

## Heredity/Development in the United States, circa 1900

Jane Maienschein

Department of Philosophy  
Arizona State University  
Tempe, Arizona 85287, USA

**ABSTRACT** – Historians have emphasized the appearance of a productive research program in genetics after 1910, and philosophers and biologists have considered endorsement of genetics as a progressive move, indeed as a starting point for modern experimental biology. These efforts focus on what biology had changed *to*. This paper examines the condition *from* which biology moved, stressing the way in which Americans held heredity and development as a natural, intimately intertwined couple. Heredity accounts for likenesses, development for variation, and the two act together throughout an individual's life. This discussion establishes the antecedent conditions necessary to explain the split of genetics and embryology and addresses the reasons for the split.

A number of historians and philosophers of biology have focused on the emergence of an exciting and productive program in genetics after 1910. Many have then looked back for the roots of that program. While a recent article by Iris and Laurence Sandler considers what they identify as the heredity/development concept as a unified idea from Hippocrates and Aristotle into the twentieth century, most have explored the complex relations of genetics to embryology primarily in order to illuminate the emergence of the gene theory and genetics. Frederick Churchill has examined the way in which Wilhelm Johannsen (1857-1927) moved in 1909 away from the unified concept with his genotype/phenotype distinction, for example. Garland Allen has discussed the importance of that distinction for allowing Thomas Hunt Morgan (1866-1945) to establish his own genetics program, while Scott Gilbert has shown the significance of a developmental perspective for Morgan and others who constructed the gene theory.<sup>1</sup> The rediscovery of Gregor Mendel's ideas of particulate heredity, according to the Sandler, and Johannsen's and Morgan's distinc-

<sup>1</sup> Iris Sandler and Laurence Sandler, 'A Conceptual Ambiguity that Contributed to the Neglect of Mendel's Paper', *History and Philosophy of the Life Sciences*, 7 (1985), 3-70; Frederick Churchill, 'William Johannsen and the Genotype Concept', *Journal of the History of Biology*, 7 (1974), 5-30; Garland Allen, 'T. H. Morgan and the Split Between Embryology and Genetics, 1910-1926', in T. J. Horder, J. A. Witkowski, and C. C. Wylie, editors, *A History of Embryology*, Cambridge, Cambridge University Press, 1985, pp. 113-146; Scott Gilbert, 'The Embryological Origins of the Gene Theory', *Journal of the History of Biology*, 11 (1978), 307-351.

tions, according to Churchill, Allen, and Gilbert, reflected the practical value of separating heredity from development. By 1915 at least, these had become largely differentiated subjects of study, recent scholarship emphasizes. That general conclusion certainly seems well founded.

Yet relatively little attention aside from that of the Sandler has turned to detailed examination of the relation of heredity and development before the split. Even though a few such excellent studies as William Coleman's 'Cell, Nucleus, and Inheritance' or Frederick Churchill's work in progress address the role of heredity or even of heredity and development in the late nineteenth century, these concentrate mainly on German work.<sup>2</sup> Yet Americans also played a role in the move to genetics and to separation of heredity and development. Little attention has been given to the reaction of American biologists. In this paper I will explore that relation in more detail, and specifically for those American biologists around 1900 who later established major productive programs in genetics and embryology. The emergence of a program in genetics has served for scholars as a favorite example of productive scientific change, specifically of theory change, and research has focused on the apparently more productive program after the change *to* genetics.<sup>3</sup> I wish, therefore, to establish more concretely what that highly publicized biological work in genetics and alternative programs in experimental embryology were changing away *from*. What commitments characterized the field of biological research before and after, and what changes within the research traditions in heredity and development brought the move toward genetics?

Specifically, I will focus on selected American biological leaders, particularly those concerned with development and those who visited the summer mecca for many of the best American biologists, the Marine Biological Laboratory, those also representing major biological programs. That summer laboratory in Woods Hole, Massachusetts (M.B.L.) had a series of lectures, inaugurated by director Charles Otis Whitman (1842-1910), which addressed what the group regarded as outstanding problems of the day. Not reports of research results, the 'evening course of biological lectures' raised current problems and discussed areas of concern or disagreement among researchers. They therefore provide a particularly valuable primary source for historical perspective on the 1890s. From

<sup>2</sup> William Coleman, 'Cell, Nucleus, and Inheritance: An Historical Study', *Proceedings of the American Philosophical Society*, 109 (1965), 124-58; Frederick Churchill, 'Transformation of Heredity as an Object of Scientific Study, 1840-1915', unpublished paper presented at Columbia History of Science Group, April 1986.

<sup>3</sup> Lindley Darden has presented a number of papers discussing the emergence of genetics as a theory: for example, 'Theory Construction in Genetics', in T. Nickles, editor, *Scientific Discovery: Case Studies*, Dordrecht, D. Reidel, 1980, pp. 151-170.

them we can gain evidence about what the terms 'heredity' and 'development' meant, and what it might mean to say that those areas of discussion were unified or that they later diverged. Given that a divergence did occur and eventually resulted in separate specialties of genetics and embryology, I will consider whether that parting of the ways represented to other American biologists around 1900 the irreconcilable divorce which Henry Fairfield Osborn (1857-1935) saw.

'Unnatural divorce' was, in fact, occurring between various couples of scientific areas of study, Osborn lamented in a public lecture at the Marine Biological Laboratory in 1894. Osborn, an internationally known paleontologist at Columbia University, regarded himself as a biologist. Even though a paleontologist, he spent time at the M.B.L. and worried about trends in biology. Biology, he complained, was suffering from an overabundance of different opinions and from related overspecialization. In particular, study of heredity had become unnaturally divorced from evolution study. We might expect Osborn to see a similar separation of heredity and development since he was explicitly concerned about specialization. Yet Osborn did not; these two were not 'divorced' in 1894. Rather, Osborn believed that 'in modern embryology certainly the most brilliant discovery is that the physical basis of all inheritance is the same - and growing out of this is the higher probability that the laws of heredity are the same in the whole organic world...'.<sup>4</sup> If a discovery about inheritance was the most brilliant in embryology, the two areas must be very closely related indeed. Neither Osborn nor his contemporaries saw heredity and development as identical, as is clear from their continued use of both terms and from their elaborations of the two. Yet in his 1894 lecture Osborn treated them as effectively inseparable. Heredity, he maintained, accounts for both variation (or 'the exponent of old hereditary forces developing under new or unstable conditions') and repetition (bringing old forces under old conditions). Heredity would therefore explain how both likenesses and differences are carried on, said Osborn.<sup>5</sup>

Whitman regarded biology from a different perspective than Osborn's, but similarly saw study of heredity and development as connected. As first director of the Marine Biological Laboratory and first chairman of the Biology Department at Clark University and then the University of Chicago, Whitman played an extremely influential role in American biology. He served as inspiration for many of the young biologists who

<sup>4</sup> Henry Fairfield Osborn, 'The Hereditary Mechanism and the Search for the Unknown Factors of Evolution', *Biological Lectures 1894* (1895), 79-100: 81; reprinted in Jane Maienschein, editor, *Defining Biology*, Cambridge, Harvard University Press, 1986, as are other *Biological Lectures*.

<sup>5</sup> *Ibid.*; also see Henry Fairfield Osborn, 'Evolution and Heredity', *Biological Lectures 1890* (1891), 130-141.

became leaders in studies of both heredity and development.<sup>6</sup> His views were taken seriously by a wide range of younger American biologists and therefore merit close attention.

Whitman regarded specialization in biology as desirable, indeed necessary, for progress in a growing scientific field such as biology in the 1890s. Specialization, he pointed out, allows division of labor, which in turn brings efficiency. Of course, specialists should not rush off in all different directions to pursue their own selfish interests; they must work cooperatively together. There is no serious risk from too much specialization for there is always a corrective: 'there are centripetal forces that keep pace with the centrifugal ones; and the danger of any science flying into disconnected atoms is about as dreamy and remote as the dissolution of the earth itself.'<sup>7</sup> With proper cooperative union such as occurs among the cells of an individual organism, this persistent idealist insisted, success will come for biology.

In his work at the Marine Biological Laboratory and the University of Chicago, Whitman was directly concerned with identifying appropriate specializations in biology and was thus presumably alert to newly emerging specialties. Nonetheless, he regarded heredity and development as intimately related, as distinguishable but not as independent specialties. In an essay of 1898, he identified embryology as

the science which deals directly with the phenomena of heredity, and which is, therefore, the touchstone of every theory of inheritance. It is a fundamental tenet of embryology that all organisms reproducing exclusively by germs owe their inherited characters to the germs from which they arose, and that germs carry the primordial characters of adult structure, not by virtue of any mysterious transference of parental features, but by virtue of the constitution they bring with them when they arise by division of preexisting germs. That is, I believe, a fair statement of the embryological doctrine of inheritance, which must be the final test of our theories.<sup>8</sup>

With 'The embryological doctrine of inheritance' Whitman meant to emphasize the fact that development involves the inherited structure and 'potentialities' of the egg. Development and inheritance work together at all times. Heredity certainly does not end with germ production, since the particular organization of the egg and later structural influences or directs development at all stages. Neither does development begin only at fertili-

<sup>6</sup> Charles Otis Whitman, 'Specialization and Organization', *Biological Lectures 1890* (1890), 1-26; Whitman, 'The Naturalist's Occupation', *Biological Lectures 1890* (1890), 1-26; Jane Maienschein, 'Agassiz, Hyatt, Whitman, and the Birth of the Marine Biological Laboratory', *Biological Bulletin* 168 Supplement (1985), 26-34.

<sup>7</sup> Whitman (footnote 6), p. 22.

<sup>8</sup> Charles Otis Whitman, 'Animal Behavior', *Biological Lectures 1898* (1899), 285-338.

zation or thereafter, since the germ cells change continually. Heredity and development are two closely related aspects of the ongoing production of a new differentiated individual.

Many of the other American researchers at the M.B.L. agreed, explicitly or implicitly. Morgan, for example, said even as late as 1910 that he had 'come to look upon the problem of heredity as identical to the problem of development'.<sup>9</sup> Thus we see that the two problems were closely, if not inextricably, related. There were, for these Americans at least, no separate disciplines to study heredity and development. Rather many of the leading problems of biology centered on heredity and development or heredity/development, all of which in turn were shaped by evolutionary factors. A researcher might focus on patterns of embryonic development or on cytological changes in the nucleus, but he still considered himself concerned with heredity/development generally. Nonetheless, these two sets of problems and phenomena were not really identical; each meant something different.

Heredity for American biologists of the 1890s generally concerned the passing on of likenesses of structural features from one generation to the next through the structure of the fertilized egg cell.<sup>10</sup> Thus, studies of heredity were largely morphological (concerned with structure). Heredity also embraced the occurrence of variations, or differences from the parents. But discussions of heredity also concentrated on factors internal to the organism, which tended to focus attention on stability and continuity instead of change and variation. Evolutionary adaptation brings stability, and thus heredity and evolution are closely allied. In Osborn's words, 'the theory of the evolutionary process is inseparably connected with some theory of inheritance'. For Edmund Beecher Wilson (1856-1939), every organic being has a two-fold nature: it is a complicated mechanism in equilibrium with its parts and its environment and is also an adaptation from the past. Thus embryological developments depend also on both present mechanical adaptations and on heredity of evolutionary adaptations to past conditions. As Jacques Loeb (1859-1924) pointed out, heredity served as a collective term referring to a number of different circumstances.<sup>11</sup> Only gradually did this group of researchers realize that one

<sup>9</sup> Thomas Hunt Morgan, 'Chromosomes and Heredity', *American Naturalist*, 44 (1910), 449-496: 449.

<sup>10</sup> Alpheus Hyatt, 'Some Governing Factors Usually Neglected in Biological Investigations', *Biological Lectures 1899* (1900), 127-156: 129; Coleman (footnote 2) discusses similarities for the Germans.

<sup>11</sup> Henry Fairfield Osborn (footnote 5), 'Evolution and Heredity', 1890, p. 131; Edmund Beecher Wilson, 'Cell-Lineage and Ancestral Reminiscence', *Biological Lectures 1898* (1899), 21-42: 21; Jacques Loeb, 'On the Heredity of the Marking in Fish Embryos', *Biological Lectures 1898* (1899), 227-234: 227.

single unified theory to explain all hereditary phenomena might prove impossible to achieve.

In contrast to the stabilizing function of heredity, development concentrated on the production of differentiations or variations. Development represented the response to conditions both internal and external to the individual, the individual which was strongly directed by the inherited chemical or formal structure of the egg. Development was largely physiological, or concerned with the process of producing a new organism. While heredity represented the growth and differentiation of one individual into another of the next generation, development involved the growth and differentiation of one individual. As Edwin Grant Conklin (1863-1952) summarized, 'Development is progressive differentiation coordinated as to time and place; hereditary likenesses consist in the repetition by the offspring, at certain stages of its life cycle, of definite differentiations of the parent... The phenomena of differentiation are therefore of the greatest interest, and their causes one of the most important problems of biology'.<sup>12</sup>

This interpretation of heredity as primarily bringing stability and development as primarily yielding variation, dominant among American biologists at the M.B.L. and at major biological programs (Chicago, Johns Hopkins, Yale, Princeton, Harvard, and Columbia), directly and explicitly rejected the suggestions of August Weismann (1834-1914) and Wilhelm Roux (1850-1924), which might have brought a different perspective. This rejection is significant, though certainly not unique to this selected group of Americans.

#### *American Rejection of Weismann-Roux Preformationism*

Weismann was too exclusively morphological, placing all his emphasis on the biophore structures, these Americans felt as they attacked his ideas in paper after paper in the 1890s. As Wilson maintained, for example, the researchers' 'point of view has been too largely morphological while the physiological aspect of development has been thrown into the background'. The developing organism may experience effects of congenital changes in idioplasm or changes in its environment. Either may affect the organism. Development and inheritance have a more complex relationship than biologists such as Weismann recognized, Wilson urged. In fact,

<sup>12</sup> Edwin Grant Conklin, 'Protoplasmic Movement as a Factor of Differentiation', *Biological Lectures 1898* (1899), 69-92: 69.

The greatest fault of embryology has been the tendency to explain any and every operation of development as merely the result of 'inheritance', overlooking the vital point that every such operation must have some physiological meaning for the individual development, hard though it may be to discover.<sup>13</sup>

Analyzing this physiological component of development was a primary task for a number of the American biologists such as Morgan or Loeb in the 1890s.

The repeated criticisms of Weismann and Roux served to focus attention on the importance of development and to emphasize the working together of development and heredity which Weismann's continuous and independent germ plasm set apart. Weismann's failure to acknowledge the complex and subtle relationship between heredity and development, his emphasis on the nucleus and heredity, could lead to the sort of unnatural divorce which Osborn had regretted. This result Wilson and other Americans (as well as German epigenesists Hans Driesch (1867-1941), Oscar Hertwig (1849-1922), Swiss Wilhelm His (1831-1904), and German/American Jacques Loeb) sought to avoid in the 1890s.

The American community at the M.B.L., at least, consisted almost uniformly of neo-epigenesists of some form in the 1890s, or else the researchers adopted some compromise position between epigenesis and preformation. They explicitly rejected what they saw as Weismann's and Roux's neo-preformationism. Whitman and William Morton Wheeler (1865-1937) both explicitly addressed the issue of preformation vs. epigenesis in general lectures at the M.B.L. As Whitman put it, the modern biologist must proceed carefully in order to avoid the Scylla and Charybdis of the old extreme preformationism and epigenesis. In particular, it was important not to move too far toward preformationism just because it seemed that development might be largely directed by internal factors. 'It seems to be forgotten that determination from within may proceed quite as epigenetically as determination from without', Whitman said.<sup>14</sup> Something of inheritance of internal factors in the heterogeneous constitution of the egg directs the developmental process, according to Whitman, and thus his view represented a moderate version of predelineation. But Weismann's view was too simple and risked being sucked into that Charybdis

<sup>13</sup> Edmund Beecher Wilson, 'The Embryological Criterion of Homology', *Biological Lectures 1894* (1895), 101-124: 118, 119, 123; Also Edmund Beecher Wilson emphasized the close relations of heredity and development beginning with his classic *The Cell in Development and Inheritance*, New York, Macmillan, 1896; reprinted New York, Johnson Reprint Corporation, 1966.

<sup>14</sup> Charles Otis Whitman, 'Evolution and Epigenesis', *Biological Lectures* (1895), 205-224: 223; see also, Jane Maienschein, 'Preformation or New Formation - or Neither or Both', in T. H. Horder et al., *A History of Embryology*, 1985, pp. 83-108.

of excessive preformationism. As Wheeler agreed in his essay praising Caspar Friedrich Wolff, neither extreme would do:

The pronounced 'epigenesist' of to-day who postulates little or no predetermination in the germ must gird himself to perform Herculean labors in explaining how the complex heterogeneity of the adult organism can arise from chemical enzymes, while the pronounced 'preformationist' of to-day is bound to elucidate the more elaborate morphological structure which he insists must be present in the germ. Both tendencies will find their correctives in investigation.<sup>15</sup>

The evidence brought by the best investigations to date pointed more toward the gradual unfolding and importance of physiological processes of development and away from Weismannian preformationism.

Some American attacks on Weismann and Roux centered on the ad hoc nature of their theories, which the critics regarded as artificial. The various after-the-fact attempts to save the theory, such as from the problems of regeneration, meant to them that Weismann and Roux were logically abandoning their original ideas.<sup>16</sup> Some of the Americans rejected the speculative nature of Weismann's and Roux's work, citing the lack of accord with observed evidence and the weak empirical basis for the conclusions, which were not in accord with the general direction of thinking at Woods Hole about what constituted the interesting problems and appropriate methods and answers. Still others reacted against the concentration which Weismann and Roux, along with other European researchers, placed on the nucleus while ignoring the cytoplasm.<sup>17</sup> The most important criticism centered on the claim that Weismann and Roux had oversimplified the all-important problems of heredity and development and had thus failed to explain anything at all. Weismann's unjustified emphasis on the germ plasm and its predetermined 'microcosm of biophores' and Roux's insistence on cellular self-differentiation which held that heredity directed development shut out the possibility of a flexible internal response to environmental conditions. As Morgan said, such views simply threw explanations back to the ancestral 'shadowy past'. Physiologist Albert Prescott Mathews (1871-1957) considered such a theory as Weismann's a 'scientific misdemeanor'.<sup>18</sup> This response reflected fundamental assumptions by the Americans.

<sup>15</sup> William Morton Wheeler, 'Caspar Friedrich Wolff and the *Theoria Generationis*', *Biological Lectures 1898* (1899), 265-284: 284.

<sup>16</sup> Edmund Beecher Wilson, 'The Mosaic Theory of Development', *Biological Lectures 1893* (1894), 1-14; John Ryder, 'A Dynamical Hypothesis of Inheritance', *Biological Lectures 1894* (1895), 23-54; Osborn, 'The Hereditary Mechanism', 1894, p. 79.

<sup>17</sup> Wilson (footnote 13), p. 104; Edwin Grant Conklin, 'The Fertilization of the Ovum', *Biological Lectures 1893* (1894), 15-35: 30.

<sup>18</sup> Thomas Hunt Morgan, 'Regeneration: Old and New Interpretations', *Biological Lectures 1899* (1900), 185-208: 195; Albert Prescott Mathews, 'The Physiology of Secretion', *Biological Lectures 1899* (1900), 165-183: 183.

Some biologists saw heredity and development as separated mainly in time, with heredity acting first and development following, as the Sandler suggest, but these Americans would generally not have agreed.<sup>19</sup> Rather, both heredity and development work together at all times, just as there is always simultaneously movement toward conservative sameness and toward difference. The idea of hereditary transmission of characters was not a completely foreign idea, but it held no useful meaning for those Americans who rejected the importance of Weismannian inherited determinants. Some structure was surely transmitted in the complex, heterogeneous egg, but physiological development also worked at all times to bring characteristics to reality. They could see this happening. Even at the earliest developmental stages, even at fertilization, a complex of developmental changes took place so that developmental processes of change always occurred. Likewise, heredity always had an effect since the inherited chemical and formal arrangement exerted an influence as the physiological processes acted and continued to play a part throughout development.

To reemphasize this essential point, then, development and heredity work together at all times according to the dominant opinion of the American biologists of the 1890s. As Whitman said rather vaguely, the life of an individual begins with a 'ready-formed, living germ, with an organization cut directly from a preexisting, parental organization of the same kind'.<sup>20</sup> He did not explain how.

To sort out the discussion around 1900 a bit further, let me outline some of the distinctions which researchers saw as relevant and useful. We have already seen the persistence of problems of both heredity and development. In addition, biologists distinguished between morphological and physiological studies as those concerned respectively with structure and with process. Heredity studies tended to be morphological, with developmental study physiological. These were not sharp dichotomies with no middle ground. Heredity was just more morphological, development more physiological. Both co-existed, just as both empirical observations and experimental manipulations co-existed as proper methods for biological research. Again, factors internal and external to the individual both influenced development and heredity. Both nuclear and cytoplasmic factors worked together. Cellular parts and organic whole organisms both provided appropriate subjects for study. These distinctions and awareness of alternatives pervaded biology around 1900. Sometimes discussion cut across the lines in unusual ways, but more often, researchers saw the legiti-

<sup>19</sup> Sandler and Sandler (footnote 1), p. 67.

<sup>20</sup> Wheeler (footnote 15), p. 281, reporting Whitman's words.

macy and value of pursuing alternatives, even while stressing one or another for the purpose at hand.<sup>21</sup> Biologists differed in their research emphases, of course, but those leading American biologists at the M.B.L. in the 1890s shared their basic assumptions about heredity and development.

### *The Breakup*

By 1915, however, this situation had changed, as mentioned earlier. Heredity and development had each undergone changes. The new separated disciplines which resulted appeared sufficiently different and the results sufficiently irreconcilable that the specialized fields of genetics and experimental embryology had effectively separated. What had brought the change? Two factors contributed: the evidence from empirical studies and a pragmatic desire for progress. The wealth of empirical results around the turn of this century detailed much of what happens in virtually all visible parts of the cell during all the early points during development. In the 1890s such work had reinforced the conclusion that heredity and development remain extremely complex and intertwined. Complexity had seemed to serve as a barrier to further analysis. But after 1900 further evidence mounted to suggest a chink in the embryo's armor of complexity, namely through study of chromosomes and sex determination. At the same time, the desire for productive and progressive results rather than 'dreamy speculations' in biology led these Americans to embrace a pragmatic program of study which promised conclusive results. These two factors supported the formation of a new specialty field of study in genetics. Heredity thus gained glamour and independence. The resulting divergence of interest ultimately brought separation of heredity from development.

More specifically, the empirical studies surrounding sex determination began with breeding and population studies, primarily in Europe. Assuming that external environmental factors determined sex in individuals, researchers believed they could examine the effects of different environments on sex ratios and therefore discover what factors produce which sex. They changed environments and examined changes in ratios. This breeding and population work attracted advocates, including a few Mendelians, but did not really become a viable program for understanding

<sup>21</sup> Wilhelm His, especially in *Unsere Körperform und das physiologische Problem ihrer Entstehung*, Leipzig, F.C.W. Vogel, 1874, stressed inherited and external factors rather than making the usual inherited/developed or external/internal distinctions; Wilson (footnote 17), p. 118.

how heredity works since heredity acts on individuals and such population change affects groups. No one could gain useful experimental results on individuals by changing external conditions because one could not both know what the sex of an individual would have been and also what it was after the conditions changed. Then in the twentieth century, accumulating evidence convinced most researchers, even many of the ardent epigenesists and environmentalists, that internal rather than external factors play the decisive role.<sup>22</sup> By then work on chromosomes and the ongoing research into sex determination had begun to converge.

By 1902 Theodor Boveri (1862-1915) and Walter Sutton (1877-1916) had reinforced the conviction that chromosomes have physical reality and continuity in some interesting and meaningful sense.<sup>23</sup> They persist and retain autonomy through time rather than disappearing and reappearing as the matter of which they consist rearranges itself. Chromosomes must play some important role in the life of the individual, even the most sceptical of biologists acknowledged in the first decade of this century. And since these chromosomes apparently become active early in development and during cell divisions, they must play some important role for development. Presumably, since they exist from the beginning and persist, they play a similarly important role for heredity.

It might even seem that the chromosomes, and thus the nucleus, play the central role in heredity. Weismann, Roux, and others certainly drew that conclusion.<sup>24</sup> Before 1905, the Americans generally did not. Based on their detailed cytological studies of early developmental stages, they recognized that chromosomes were only part of the complex cellular structure.<sup>25</sup> Their writings stress over and over the importance of the seemingly inherited and non-chromosomal centrosomes, the spindle fibers, the asters, etc. These are all cytoplasmic factors, such writers as Whitman, Wilson, Edwin Grant Conklin (1863-1952), Shosaburo Watase (1862-1929), Katherine Foot (1857-1944 (?)), Cornelia Clapp (1849-1939), and others

<sup>22</sup> Thomas Hunt Morgan, 'Recent Theories in Regard to the Determination of Sex', *Popular Science Monthly*, 64 (1903), 97-116, especially p. 101; Leonard Doncaster, 'Recent Work on the Determination of Sex', *Science Progress* (1909), 13: 90-104. For further discussion, see John Farley, *Gametes and Spores*, Baltimore, Johns Hopkins University Press, 1982.

<sup>23</sup> Theodor Boveri, 'Über mehrpolige Mitose als Mittel zur Analyse des Zellkerns', *Verhandlungen der physikalisch-medizinischen Gesellschaft zu Würzburg*, 35 (1902), 67-90, also reprinted in B. H. Willier and J. M. Oppenheimer, editors, *Foundations of Experimental Embryology*, Englewood Cliffs, New Jersey, Prentice Hall, 1964, pp. 76-97; Walter Sutton, 'On the Morphology of the Chromosome Group in *Brachystola magna*', *Biological Bulletin* 4 (1902), 24-39; see Coleman (footnote 2), on earlier work.

<sup>24</sup> For example, see Gilbert (footnote 1), pp. 312-319.

<sup>25</sup> The *Biological Lectures* as well as articles in the *Journal of Morphology*, which Whitman also edited, reveal the importance of cytological work and particularly work on early cell lineage stages for the Americans. The archival collections of correspondence among the various members of the Woods Hole group reveal a similar preoccupation.

emphasized in the series of papers at the M.B.L. in the mid 1890s. Those elements were *not* in the nucleus and therefore did not reside within some special boundary of inherited material in the nucleus.

For example, Conklin pointed out that Boveri, Weismann, and Hertwig (presumably Richard (1850-1937)) regarded the hereditary substance 'by means of which heritable qualities are transmitted from one generation to another' as residing wholly in the nucleus and particularly in the chromatin. They based their idea on the faulty assumption that only the male nucleus and chromatin and nothing else of the spermatozoon enters the egg at fertilization. It seemed to Conklin 'probable that this sperm cytoplasm does not act as so much dead matter, but that it also takes part in this union of the essential constituents of the two cells'. Not denying the importance of the nucleus, Conklin nonetheless regarded himself as a 'friend of the cell', the whole cell, with the nucleus and cytoplasm working cooperatively together just as Whitman wanted all biologists to do. As Whitman's protegee Watase said, the nucleus and cytoplasm keep each other in control, through the exercise of a 'reciprocal physiological influence'.<sup>26</sup> Ultimately what directs both heredity and development is the whole organism, these researchers agreed with their mentor Whitman.

Chromosomes were fine, then, and provided one possible way that heredity might act, but the definite heterogeneous organization of the egg cell and its rearrangements after fertilization were also unquestionably the result of heredity. Focus on chromosomes alone, or on the nucleus alone as if there were a neat boundary around it, was unacceptable to nearly all the American biologists with their cytological bias, prior to 1905. This includes those later architects of a chromosomal theory of sex determination, Wilson, Nettie Stevens (1861-1912) and Thomas Hunt Morgan, a point which has often been overlooked.

In effect, the convergence of work on sex determination and study of chromosomes after 1905 began to change the perspective and assumptions of at least a subset of American biologists. That work, discussed in more detail elsewhere, focused attention on the possibility that one particular chromosome might determine which of the two available sexes an individual would become. H. Henking had suggested in 1891 that an accessory chromosome might determine sex, a possibility reinforced by

<sup>26</sup> Conklin (footnote 17), pp. 30, 31; Shosaburo Watase, 'On the Nature of Cell-Organization', *Biological Lectures 1893* (1894), 83-103: 103; Whitman, 'The Inadequacy of the Cell Theory of Development', *Journal of Morphology*, 8 (1893), 639-658.

Clarence E. McClung's (1870-1946) work of 1902.<sup>27</sup> Generally, that suggestion had little immediate direct impact on the American researchers since they believed that a mere chromosome could not hold such importance for the central problems of heredity and development. But the associated questions did stimulate some American research. In particular, Nettie Stevens undertook with work in 1905 and 1906 to determine what role the particular chromosomes play in heredity and development. Evidently she expected the chromosomes to play some role but not a leading or directive one. Wilson became convinced by Stevens's work and confirming evidence from his own studies that chromosomes are indeed at least among the primary bearers of heredity. The sex determination work convinced him after 1907 that chromosomes may determine sex.<sup>28</sup>

Indeed, chromosomes might be bearers of heredity. Few others agreed yet, however, and Conklin was one who staunchly articulated his denial that the chromosomes hold any special importance. Morgan was perhaps the strongest of the physiological epigenesists, holding that heredity, while related to development, plays only a secondary role, while physiological reactions to changing external environmental conditions direct most of normal development. Recall that heredity meant evolution and stability for Morgan, who persisted in his view of 1899 that the 'younger investigators' were trying to address the same problems that Weismann, who had criticized them, was also addressing. Yet 'the younger investigators' based their interpretations on the assumption that when a change takes place a sufficient cause for the change is to be sought in the organ itself and in the external conditions surrounding that organ. They were not content to rest their 'explanations' on 'the phyletic origins' of the changes.<sup>29</sup>

The case for chromosomes, for the nucleus, for heredity as a dominant director of developmental processes and of differentiation had not gained many American converts or new recruits even by 1910. The discovery of a

<sup>27</sup> H. Henking, 'Untersuchungen über die ersten Entwicklungsvorgänge in den Eiern der Insekten, II: Über Spermatogenese und deren Beziehung zur Eientwicklung bei *Phyrrhocoris apterus*', *Zeitschrift für wissenschaftliche Zoologie*, 51 (1891), 685-741; Clarence E. McClung, 'The Accessory Chromosome - Sex Determinant?', *Biological Bulletin*, 3 (1902), 43-84; Jane Maienschein, 'What Determines Sex? A Study of Converging Approaches, 1880-1916', *Isis* 75 (1984), 457-480.

<sup>28</sup> Nettie Marie Stevens, *Studies in Spermatogenesis, Part II: A Comparative Study of the Heterochromosomes in Certain Species of Coleoptera, Hemiptera, and Lepidoptera, with Especial Reference to Sex Determination* (Carnegie Institution of Washington Publication 26, Part II, October 1906); Edmund Beecher Wilson, 'The Chromosomes in Relation to the Determination of Sex', *Science Progress*, 16 (1910), 570-592.

<sup>29</sup> Garland Allen, 'Thomas Hunt Morgan and the Problem of Sex Determination, 1903-1910', *Proceedings of the American Philosophical Society*, 110 (1966), 48-57; Morgan (footnote 9); Thomas Hunt Morgan, 'Regeneration: Old and New Interpretations', *Biological Lectures 1899* (1900), 185-208; 194-195.

white-eyed male *Drosophila*, where those two characteristics (white-eyedness and maleness) were always associated, provided a major stimulus for change. Then it seemed certain that at least some of inheritance took place by way of some association of transmitted particulate factors, quite possibly on the chromosomes.<sup>30</sup>

This discovery in itself need not have brought a divergence of heredity from development. But the prospects for research which would produce definitive results attracted new recruits. The desire for definite results introduces the second major factor explaining the separation of heredity from development. Those Americans who had criticized Weismann and Roux for their excessive speculation and overreliance on ad hoc auxiliary hypotheses wanted reliable products from their research. As Morgan said, he wanted a real explanation, an explanation based on proximate physiological and hence mechanical factors, not some reference to a vague and shadowy past.<sup>31</sup> A research program in genetics, even if the fundamental units remained theoretical, could nonetheless achieve certain results. Careful study could produce chromosome maps to determine which traits are associated with which chromosomes. Never mind *how*. Never mind the complex connections of heredity and development. The search for definite results dictated the pragmatic separation of heredity studies, specifically genetics, from development. Morgan and other geneticists embraced genetics, formed a new union with Mendelian theory, and wandered away from development. Morgan, as a spokesman, said that he hoped to reconcile the old couple, but found he could not. In the end, with his book *Embryology and Genetics* of 1934, he did not even find it profitable to try very hard.<sup>32</sup> Heredity had moved in different directions from its old partner.

What of development, then? For a while, some developmentalists such as Conklin denied that a separation had really occurred. Heredity and development remained essentially together for Conklin, who stressed the importance of cytoplasmic and nuclear inheritance and of both the cells and the organism as a whole. Others such as Ross Granville Harrison (1870-1959) accepted the separation, bid a quick farewell to the suspect program in genetics, and turned attention to the developmental processes with his experimental embryology. His concern with transplantation techniques and changes in form moved his work

<sup>30</sup> For example: Thomas Hunt Morgan, 'An Attempt to Analyze the Constitution of the Chromosomes on the Basis of Sex-limited Inheritance in *Drosophila*', *Journal of Experimental Zoology* 11 (1911), 365-414.

<sup>31</sup> Morgan (footnote 29), p. 195.

<sup>32</sup> Thomas Hunt Morgan, *Embryology and Genetics*, New York, Columbia University Press, 1934.

away from heredity as surely as genetics was carrying heredity away from development.<sup>33</sup>

After 1910, then, study of heredity and development had actually separated, in a divorce that allowed both parties to mature as independent research programs. Yet the separation also entailed some cost, some loss of understanding of problems falling between the new research programs. Genetics, embryology and evolution do, as we have seen, share a common tradition. It would be well for historians and biologists to recall that tradition as the Sandlers and others have begun to do.

#### *Acknowledgements*

Research for this project was completed with support of National Science Foundation Grant SES 83-09388 and an Arizona State University Grant. Thanks to Fred Churchill and Bernardino Fantini for helpful comments.

<sup>33</sup> Ross Harrison repeatedly refused to hire a geneticist and regarded genetics generally as much too speculative, Ross Granville Harrison Collection, Yale University Manuscripts and Archives.