blood scientists but disembodied philosophical stances put in a logical and neutral space where they interact, confront and dance in different ways: the theoretical antireductionism agrees with the structural one, the conceptual antireductionist may, sometime, agree (but also disagree) with the substantive and theoretical reductionist, even though the theoretical reductionist may squabble with the substantive reductionist... In sum, the concepts examined are invented figures like those of the dramatists – the theatrical figures that often symbolise concepts like greed, dissoluteness or goodness but do not refer to any real individual. Jones' concepts alas are in a much sorrier state. They do not speak either for the scientists or for the dramatists, but only for a few creative philosophers interested in such devices.

The historical approach I have used instead shows that such a rhetorical strategy is, at best, ineffective or empty. There is no clarification of what reductionism or antireductionism is outside of scientific practices and outside of the specific uses, times and places where these notions first emerged. Analysing general stances, whether as ideas, concepts, arguments or statements, and pretending that these positions could, in principle, correspond to specific real-life thinkers is a delusive technique. The problem indeed is not with the generalisations or abstractions themselves – that is, with simplified stances aiming to abridge and synthesise possible positions in order to frame clearer arguments. The problem arises from the specific *modality* of generalisation and abstraction. For it is one thing to generalise about a trend, a school, a tradition or a group of thinkers, and quite another thing to generalise about more or less consistent notions or concepts. In the first case, a generalisation or abstraction would be *testable*; it is an inductive generalisation about concrete cases that could be either reliable and convincing or baseless and unsupported by the evidence. In the second case – in the case of an abstraction of Jones' kind – success or

failure is ultimately a matter of philosophical tastes, informed (if that is the right word) by ‘intuition’ or ‘common sense’ about what a coherent position on reductionism or holism would look like.¹⁷ There is no way out. In a philosophical debate so disconnected from the life of scientific reason as actually pursued, to explain or understand notions such as reductionism or holism (or ‘isms’ in general) is like explaining or understanding what Protestantism is without mentioning the 16th-century Christian schism.

This dissertation began with the 1931 philosophico-scientific reflections of J. S. Haldane. Let me in closing turn to his son, the equally distinguished biologist J. B. S. Haldane. Around the same time, the latter explained his wariness toward the unhelpful scholasticism that, in his day too, academic philosophy represented:

...some of my biological readers will doubtless object that it is unscientific to describe animal and human behaviour in terms of mind. We should always try to explain it (they will say) on physico-chemical lines. *This objection seems to me to savour of philosophy rather than science.* As a scientist I am engaged in an attempt to unify my experience, and will describe A in terms of B, or B in terms of A, as it suits my convenience. The idealist wants me always to describe matter in terms of mind, the materialist makes the opposite demand. Now in plane geometry I use point coordinates or line-coordinates as it suits me. Although on the whole the point is the simpler idea, it may suit my convenience to describe every point by specifying two lines which meet in it. The idealists, to speak metaphorically, would like me always to do this: the materialists would forbid it. Personally I find geometry difficult enough to excuse my employing any coordinate system I choose. So with biology.¹⁸

Closer to the present, we find, among thoughtful biologists, similar views. The developmental-evolutionary biologist J. T. Bonner confessed: “What is utterly baffling to me is why one cannot be a *reductionist* and a *holist* at the same time.”¹⁹ Bonner’s sense of holding a position not well captured by that dichotomy of isms reflects precisely what the protagonists of the story of the neo-Kantian bio-

¹⁷ For a general introduction to the reductionist and holist debate, see Beckner, 1959, Ayala and Dobzhansky, 1974; Beckermann, Flohr and Kim, 1992; Brandon, 1996; Gilbert and Sarkar, 2000; des Chene 2001; Andersen, 2001; Delehanty 2005.

¹⁸ J.B.S Haldane, 1929

¹⁹ See Bonner, 1988, p. IX.

philosophical tradition intended with their understanding of biology – a science which needs both reductionism and holism.

Philosophers seeking to understand science should never lose touch with scientific practice, because it is there that notions such as reductionism, materialism, mechanism and holism first emerged and there that they are framed. Talking about holism and reductionism without mentioning, for instance, Child's struggles to understand how pieces of *Planaria* or tubularia were able to organise themselves to form functional wholes, or J. S. Haldane's attempts to understand breathing's complex regulation, or Lillie's efforts to figure out how the development of the invertebrate eggs works, or Spemann's attempts to shed light on the regulation of cells in tissue transplantations (to name only a few examples from this dissertation), hardly advances our understanding of these philosophical categories. For these purposes, the history of science can be seen an inexhaustible source of inspiration for improving our acquaintance with some of the most enduring, and still pressing, philosophical issues.

Bibliography

Manuscript Sources

William Emerson Ritter Papers, Scripps Institution of Oceanography, Historical Archives, University of California, San Diego, La Jolla, CA, USA

William Emerson Ritter Papers, Bancroft Library, University of California, Berkeley, CA, USA

Frank Rattray Lillie Papers, Woods Hole Oceanographic Institution, Historical Archives, MA, USA.

John Henry Woodger Papers, University College London, Special Collections, UK

Printed sources

Abir-Am, P., 1987, 'The Biotheoretical Gathering, Trans-Disciplinary Authority and the Incipient Legitimizing of Molecular Biology in the 1930s: New Perspective on the Historical Sociology of Science', *Hist. Sci.* 25 (67 pt 1):1-70

Agar, W. E., 1936. 'Whitehead's Philosophy of Organism an Introduction for Biologists'. *The Quarterly Review of Biology*, Vol. 11, No. 1: 16-34

Allen, G. E., 1967, 'J. S. Haldane: The Development of the Idea of Control Mechanisms in Respiration', *Journal of the History of Medicine*, Vol. XXII, pp. 392-412

Allen, G. E., 1975, *Life Science in the Twentieth Century*, Wiley, New York

Allen, E. G., 1978, *Thomas Hunt Morgan: The Man and His Science*, Princeton University Press

Allen, G. E., 1985b, 'Heredity under an Embryological Paradigm: The case of genetics and Embryology', *Biol. Bull.* 168, pp. 107-121

Allen, G. E., 1985, 'T.H. Morgan and the split between embryology and genetics, 1910-1935', in T.J. Horder, J.A. Witkowski and C.C. Wylie (eds), *A History of Embryology*, N.Y., Cambridge University Press, pp. 113-146

Allen, G. E., 2005, 'Mechanism, Vitalism and Organicism in Late Nineteenth and Twentieth-Century Biology: the Importance of Historical Context', *Studies in History and Philosophy of Science Part C, Studies in History and Philosophy of Biological and Biomedical Sciences*, Vol. 36, Issue 2, pp. 261–283

Amundson, R., 2005, *The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo*, Cambridge University Press

Andersen, H., 2001, 'The History of Reductionism versus Holistic Approaches to Scientific Research', *Endeavour*, Vol. 25, N. 4

Ashton, R., 1980, *The German Idea: Four English Writers and the Reception of German Thought 1800-1860*, Cambridge University Press

Ayala, F.J. and Dobzhansky, T., 1974, *Studies in the Philosophy of Biology. Reductionism and Related Problems*, University of California Press, Berkeley

Barzun, J., 1937, *Race: a Study in Modern Superstition*, Methuen & Co. Ltd

- Beckner M., 1959, *The Biological Way of Thought*, University of California Press
- Beckner M., 1969, Organismic Biology, in "Encyclopedia of Philosophy" ed. Paul Edwards, MacMillan Publishing & CO.
- Beckermann, A., Flohr, H. and Kim, J., 1992, *Emergence or Reduction? Essays on the Prospects of Nonreductive Physicalism*, Berlin, De Gruyter.
- Beiser F. C., 2002, *German Idealism: The Struggle Against Subjectivism 1781-1801*, Harvard University Press
- Beiser, F., 2006, 'Kant and Naturphilosophie', in *The Kant Legacy in the Nineteenth-Century Science*, Ed. M. Friedman & A. Nordmann, The MIT Press, USA
- Ben-David J. and T. A. Sullivan, 1975, 'Sociology of Science', *Annu. Rev. Sociol.* 1: 203-222
- Benson, K. R., 1988, 'Why American Marine Stations?: The Teaching Argument', *American Zoologist*, Vol. 28, No. 1, pp. 7-14
- Bergson, H., 1907, *L'Évolution Créatrice*, Paris, Les Presses universitaires de France
- Bernard C., 1984, *Introduction a L'Etude de la Médecine Expérimentale*, Flammarion, Paris,
- Blackman, H., 2003, 'A spiritual leader? Cambridge zoology, mountaineering and the death of F.M. Balfour', *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical sciences* Vol. 35, Issue 1, pp. 93-117
- Blanchard, R., 1898, 'Notices biographiques: Rodolphe Leuckart', in *Archives de parasitologie*, 1 :185-190
- Bonner, J. T., 1988, *The Evolution of Complexity by Means of Natural Selection*, Princeton University Press, Princeton
- Bowler, P. J., 1989, *The Mendelian Revolution: The Emergence of Hereditarian Concepts in Modern Science and Society*, Continuum International Publishing Group, Athlone.
- Bowler, P. J., 2001, *Reconciling Science and Religion. The Debate in Early-Twentieth-Century Britain*, University of Chicago Press, Chicago
- Brachet, A., 1917, *L'Œuf et les Facteurs de L'Ontogenèse*, G. Doin et Cie, Paris
- Brauckmann, S., 2003, 'The Scientific Life of Paul A. Weiss (1898-1989)', *Mendel Newsletter*, 12, pp. 2-7
- Brandon, R. 1996, 'Reductionism versus holism versus mechanis', in *Concepts and Methods in Evolutionary Biology*, Cambridge University Press, pp. 179-204
- Burian R., 2005, *The Epistemologies of Development, Evolution, and Genetics*, Cambridge University Press, Cambridge
- Butts, R. E., 1990, 'Teleology and Scientific Method in Kant's Critique of Judgment', *Nous*, Vol. 24, No. 1 pp. 1-16
- Burroughs, J., 1901, *Far and Near: The Writings of John Burroughs Part Thirteen*, Riverby, 2004

- Byrnes, W. M., 2009, 'Ernest Everett Just, Johannes Holtfreter, and the Origin of Certain Concepts in Embryo Morphogenesis', *Mol. Reprod. Dev.* Vol. 76, pp. 912-921
- Cain J., 2000, 'Woodger, Positivism and evolutionary Synthesis', Vol. 15, N. 4, pp. 535-551
- Cain, J., 2009, 'Rethinking the Synthesis Period in Evolutionary Studies', *Journal of the History of Biology*, 42:621-648
- Carr, E. H., 1963, *What is History: The George Macaulay Trevelyan Lectures Delivered in the University of Cambridge January-March 1961*, Penguin Books
- Child, C. M., 1906 'Some Considerations Regarding So-Called Formative Substances', *Biological Bulletin*, Vol. 11, No. 4
- Child, C. M., 1911, 'Studies on the Dynamics of Morphogenesis and Inheritance in Experimental Reproduction. 1. The Axial Gradient in *Planaria dorocephala* as a Limiting Factor in Regulation', *Journal of Experimental Zoology*, Vol. 13, Issue 1, pp. 103-152
- Child, C. M., 1912 'Certain Dynamic Factors in Experimental Reproduction and their significance for the Problem of Reproduction and Development', *Journal of Experimental Zoology*, Vol. 35, N. 4, pp. 598-641
- Child C. M., 1912b, 'The Process of Reproduction in Organisms', *Biological Bulletin*, Vol.23, No.1
- Child 1913, 'Studies On the Dynamic of Morphogenesis and Inheritance in Experimental Reproduction. VI. The Nature of the Axial Gradients in *Planaria* and their Relation to Antero-Posterior Dominance, Polarity and Symmetry', *Journal of Experimental Zoology*, Vol. 37, N. 1, pp. 108-158
- Child, C. M., 1915, *Senescence and Rejuvenescence*, University of Chicago Press, Chicago
- Child C. M., 1915b, *Individuality in Organisms*, University of Chicago Press, Chicago
- Child C. M., 1921, *The Origin and Development of the Nervous System from a Physiological Viewpoint*, The University of Chicago Press.
- Child, C. M., 1924, *Physiological Foundations of Behavior*, Henry Holt & Co, New York
- Child C. M., 1946, 'Biographical Memoir of Francis Bertody Sumner', 1874-1945, *National Academy of Science*, Washington
- Churchill, F. B., 1969, 'From Machine-Theory to Entelechy: Two Studies in Developmental Teleology', *Journal of the History of Biology*, Vol. 2, N. 1, pp. 165-185
- Churchill F. B., 1974, 'William Johannsen and the Genotype Concept', *Journal of the History of Biology*, Vol. 7, N. 1., pp. 5-30
- Cobb, M., 2006, 'Heredity before Genetics: A History', *Nature*, Vol. 7, pp. 995-997
- Cohen, D. R., 2006, 'Living Precisely in the Fin-de-Siècle Vienna', *Journal of the History of Biology*, 39(3): 493-532
- Coleman, W., 1971, *Biology in the Nineteenth Century: Problems of Form, Function and Transformation*, Cambridge University Press
- Conklin, E G., 1908, 'The Mechanism of Heredity', *Science*, Vol. 27. no. 681, pp. 89 – 99

- D'Arcy W. Thompson, R., 1958, *D'Arcy Wentworth Thompson, The scholar-Naturalist, 1860-1948*, Oxford University Press
- D'Arcy W. Thompson, 1884, 'The Regeneration of Lost Parts in Animals', *Mind*, Vol. 9, No. 35, p. 419
- D'Arcy W. Thompson, 1942, *On Growth and Form*, Cambridge University Press
- D'Arcy W. Thompson, 1966, *On Growth and Form*, J. T. Bonner (editor), Cambridge University Press; Rei/Abridg edition
- Dawson V.(1987), *Nature's Enigma: The Problem of the Polyp in the Letters of Bonnet, Trembley, and Reaumur*, Amer Philosophical Society
- Delage, Y., 1903, *L'Hérédité et les Grandes Problèmes de la Biologie Générale*, 2nd Edition, Paris: Reinwald.
- Delehanty, M., 2005, 'Emergent Properties and the Context Objection to Reduction', *Biology and Philosophy*, 20:715–734
- Dembowski, J, 1926, 'Zur Kritik der Faktoren – und Chromosomenlehre', *Zts. Indukt. Abstamm. Vererbungslehre*, xli, pp. 216-147
- Desmond A., 1989, *The Politics of Evolution. Morphology, Medicine, and Reform in Radical London*, University of Chicago Press
- Des Chene, D. 2001, *Spirits and Clocks: Machine and Organism in Descartes*. Cornell University Press
- Diderot, 1976, *D'Alambert's Dream*, Penguin Classics
- Dinsmore C. E., (1991), *History of Regeneration Research: Milestones in the Evolution of a Science*, Cambridge University Press
- Drack, M., Apfalter, W., Pouvreau, D., 2007, 'On the Making of a System Theory of Life, Paul A. Weiss and Ludwig von Bertalanffy's Conceptual Connections', *Q. Rev. Biol.*, 82(4)
- Schwarz-Weig E, 2002, 'Science in a Constant Flow: Life and Work of Eduard Strasburger (1844-1912)', *German Botanical Society*, in <http://www.deutsche-botanische-gesellschaft.de>
- Ede A., 2007, *The Rise and Decline of Colloid Science in North America, 1900-1935: The Neglected Dimension*, Ashgate Publishing
- Edwards, C. L. 1911, 'The Vienna Institution for Experimental Biology', *The Popular Science Monthly*, Vol. 78, N. 37, pp. 584-601
- Emmett, D. M., 1932, *Whitehead's Philosophy of Organism*, London, MacMillan and Co.
- Enriques F.,1930, I Motivi dell Filosofia di Eugenio Rignano, *Scientia*, XXIV
- Evans, M. A. and Howard E., 1999, *William Morton Wheeler, Biologist*. New York: iUniverse
- Fantini, B, 1985, 'The Sea Urchin and the Fruit Fly: Cell Biology and Heredity, 1900-1910', *Biol. Bull.*: pp. 99-106
- Farley, J., 1982, *Gametes and Spores, Ideas about Sexual Reproduction: 1750-1914*, The Johns Hopkins University Press
- Foster M. and Balfour F. M., 1874, *The Elements of Embryology* , Macmillan and Co.

- Friedman, M. Nordmann, A., 2006, *The Kantian Legacy in Nineteenth-Century Science*, MIT Press, Cambridge, USA
- Furbank P. N., 1992, *Diderot: A Critical Biography*, Knopf, New York
- Gasking E.(1968), *Investigations into Generation*, John Hopkins University Press, Baltimore
- Geison, G. L., 1978, *Michael Foster and the Cambridge School of Physiology, The Scientific Enterprise in the late Victorian Society*, Princeton University Press, Princeton
- Gelbart W., 1998, 'Databases in genomic research', *Science*, Vol. 282 no. 5389, pp. 659-661
- Gilbert F. S., 1988, 'Cellular Politics: Ernest Everett Just, Richard B. Goldschmidt, and the attempt to Reconcile Embryology and Genetics', In *The American Development of Biology* (R. Rainger, K. R. Benson, and J. Maienschein, eds.) University of Pennsylvania Press, Philadelphia. pp. 311-346
- Gilbert, S. F., 1998, 'Bearing Crosses: The Historiography of Genetics and Embryology', *Amer. J. Med. Genet.* 76: 168 – 182
- Gilbert, S.F., and S. Sarkar, 2000, 'Embracing Complexity: Organicism for the 21st Century', *Developmental Dynamics*, Vol. 219, pp. 1–9
- Ginsborg, H., , 'Kant on Understanding Organisms as Natural Purposes' in *Kant and the Sciences*, ed. E. Watkins, pp. 231–59, 2001, Oxford University Press
- Gliboff, S., 2006, 'The Case of Paul Kammerer: Evolution and Experimentation in the Early 20th Century', *Journal of the History of Biology*, 39(3): 525-563
- Goodman, M., 2007, *Suffer and Survive*, Simon & Schuster, London
- Goodwin, B., 1994, *How the Leopard Changed Its Spots*, Princeton University Press
- Gould, S. J., 1971, 'D'Arcy Thompson and the Science of Form', *New. Literary. Hist.* 2: 229-258
- Gould S. J., 1977, *Ontogeny and Phylogeny*, Harvard University Press
- Gould S. J., 1983, 'Thwarted Genius', *The New York Review of books*, November 24
- Gould, S. J., 1985, *The Flamingo's Smile: Reflections in Natural History*, Norton & Company
- Gould, S. J. 2002, *The Structure of Evolutionary Theory*, Cambridge, Harvard University Press
- Graham, M., 1954, 'E. S. Russell 1887-1954', *ICES Journal of Marine Science*, Vol. 20, 2, pp. 135-139
- Gregg J. R. and Harris, F. T. C., 1964, *Form and Strategy in Science, Studies Dedicated to Joseph Henry Woodger on the Occasion of his Seventieth Birthday*, Reidel Publishing Company, Dordrecht
- Gregory, F., 1989, 'Kant's Influence on Natural Scientists in the German Romantic Period', in *New Trends in the History of Science*, ed. Robert P. W. Visser, Radopi, Amsterdam
- Grene M. G., Depew, D. J., 2004, *Philosophy of Biology: An Episodic History*, Cambridge University Press, Cambridge
- Guyer, P. 2001, 'Organisms and the Unity of Science'', in *Kant and the Sciences*, ed. E. Watkins, 2001, Oxford University Press, pp. 259–82

- Haldane J. S. and Haldane R. S., 1883, 'The Relation of Philosophy to Science', in A. Seth & R. S. Haldane, *Essays in Philosophical Criticism*, Burt Franklin, New York
- Haldane, J. S., 1884, 'Life and Mechanism', *Mind*, IX, No. 33
- Haldane, J. S., 1913, *Mechanism, Life and Personality. An Examination of the Mechanistic Theory of Life and Mind*, London, Murray
- Haldane, J. S., 1917, *Organism and Environment as Illustrated by the Physiology of Breathing*, Yale University Press
- Haldane, J. S., D'Arcy W. Thompson, Mitchell, P. C., Hobhouse, L. T., 1918, 'Symposium: Are Physical, Biological and Psychological Categories Irreducible?' *Proceeding of the Aristotelian Society: Supplementary Volumes*, Vol. 1, Life and Finite Individuality, London
- Haldane, J. S., 1919, *The New Physiology and Other Addresses*, London, C. Griffin
- Haldane J. S., 1921, *Respiration*, Yale University Press
- Haldane, J. S., 1931, *The Philosophical basis of Biology*, London, Hodder and Stoughton
- Haldane, J. S., 1932, *Materialism*, London, Hodder and Stoughton
- Haldane, J. S., 1935, *The Philosophy of a Biologist*, Clarendon Press
- Haldane, J. B. S., 1929, *The Causes of Evolution*, Longmans, Green & Co, London
- Hall, B. K., 1999, *Evolutionary Developmental Biology*, Kluwer Academic Publishers, Netherlands
- Hall, B. K., 2003, 'Francis Maitland Balfour (1851-1882): A founder of Evolutionary Embryology', *Journal of Experimental Zoology*, 299, pp. 3-8
- Hamburger, V., 1988, *The Heritage of Experimental Embryology, Hans Spemann and the Organizer*, Oxford University Press
- Hangstrom W. O., 1975, *The Scientific Community*, Southern Illinois University Press
- Haraway, D., 1976, *Crystals, Fabrics, and Fields*, Johns Hopkins University Press
- Harrington A., 1996, *Reenchanted Science. Holism in German Culture from Wilhelm II to Hitler*, Princeton University Press
- Harrison, R. G., 1937, 'Embryology and its Relations', *Science*, 85: 369-374
- Harwood, J., 2003, *Styles of Scientific Thought: The German Genetics Community, 1900-33*, University of Chicago Press, Chicago
- Hofstadter, R., 1963, *Anti-intellectualism in American Life*, New York, Random House
- Hoppe P. and U. Kutschera, 2010, 'In the shadow of Darwin: Anton de Bary's origin of myxomycetology and a molecular phylogeny of the plasmodial slime molds', *Theory Biosci.*, 129(1):15-23
- Hubner K., 1985, *Critique of Scientific Reason*, University of Chicago Press, Chicago
- Huneman P., 2006, 'From the Critique of Judgment to the Hermeneutics of Nature: Sketching the fate of philosophy of Nature after Kant', *Continental Philosophy Review*, Vol. 39, (1)

- Huneman, P., 2007, *Understanding Purpose, Kant and the Philosophy of Biology*, University of Rochester Press, Rochester
- Lurie, E. 1960. *Louis Agassiz: A Life in Science*. University of Chicago Press, Chicago
- Jardine, N., 1996, *Naturphilosophie and the Kingdoms of Nature*, In *Cultures of Natural History*, Ed. N. Jardine, J. Secord, and E. Sparry, Cambridge University Press, Cambridge
- Johannsen, W., 1909, *Elemente der exakten Erblichkeitslehre*, Gustav Fisher, Jena
- Johannsen W., 1911, 'The Genotype Conception of Heredity', *American Naturalist* 45, pp. 129-159
- Johannsen, W., 1923, 'Some Remarks about Units in Heredity', *Hereditas*, 4: 133-141
- Jones R. H., 2000, *Reductionism: Analysis and the Fullness of Reality*, Bucknell University Press
- Just, E. E., 1932, 'On the Origins of Mutations', *American Naturalist*, 66 (1932): 61-74
- Just, E. E., 1933, 'Cortical Cytoplasm and Evolution', *American Naturalist*, 66: 22-29
- Just, E. E., 1936, 'A single theory for the physiology of development and genetics'. *Am. Nat. Suppl.*, 70, pp. 267-312
- Just, E. E., 1937, 'Phenomena of embryogenesis and their significance for a theory of development and heredity'. *Am. Nat.*, 71, pp. 97-112
- Just E. E., 1939, *The Biology of the Cell Surface*, The Technical Press, London
- Just, E. E., 1940 'Unsolved Problems of General Biology', *Physiological Zoology*, Vol. 13, No. 2, pp. 123-142
- Kant, I., 1914, *Kritik of Judgment, Translated with Introduction and notes of J. H. Bernard*, 2nd Ed., Rev., MacMillan, London
- Keller, E. F., 2000, *The Century of the Gene*. Harvard University Press
- Keller, E. F., 2002, *Making Sense of Life : Explaining Biological Development with Models, Metaphors, and Machines*. Harvard University Press
- Keller, E. F., 2010, *The Mirage of a Space between Nature and Nurture*. Duke University Press
- Kimball, G. K., 1953, 'D'Arcy Thompson: His Conception of the Living Body', *Philosophy of Science*, Vol. 20, N. 2
- Kitchen, P., 1975, *A Most Unsettling Person: An Introduction to the Ideas and Life of Patrick Geddes*, Gollancz, London
- Koestler, A., 1971, *The Case of the Midwife Toad*, Hutchinson, London
- Kohler, R. E., 2002, *Landscapes and Labscapes, Exploring the Lab-Field Border in Biology*, The University of Chicago Press
- Kolakowski L., 1985, *Bergson*, Oxford University Press
- Kovarik, B., 2001, *Revolution in Communications, Media History from Gutenberg to the Digital Age*, Continuum Publishing Corporation

- Larson, E. J., 1997, *Summer for the Gods: The Scopes Trial and America's Continuing Debate Over Science and Religion*, BasicBooks
- Le Gros Clark, Wilfred, and Peter Medawar, eds. *Essays on Growth and Form: Presented to D'arcy Wentworth Thompson*. Oxford: Clarendon, 1945
- Lecourt, D., 1977, *Proletarian Science?: The Case of Lysenko*, NLB, London
- Lenoir, T., 1982, *The Strategy of Life: Teleology and Mechanics in Nineteenth-Century German Biology*, University of Chicago Press, Chicago
- Lenoir, T., 1988, 'Kant, von Baer, and the causal-Historical Thinking in Biology', *Poetics Today*, Vol. 9, N. 1
- Lewontin, R. C., 1983, 'The Organism as Subject and Object of Evolution', *Scientia* vol. 188 pp. 65-82
- Lewontin, R. C., Rose S., and Kamin L. J., 1984, *Not in Our Genes: Biology, Ideology and Human Nature*, Penguin Books
- Lewontin, R. C., R. Levinas, 1985, *The Dialectical Biologist*, Harvard University Press, Cambridge
- Lewontin, R. C., 1992, *Biology as Ideology, The Doctrine of DNA*, Harper Collins Publishers, New York
- Lewontin, R. C., 2000, *The Triple Helix: Gene, Organism, and Environment*, Harvard University Press
- Lightman, B., 2004, *The Dictionary of Nineteenth-Century British Scientists*, Thoemmes Continuum
- Lillie, F. R., 1901, 'The Organization of the egg in *Unio*, based on a study on its maturation, fertilization, and cleavage', *Journal of Morphology*, Vol. 17, pp. 277-292
- Lillie, F. R., 1906, 'Observations and Experiments concerning the elementary Phenomena of Embryonic Development in *Chaetopterus*', *J. Exp. Zool.* 3, pp.153-268
- Lillie, F. R., 1914, 'Studies on Fertilization: VI. The Mechanism of Fertilization in *Arbacia*', *Journal of Experimental Zoology*, Vol. 16
- Lillie, F. R., 1919, 'The Theory of Individual Development', *Popular Science Monthly*, Vol. 75, No. 14, pp. 239-252
- Lillie, F. R., 1927, 'The Gene and the Ontogenetic Process', *Science*, Vol. LXVI, N. 1712, pp. 361-368
- Lillie, F. R., 1929, 'Embryonic Segregation and its Role in the Life History', *Development Genes and Evolution*, Vol. 118, N. 1
- Lillie, F. R., 1932, 'The Physiology of Feather Pattern', *The Wilson Bulletin*, Vol. 44 No. 4, pp. 193-211
- Lillie F. R. and Juhn, R., 1932, 'The Physiology of Development of Feathers I. Growth-Rate and Pattern in the Individual Feather', *Physiological Zoology*, Vol. 5 No. 1, pp. 124-184
- Lillie, F. R., 1938, 'Zoological Science in the Future', *Science*, Vol. 88, N. 2273
- Lillie, F. R., 1938, 'Physiology of Development of the Feather. II. General Principles of Development with Special Reference to the After-Feather', *Physiological Zoology*, Vol. 11, No. 4, pp. 434-450
- Lillie, F. R., 1941, 'Physiology of Development of the Feather V. Experimental Morphogenesis', *Physiological Zoology*, Vol. 14, No. 2, pp. 103-135

- Lillie, F. R., 1942, 'E.E. Just: August 14, 1883, to October 27, 1941', *Science, New Series*, Vol. 95, No. 2453
- Lillie, F. R., 1942, 'On The Development of Feathers', *Biological Reviews*, Vol. 17. No. 3, pp. 247-266
- Lillie, F. R., 1944, *The Woods Hole Marine Biological Laboratory*. Chicago: University Press
- Lindsay A. A., 1978, 'The Harriman Alaska Expedition of 1899, Including the identity of Those in the Staff Picture', *Bioscience*, Vol. 28, No. 6, pp. 383-386
- Linguetti S., 2005, *La Grande Festa della Scienza. Eugenio Rignano e Federico Enriques. Lettere*. Franco Angeli
- Litwin, T., 2005, *The Harriman Alaska expedition retraced: A century of change, 1899–2001*. New Brunswick, NJ: Rutgers University Press
- Loison, L., 2010, *Qu'est-ce que le Néo-Lamarckisme, Les Biologistes Français et la Question de L'évolution des Espèces*, Vuibert, Paris
- Lurie, E. 1960. *Louis Agassiz: A Life in Science*. University of Chicago Press
- Lysenko, T. D., 2002, *Heredity and its Variability*, University Press of the Pacific
- MacFarland, J., 1970, *Kant's Concept of Teleology*, Edinburg University Press, Edinburg
- Maienschein, J., 1985, 'First Impressions: American Students at Naples', *Biological Bulletin*, 168 Suppl: 26-34
- Maienschein, J., 1985, 'Agassiz, Hyatt, Whitman and the birth of Marine Biological Laboratory'. *Bio Bull.* 168 (suppl.) pp. 26-34
- Maienschein, J., 1987, 'H. N. Martin and W. K. Brooks: Exemplars for American Biology?' *Amer. Zool.*, 27 (3): 773-783
- Maienschein, J., 1991a, *Transforming Traditions in American Biology, 1880-1915*, The John Hopkins University Press, London
- Maienschein, J., 1991b, 'Whitman at Chicago: Establishing a Chicago Style of Biology?', in R. Rainger, K. R. Benson, J. Maienschein, *The American Development of Biology*, University of Pennsylvania Press, pp. 151-180
- Maienschein, J., 'The Origins of Entwicklungsmechanik', in S. F. Gilbert (1991) *A Conceptual History of Modern Embryology*, Plenum Press, New York, pp. 43-59
- Manning, K. R., 1983, *Black Apollo of Science. The Life of Ernest Everett Just*, Oxford University Press, Oxford
- Mayr E., 1982, *The Growth of Biological Thought. Diversity, Evolution, and Inheritance*, Harvard University Press
- McDowall, J. S., 1936, 'Sir Michael Foster', *Post-Graduate Medical Journal*, 12, pp. 78-79
- McLaughlin, P., 1990, *Kant's Critique of Teleology in Biological Explanation, Antinomy and Teleology*, Mellen Press

- Medawar, Peter. 'Postscript: D'Arcy Thompson and Growth and Form'. In *D'Arcy Wentworth Thompson: The Scholar Naturalist (1860-1948)*, by Ruth D'Arcy Thompson, 219–33. London: Oxford University Press, 1958
- Mesle, R. 2008, *Process-Relational Philosophy, An Introduction to A. N. Whitehead*, Templeton Foundation Press
- Mitman G. and Fausto-Sterling A. 1992, 'Whatever happened to Planaria? C.M. Child and the physiology of inheritance'. In: Clarke A. E. and Fujimura J. H., (eds) *The Right Tools for the Job: At Work in Twentieth-Century Life Sciences*, pp. 172–197, Princeton University Press, Princeton
- Mitman G., 1992, *The State of Nature. Ecology, Community, and American Social Thought, 1900-1950*, University of Chicago Press
- Morange, M., 2000, *A History of Molecular Biology*, Harvard University Press
- Morgan C. L., 1923, *Emergent Evolution*, New York, Henry Holt and Co.
- Morgan, T. H., 1901, *Regeneration*, New York, Macmillan
- Morgan T. H., 1915, *The Mechanism of Mendelian heredity*, New York, Henry Holt and Co.
- Morgan T. H., 1919, *The Physical Basis of Heredity*, Lippincott Company, Philadelphia
- Morgan T. H., 1926b, *The Theory of the Gene*, Yale University Press, New Haven
- Morgan, T. H., 1926, 'Genetics and Physiology of Development', *American Naturalist*, 60 (671): 489-515
- Morse, E. S., 1912, 'Biographical memoir of Charles Otis Whitman, 1842-191, *National Academy of Sciences*, Washington
- Morse, E. S., 1920, 'Biographical Memoir of Charles Sedgwick Minot 1852-191, *National Academy of Sciences*, Washington
- Moscoso J., 1995, 'Experimentos de Regeneración Animal: 1686-1765. Come defender la Preexistencia?', *Dynamis*, 15
- Muller, I., 1996, 'The Impact of the Zoological Station in Naples on Developmental Physiology', *Int. J. Dev. Bio.* N. 40
- Muller, J., 1837, *Handbuch der Physiologie des Menschen: für Vorlesungen*, Vol. 1, Verlag von J. Holscher, Coblenz
- Mulnard, J. G., 1992, 'The Brussels School of Embryology', *Int. J. Dev. Biol*, Vol. 36, pp. 17-24
- Needham, J., 1927, *Man a machine: in answer to a romantical and unscientific treatise written by Sig. Eugenio Rignano & entitled "Man not a machine"*, London: Kegan Paul, Trench, Trübner & Co.
- Newmann H. H., 1948, 'History of the Department of Zoology in the University of Chicago', *Bios*, Vol. 19, No. 4, pp. 215-239
- Nils Roll-Hansen, 1984, 'E. S. Russell and J. H. Woodger: The Failure of Two Twenty Century Opponents of Mechanistic Biology', *Journal of the History of Biology*, Vol. 17, n. 3
- Nyhart L. K., 1995, *Biology Takes Form. Animal Morphology and the German Universities, 1800-1900*, University of Chicago Press, Chicago

- Nyhart L. K., and Lidgard, S., 2011, 'Individuals at the Center of Biology: Rudolf Leuckart's *Polymorphismus* and the Ongoing Narrative of Parts and Wholes. With An Annotated Translation', *Journal of the History of Biology*, Online first: <http://www.springerlink.com/content/b1n5h32v51582385/>
- Olby, R. B., *Origins of Mendelism*, University of Chicago Press, Chicago
- Osborn, H. F. 1891, 'The Present Problem of Heredity', *The Atlantic Monthly* (1891), 57, 363
- Ospovat, D., 1976, 'The Influence of Karl Ernst von Baer's Embryology, 1828-1859: A Reappraisal in Light of Richard Owen's and William B. Carpenter's "Paleontological Application of 'Von Baer's Law'", *Journal of the History of Biology*, vol.9 no.1, pp. 1-28
- Ospvat, D., 1978, 'Perfect Adaptation and Teleological Explanation: Approaches to the Problem of the History of Life in the Mid-nineteenth Century', *Stud. Hist. Biol.*, 2: 33-56
- Outram, D., 1984, 'Georges Cuvier: Vocation, Science, and Authority in Post-Revolutionary France', Manchester University Press, Manchester
- Outram, D., 1986, 'Uncertain Legislator: Georges Cuvier's Laws of Nature in Their Intellectual Context', *Journal of the History of Biology*, Vol. 19, N.3
- Overton J., 1997, 'Paul Alfred Weiss 1898-1989', *National Academy of Sciences*, National Academy Press, Washington
- Pauly, P.J., 1984, 'American Biologists in Wilhelminian Germany: Another Look at the Innocents Abroad', Paper delivered at the annual meeting of the *History of Science Society*, Chicago
- Pauly, P. J., 2000, *Biologists and the Promise of American Life: From Meriwether Lewis to Alfred Kinsey*, Princeton University Press
- Pearl, R., 1916, *Modes of Research in Genetics*, Macmillan, New York
- Persell, S. M., 1999, *Neo-Lamarckism and the evolution controversy in France, 1870-1920*, The Edwin Mellen Press
- Peters, P., 2000, 'Frank Lillie: The cultivator of an embryonic Woods Hole scientific community', *Cape Cod Times*
- Phillips D. C., 1970, 'Organicism in the Late Nineteenth and Early Twentieth Century', *Journal of The History of Ideas*, Vol. 31, N. 3
- Pierce, M., 1973, 'Kafoid, Charles Atwood', *Dictionary of Scientific Biography* 7: 447
- Planck, M. 1931, Letter to *Nature*, 127 (3207)
- Poivreau, D., 2006, *Une Biographie Non Officielle de Ludwig von Bertalanffy (1901-1972)*, Bertalanffy Center for the Study of System Science, Vienna
- Preyer, W. T., 1884, *Eléments de physiologie générale*, Alcan, Paris
- Provine, W. B., 1971, *The Origins of Theoretical Population Genetics*, University of Chicago Press, Chicago
- Provine, W. B., 1979, 'Francis B. Sumner and the evolutionary synthesis', *Stud Hist Biol.*, 3:211-40

- Przibram, H., 1913, 'Regeneration und Transplantation im Tierreich', *Kultur der Gegenwart, Band Allgemeine Biologie*, pp. 347-377
- Radick, G., 2005, 'Other Histories, Other Biologies', *Royal Institute of Philosophy Supplement*, 56: 3-4
- Rainger, R., 1981, 'The Continuation of the Morphological Tradition: American Palaeontology', 1880-1920, *Journal of the History of Biology*, Vol. 14, N. 1, pp. 129-158
- Rainger, R., Benson, K. R., Maienschein, J., 1991, *The American Development of Biology*, Rutgers University Press
- Raitt H. and Moulton B., 1966, *Scripps Institution of Oceanography: first fifty years*, Ward Ritchie Press
- Richards, R. J., 1992, *The Meaning of Evolution: The Morphological Construction and Ideological Reconstruction of Darwin's Theory*, University of Chicago Press, Chicago
- Richard, R., 2002, *The Romantic Conception of Life: Science and Philosophy in the Age of Goethe*, University of Chicago Press, Chicago
- Richards, R. J. 2006, 'Goethe's Use of Kant in the Erotics of Nature', in *Understanding Purpose, Kant and the philosophy of Biology*, Ed. by P. Huneman, Vol. 8, University of Rochester Press, Rochester
- Richards, R., 2008, *The Tragic Sense of Life, Ernst Haeckel and the Struggle over Evolutionary Thought*, The University of Chicago Press, Chicago
- Richmond, M., 1997, 'A Lab of One's Own: The Balfour Biological Laboratory for Women at Cambridge University', 1884-1914, *ISIS*, Vol. 88, No. 3, pp. 422-455
- Richmond, M., 2004, 'Sedgwick, Adam (1854–1913)', *Oxford Dictionary of National Biography*
- Rignano, E, 1906, *Sur la Transmissibilité des Caractères Acquis : Hypothèse d'une Centro-épigénèse*, Félix Alcan
- Rignano E., 1926, *Man not a machine: a study of the finalistic aspects of life, with a foreword by Professor Hans Driesch*, K. Paul, Trench, Trubner & Co., Ltd, London
- Rignano, E., 1926, *Biological Memory*, K. Paul, Trench, Trubner & Co., Ltd, London
- Rignano, E. 1931, *Das Gedächtnis als Grundlage des Lebendigen; mit einer einleitung von Ludwig von Bertalanffy*, Wilhelm Braumuller, Wien
- Ritter, W. E., 1903, 'On the Nature of Heredity and Acquired Characters, and the Question of Transmissibility of these Characters', *University Chronicle*, Vol. III, No. 5 and 6
- Ritter, W. E., 1904, 'Organization in Scientific Research', *Popular Science Monthly*, No. 67, pp. 49-53
- Ritter, W. E., 1905, 'A General Statement of the Ideas and the Present Aims and Status of the Marine Biological Association of San Diego', *University of California Publications in Zoology* 2: i-xvii
- Ritter, W. E., 1909, 'Life from a Biologist's Standpoint', *Popular Science Monthly*, Vol. 75, pp. 174-190
- Ritter, W. E., 1909, 'The Hypothesis of "presence and absence" in Mendelian inheritance', *Science*, Vol. XXX, No. 768, pp. 367-368
- Ritter, W. E., 1912, *The Marine biological station of San Diego, its history, present conditions, achievements, and aims*, Berkeley, University of California press

- Ritter, W. E., 1919, *The Unity of the Organism, or, the Organismal Conception of Life*, Gorham Press, Boston, II Volumes
- Ritter, E. W. 1919, *The Unity of the Organism, or the Organismal Conception of Life*, Richard G. Badger, Boston, Vol. 1, p. 305
- Ritter W. E. and Bailey E. W., 1928, 'The Organismal Conception, Its Place in Science and Its Bearing on Philosophy', *UC Publications in Zoology*, Vol 31, No. 14 pp. 307-358
- Ritter, W.E. 1933, 'Historical and contemporary relationships of the physical and biological sciences. Second International Congress on the History of Science', 3rd session, in *Archeion*, 14(4), 497-502
- Roger J., 1963, *Les Sciences de la Vie dans la Pensée Française du XVIII^e Siècle*, Armand Colin, Paris
- Ronald, J. A., 2004, 'Libbie Henrietta Hyman (1888-1969): from developmental mechanics to the evolution of animal body plans'. *J. Exp. Zool. B Mol. Dev. Evol.*, 302 (5): 413-23
- Rudmose B. R. N., 'Sir William Abbott Herdman' (1858-1924)' in *Dictionary of National Biography 1922-1930*, pp. 415-6
- Ruse, M., 1975, 'Woodger on Genetics, A Critical Evaluation', *Acta Biotheoret.*, 24, pp. 1-13
- Russell, E. S., 1910, 'Évolution ou épigénèse', *Scientia*, Vol. 8, pp. 225-246
- Russell, E. S., 1911, 'Vitalism', *Scientia*, Vol. 9, pp. 329-345
- Russell, E. S., 1912, Review of *Sur la Transmissibilité des Caractères Acquis : Hypothèse d'une Centro-épigénèse*, *Scientia*, Vol. 11, p. 439
- Russell, E. S., 1914, Vererbungslehre, *Scientia: Rivista Internazionale di Sintesi Scientifica*, Vol. 15, pp. 274-281
- Russell, E. S., 1914b, 'Bateson, W. - Mendel's principles of heredity', *Scientia: Rivista Internazionale di Sintesi Scientifica*, Vol. 15, pp. 274-281
- Russell E. S., 1916, *Form and Function: A Contribution to the History of Morphology*, London, J. Murray
- Russell, E. S., 1924, *The Study of Living Things: Prolegomena to a Functional Biology*, Methuen & Co, Ltd., London
- Russell, E. S. , 1930, *The Interpretation of Development and Heredity*, Oxford, Clarendon
- Russell, E. S., 1932, 'Fishery Researches: Its Contribution to Ecology', *Journal of Ecology*, Vol. 20, N. 1, pp. 128-151
- Russell, E. S., 1945, *The Directiveness of Organic Activities*, Cambridge University Press
- Sander K., 1991, 'Wilhelm Roux and the rest: developmental theories 1885-1895'. *Roux's Arch.* 200:293-299
- Sapp, J., 1987, *Beyond the Gene, Cytoplasmic Inheritance and the Struggle for Authority in Genetics*, Oxford University Press
- Sapp, J., 2003, *Genesis, The Evolution of Biology*, Oxford University Press

- Sapp, J., 2009, 'Just in Time: Gene Theory and the Biology of the Cell Biology', *Molecular Reproduction and Development* 76: 1-9
- Sarton, G., 1931, 'Eugenio Rignano', *ISIS*, Vol. 15, N. 1, pp. 158-162
- Schmidt, K. P., 1957, 'Warder Allee 1885-1966', *National Academy of Science*, Washington
- Schmitt, S., 2006, 'Succession of Functions and Classifications in Post-Kantian Naturphilosophie around 1800', in *Understanding Purpose, Kant and the philosophy of Biology*, Ed. by P. Huneman, Vol. 8, University of Rochester Press, Rochester
- Secord, J. A., (1996) *Victorian Sensation*, University of Chicago Press
- Sedgwick, A., 1898, *Student's Text-Book of Zoology*, Macmillan & Co.
- Seth, R., Seth A., 1883, *Essays in Philosophical Criticism*, Burt Franklin, New York
- Sheldrake J. S., 2005, 'Joseph Henry Green (1791-1863): surgeon, philosopher and Coleridgean transcendentalist', *J Med Biogr.*, 13(3):136-41
- Shor, E. N., 1981, 'How Scripps Institution came to San Diego', *The Journal of San Diego History*, Vol. 27, N. 3
- Simons, P., 1998, 'Metaphysical Systematic: A Lesson from Whitehead', *Erkenntnis*, 48: 377-393
- Sloan, P., 2002, 'Preforming the Categories: Eighteenth Century Generation Theory and the Biological Roots of Kant's A Priori', *Journal of the History of Philosophy*, Vol. 40, No. 2, pp. 229-253
- Sloan, P. R., 2007, 'Kant and British Bioscience', in *Understanding Purpose, Kant and the Philosophy of Biology*, Vol. 8, University of Rochester Press, Rochester
- Smocovitis, V. B., 1992, 'Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology', *Journal of the History of Biology*, Vol. 25, pp. 1 - 65
- Smocovitis V. B., 1996, *Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology*, Princeton University Press
- Smuts J. C., 1926, *Holism and Evolution*, New York, MacMillan and Co.
- Soyfer, V., 1994, *Lysenko and the Tragedy of Soviet Science*, Rutgers University Press, New Brunswick
- Spemann, H., 1919, 'Experimentelle Forschungen zum Determinations und Individualitäts Problem', *Naturwissenschaften*, 7, pp. 581-591
- Stern, C., and Sherwood E. R., 1966, *The Origin of Genetics. A Mendel Source Book*, C., University of California Press, Berkeley
- Stevens, M. H., 2009, 'The Enigma of Meyer Lissner: Los Angeles's Progressive Boss', *Journal of the Gilded Age and Progressive Era*, Vol. 8, N. 1
- Stork, O., 1946, 'Berthold Hatschek - A landmark in the history of the morphology of the Austrian Academy of Sciences', *almanac for the year*, 99
- Strasburger, E., 1898, *A Text-Book of Botany*, London, MacMillan Publishers
- Sturdy, S., 1988, 'Biology as Social Theory: John Scott Haldane and Physiological Regulation', *British Journal of the History of Science*, Vol. 21, pp. 315-340

- Sumner, F. B. 1944, 'William Emerson Ritter: Naturalist and Philosopher', *Science, New Series*, Vol. 99, No. 2574, pp. 335-338
- Sunderland, M. E., 2010, 'Regeneration: Thomas Hunt Morgan's window into development'. *J. Hist. Biol.* 43(2):325-61
- Taquet, P., 2006, *Georges Cuvier, Naissance d'un Génie*, Odile Jacob, Paris
- Thomson, J. A., 1901, *The Study of Animal Life*, London, J. Murray
- Thomson J. A. and Geddes P., 1904, 'A Biological Approach'. In *Ideals and Science and Faith*, edited by J. E. Hand, George Allen, London
- Thomson, J. A., 1920, *Systems of Animate Nature, The Gifford Lectures Delivered in the University of St. Andrew in the Years 1915 and 1916*. 2 vols., London, Willams and Norgate
- Thone F. E. A. and Bailey, E. W., 1927, 'William Emerson Ritter: Builder', *The Scientific Monthly*, Vol. XXIV, pp. 256-262
- von Bertalanffy, L., 1933, *Modern Theories of Development, An introduction to Theoretical Biology*, Oxford University Press, Oxford
- Watson, D. M. S., 1955, 'James Peter Hill, 1873-1954'. *Biographical Memoirs of Fellows of the Royal Society*, pp. 101-117
- Weismann, A., 1898, *The Germ-Plasm. A Theory of Heredity*, New York, C. Scribner's Sons
- Wellek, R., 1931, *Immanuel Kant in England, 1793-1838*, Princeton University Press, Princeton
- Werskey, G., 1978, *The Visible College*, Penguin Books, Ltd, London
- Wheeler, M., 1936, 'George Baur's Life and Writings', *Amer. Nat.*, 33 (1900), 15-30
- Whitehead, A. N., 1920, *The Concept of Nature*. Cambridge University Press, 2004
- Whitehead, A. N., 1925, *Science and the Modern World*. 1997, Free Press
- Whitehead, A. N., 1929, *Process and Reality: An Essay in Cosmology*. 1979 corrected edition, edited by David Ray Griffin and Donald W. Sherburne, Free Press
- Whitman, C. O., 1893, 'The Inadequacy of the Cellular Theory of Development', *Journal of Morphology*, Vol. 8, Issue 3, pp. 639-659
- Willier, B. H., 1957, 'Frank Rattray Lillie, 1870-1947', *National Academy of Science*, Washington
- Wilson, E. B., 1896, *The Cell in Development and Inheritance*, Macmillan & Co., Ltd
- Winchester S., 2008, *The Man Who Loved China: The Fantastic Story of the Eccentric Scientist Who Unlocked the Mysteries of the Middle Kingdom*, Harper Editions
- Winsor, P. M., 1991, *Reading the Shape of Nature: Comparative Zoology at the Agassiz Museum*, University of Chicago Press
- Woodger J. H., 1924, *Elementary Morphology and Physiology for Medical Students. A guide for the First Year and a Stepping-stone to the Second*, Oxford University Press

Woodger, J. H., 1929, *Biological Principles. A Critical Study*, K. Paul, Trench, Trubner & Co., Ltd, London

Woodger, J. H., 1930, 'The Concept of Organism and the Relation between Embryology and Genetics Part I', *Q. Rev. Biol.*, 5 (1): 1-22

Woodger, J. H., 1931, 'The Concept of Organism and the Relation between Embryology and Genetics Part II', *Q. Rev. Biol.*, 5 (4): 438-462

Woodger, J. H., 1931, 'The Concept of Organism and the Relation between Embryology and Genetics Part III', *Q. Rev. Biol.*, 6 (2): 178-207

Woodger, J. H., 1937, *The Axiomatic Method in Biology*, Cambridge University Press

Woodger, Joseph H. 'On Biological Transformations', In *Essays on Growth and Form: Presented to D'Arcy W. Thompson*, eds. Wilfred Le Gros Clark and Peter Medawar, pp. 94–120. Oxford: Clarendon, 1945

Zammito, J. H., 1992, *The Genesis of Kant's Critique of Judgment*, The University of Chicago Press, Chicago, 1992

Zammito, J. H., 2006, 'Kant's Persistent Ambivalence toward Epigenesis', 1764–90, in *Understanding Purpose, Kant and the Philosophy of Biology*, Ed. P. Huneman, University of Rochester Press, Rochester, pp. 51–74

Zirkle, C., 1946, 'The Early History of the Idea of the Inheritance of Acquired Characters and of Pangenesis', *Transactions of the American Philosophical Society*, 38, pp. 91-15