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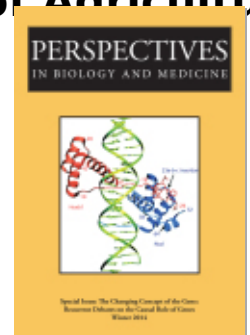
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## Origins of the Classical Gene Concept, 1900-1950: Genetics, Mechanistic, Philosophy, and the Capitalization of Agriculture

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# ORIGINS OF THE CLASSICAL GENE CONCEPT, 1900–1950: GENETICS, MECHANISTIC, PHILOSOPHY, AND THE CAPITALIZATION OF AGRICULTURE

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GARLAND E. ALLEN

**ABSTRACT** In the period of “classical genetics” (roughly 1915–1950), the common view of the gene was mechanistic—that is, genes were seen as individual, atomistic units, as material components of the chromosomes. Although it was recognized early on that genes could interact and influence each other’s expression, they were still regarded as individually functioning units, much like the chemists’ atoms or molecules. Although geneticists in particular knew the story was more complex, the atomistic gene remained the central view for a variety of reasons. It fit the growing philosophy of mechanistic materialism in the life sciences, as biologists tried to make their field more quantitative, rigorous, and predictive, like physics and chemistry. Conceptually and pedagogically, it provided a simple way to depict genes (as beads on a string) that fit with the exciting new work on chromosomal mapping. The atomistic gene also fit well with the increasing drive to move capital into agriculture, both for potential patenting purposes and for ease of experimental manipulation and prediction. It is the latter point that the present essay explores most thoroughly. The rise of agriculture as an industrialized process provided a context and material support that fueled much of the rapid growth of genetics in the first half of the 20th century.

AS MANY OF THE PAPERS IN THIS SPECIAL SYMPOSIUM ISSUE discuss, by the 21st century we have moved well beyond the notion of a gene as a single particulate unit coding for a given protein, or especially a single phenotypic trait. Yet notions

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of genes as some kind of single, particulate entity still persist, especially in textbooks and writings about genetics for the general public.

To understand this disjunct between the professional geneticist's view of genes and their complex interactions, and the more widespread public understanding of genes as distinct entities, I thought it might be useful to look back 150 years or more to the origins of the gene concept, to the origins of Mendelian genetics itself and its predecessors. In this process, I would like to raise several questions that I hope will illuminate something about how biology was practiced in the early years of the 20th century and how that understanding has led to the persistence of an older view of the gene that can inform our practice and communication about genetics today.

These questions all relate in one way or another to the interaction of biological theories and their philosophical, economic, and social contexts. Among the many aspects of the historical context in which genetics as a field evolved, five questions will form the focus of our attention: (1) how did the early portrayal of the gene, at least in the first half of the 20th century, come into being; (2) what particular form did that portrayal of the gene take; (3) how was that form perpetuated over the period 1900 to 1950; (4) what confluence of factors operated to promote this specific view of the gene; and (5) how has that picture of the gene persisted into and affected the development of genetics from the late 20th century onwards?

### **THE CONCEPT OF THE GENE IN THE EARLY 20TH CENTURY**

The view of the gene to which I am referring in this essay is what I designate as the mechanical, mechanistic, or atomistic gene, based on the generally pervasive philosophy of mechanistic materialism that was highly influential in biology in the early and mid-20th century. This view grew out of the confluence of a number of factors in late-19th and early-20th-century social and economic developments, especially in the United States and England. The atomistic/mechanistic gene was a highly successful and resilient concept that eventually became the predominant conceptualization. However, this formulation was challenged periodically during the first half of the 20th century, and as a result modified to varying degrees. At the time of the elucidation of the molecular structure of DNA in 1953, the basic view of the gene as an atomistic unit, at a specific physical location (locus) on a chromosome and associated with a particular phenotypic trait, was still the predominant picture with which most biologists and the public were familiar.

The confluence of factors that had supported this view of the gene included the particulate nature of the numerous synthetic theories of heredity developed especially in the post-Darwinian period. These theories included the work of Darwin himself, but also that of August Weismann, Ernst Haeckel, Carl von Nägeli, Hugo de Vries, and a host of other investigators (Robinson 1979).<sup>1</sup> Although these theories represented an increased interest in the nature of heredity as a biological

phenomenon, they were unsatisfactory in varying degrees because of their speculative, nonempirical foundations and their inability to predict outcomes in plant and animal crosses with any accuracy.

Another factor was the rapid growth of industry in the period between 1870 and 1920 in both Europe and the United States, which led to an accumulation of capital and thus to the need to find new areas of investment. One area that had been eyed for decades was agriculture, but it was basically a cottage industry, based on small plot holdings and rule-of-thumb practices that were ill-suited to providing predictable results and thus large-scale investment. At the same time, industrialization and its associated urbanization—which meant fewer workers on the farm, and more mouths to feed in the cities—increased the pressure for higher agricultural productivity. With government help, especially in the United States, the ideal of the industrialization of agriculture became an increasing goal, including not only mechanization and attention to environmental conditions such as soil nutrients, fertilizers, and the like, but also the development of higher-yield plant and animal varieties that could increase productivity per acre (Harwood 1997; Fitzgerald 2003).

Also important during this period was the professionalization of biology: its conversion from a more loosely organized community of naturalists isolated in widely scattered universities to organized societies of investigators with common sets of interests, professional societies, and journals. Concurrently, this period also saw the emergence of privately funded and governmental institutions dedicated to research in broad areas of biological and genetic science. One major feature of the emergence of a more highly professional consciousness among biologists was the emphasis on experimental, quantitative science as the hallmark of what was often referred to as the “new” biology—emulating, often quite consciously, the physical sciences in which these approaches were paramount. Particularly important was the fact that experimentation led to the ability to make predictions from, and then to test, hypotheses. Experimentation was explicitly touted by many younger biologists as superior to purely descriptive and speculative methods, not only for epistemological reasons but also for reasons of professionalization. (There is a wide-ranging literature on professionalization in the sciences, including biology, in the later 19th and early 20th centuries; see, for example, Appel 1988).

It was in the development of genetics—and particularly the mechanistic conception of the gene—that these various economic, social, and intellectual strands found their most successful expression. Genetics became the embodiment of a new and more scientific approach to both biological research and economic development.

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<sup>1</sup>There has been much debate as to whether Mendel himself adhered to a particulate concept for what he referred to as “factors” or “*Elemente*,” and no clear consensus has been reached. After its rediscovery in 1900, many Mendelians, including William Bateson, interpreted Mendel’s work in a particulate paradigm, regardless of what Mendel himself may have actually thought. To be fair, Mendel can be read both ways (see Allen 2000, 2003; Brannigan 1979; Kampourakis 2013; Meijer 1983; Olby 1979).

**MECHANISTIC MATERIALISM AND THE  
MECHANISTIC CONCEPTION OF LIFE**

So, what do we mean by the “mechanistic gene,” or, more broadly, the mechanistic materialist philosophy, of which the mechanistic gene was a classic example? It was particularly fitting to raise this issue at a conference sponsored by the Jacques Loeb Center, since Loeb (1859–1924), an émigré physiologist from Germany to the United States in the early 20th century, was known as the most prominent spokesperson for the “mechanistic conception of life” at the time. The mechanistic materialism of Loeb and many of his contemporaries was based on a core set of understandings or philosophical assumptions that stand in opposition to, on the one side, vitalistic and other metaphysical, non-materialist epistemologies, and on the other, more non-reductionistic views, such as “holism” and “organicism” that were being promoted at the time, especially in physiology and psychology. (What later came to be known as dialectical materialism also promoted an anti-mechanistic stance, but it only began to exert an influence in biology in the interwar period.)

Mechanistic materialism—also referred to as “Mechanism” (with a capital M) or “the mechanical philosophy”—can be summarized by the following five propositions. First, all phenomena are based on the fundamental processes of matter in motion. Mechanistic materialism is therefore generally grounded in one or another form of realism—that is, it assumes the existence of a real world accessible by our senses directly or indirectly through some form of instrumentation. Second, mechanistic materialism holds that the whole of any phenomenon or process is equal to the sum of its parts and no more. At the time, this claim was advanced in opposition to any appeal to metaphysical forces or entities, such as a “vital force,” which had regained a kind of vogue in the early decades of the 20th century and to which avowed mechanists such as Loeb were inalterably opposed. According to the mechanistic view at the time, all living processes could be explained by reference to their chemical and physical components—and nothing more. No vital force existed that differentiated living from non-living bodies.

Following from this is the third corollary, that an organism, like any machine, is composed of a distinct number and kind of separate parts, each with its own characteristics and functions. While the individual parts of organisms—such as organelles, cells, or organ-systems—interact with one another, sometimes in complex ways like the gears and other parts of machines, the characteristics of the parts, separate from each other, determine in a summary, or additive, fashion the functioning of the whole. Concomitant with this assumption is the fourth proposition, a reductionist methodology that claims, in essence, that in order to study complex systems, they must be broken down into their component parts, each of which is studied separately and in isolation from others under controlled conditions. Once each part is described and understood completely, it is possible to explain and predict the functioning of the system as a whole.

Finally, mechanistic materialists put a large amount of emphasis on experimentation as the most rigorous part of scientific practice. Partly because they drew much of their inspiration in the early 20th century from physics and chemistry, where experimentation was a key element, mechanistically oriented biologists sought to move their field from the merely observational to the experimental mode. Experimentation allowed the testing of hypotheses that simple observation often did not. Experimentation was also a way to rid biology of speculative theories: those that could not be tested were considered superficial and a waste of time.

This mechanistic approach was adopted by a variety of biologists, especially the younger generation born in the late 1880s and 1890s. It not only placed biology on the same philosophical and methodological footing as physics and chemistry, in many younger biologists' view, but it also provided a way to study systems that were too complex to investigate as a whole. And while most biologists realized that organisms were not "mere machines," the mechanistic approach was seen as an eminently practical and heuristic way of investigating the functioning of biological systems.

Although space does not permit discussing alternative approaches at the time—the so-called "holistic" or "organismic" philosophies that gained some credence in the 1920s through the 1940s—it will be useful to point out several of the key ways in which they differed from the mechanistic philosophy. To some biologists, these differences pointed to the restricted view of biological processes embodied in the purely mechanistic approach, especially as it applied to genetics. Without being vitalistic, numerous biologists recognized that organisms were not just collections of separate parts that could be interchanged at will. (For a more comprehensive review of a variety of these approaches, see Normandin and Wolfe 2013.)

One point of difference between mechanistic and more holistic approaches in early 20th-century biology lay in the way they framed the relationships between the parts of a complex system and the whole. In holistic terms, it was argued that an important property of any component of a system is its interaction with other components, something that cannot be observed by studying the component in isolation. Thus it was argued that as useful as the mechanistic method was in isolating and enumerating the various parts of a complex system, it failed to understand the nature of the system as a functioning whole because it did not study the interactions of its parts. Following from this, holistic materialists claimed that the whole was, indeed, greater than the sum of its parts, not because of the introduction of some metaphysical element or force (though some did take such an extreme position), but because the whole involved the interactions of parts, as well as the characteristics of the individual parts in isolation. The recognition of interactions at higher levels of organization than the individual parts themselves led to the notion of "emergent properties," those that arise from the interaction of two or more components, and that go beyond the properties of the components themselves. Thus, the properties of water emerge from the interaction of two hydrogens and one oxygen and are quite different from the properties of either hydrogen or oxygen as individual molecules.

There are other points of difference between a mechanistic and holistic approach, especially as embodied in the most systematically developed of these, dialectical materialism (which emphasizes the notion of the dynamics of systems being revealed by analysis of their contradictory internal processes). The important point to emphasize here, however, is that alternative approaches were known and available, but were not the point of view that most biologists—especially geneticists—adopted in the first three or four decades of the 20th century.

### **THE MECHANISTIC MATERIALIST CONCEPT OF HEREDITY, 1860–1900**

Mechanistic materialist thinking about heredity was evident in the many theories that were proliferating during the late 19th century, for example, in the various particulate theories formulated by Charles Darwin (gemmules), Ernst Haeckel (plastidules), August Weismann (determinants and biophors), Carl von Nägeli (idioplasm), and Hugo de Vries (pangenes) (Deichmann 2010). It is important to recognize the extent of this background of particulate thinking, as it influenced profoundly the framing of concepts of the “gene” once Mendel’s work was rediscovered in 1900. Gloria Robinson’s excellent study, *Prelude to Genetics* (1979), still remains one of the best sources for detailed discussion of, and comparisons between, these various models (for shorter summaries, see also Kampourakis 2013; Rheinberger 2008). Two examples—Haeckel and Weismann—will indicate how widespread the various examples of particulate, or atomistic, thinking in theories of heredity were before 1900.

#### *Haeckel’s Theory of Plastidules*

Ernst Haeckel (1834–1919) not only promoted his morphological program based on the biogenetic law, but he also developed his own theory of heredity to fill the gap in his own and Darwin’s mechanism of natural selection. Along with August Weismann, Haeckel was one of the most prominent supporters and popularizers of Darwin in Germany. Like Darwin, Haeckel maintained an important role for the inheritance of acquired characteristics, and his theory of heredity provided a mechanism for how it might work. Unlike Darwin’s theory of pangenesis, however, which was couched in the biological terms of living units (like gemmules), Haeckel framed his theory in mechanical terms, linking it closely with theories in chemistry and physics at the time, namely of matter in motion. Robinson (1979) has shown how seriously Haeckel took his theory of heredity and its relation to physiology, chemistry, and physics.

Haeckel published his hereditary theory in 1876 in a small volume with a big title, *The Perigenesis of the Plastidule, or the Wave Generation of the Small Vital Particle: An Attempt at a Mechanical Explanation of the Elementary Processes of Development*. Like Darwin, Haeckel assumed that hereditary qualities were transmitted from

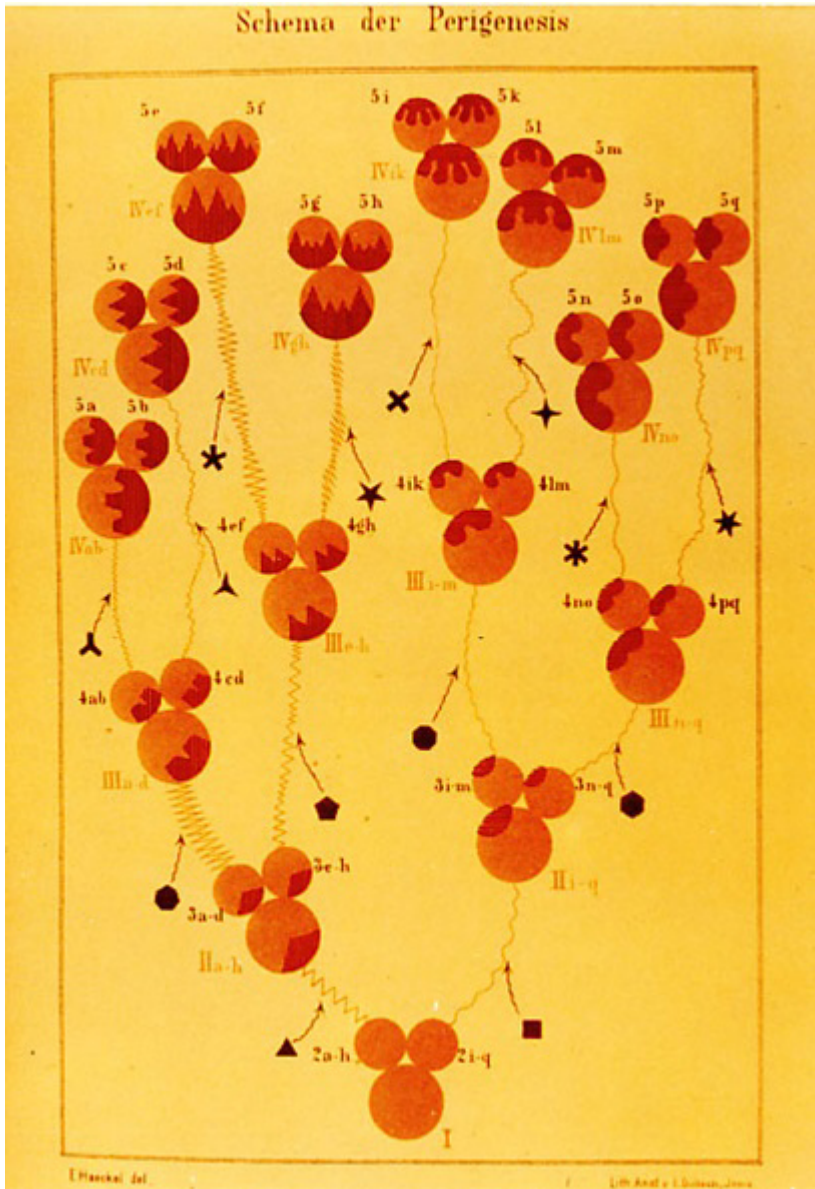


parent to offspring as particles, or molecules, which he called “plastidules.” What was characteristic of these plastidules, in addition to their molecular character, was that they were endowed, like all molecules and atoms, with an inherent motion, or “vibration.” Plastidules were the lowest level of organized molecules that made up living protoplasm, the colloidal material of the cell outside of the nucleus, and heredity was the process of the transmission from one generation to the next, not only of the material plastidule themselves, but also of their form: their frequency and amplitude of vibration. Plastidules were endowed with the property of “memory”—that is, they could reproduce themselves exactly, which they did when cells divided. According to Haeckel, exact replication meant that in its reproduction, the plastidule transmitted the same vibrational pattern, or wave-motion, as found in the original parental form. However, plastidules could also vary—that is, change their vibrational pattern—under the influence of external conditions. Here was the means by which Haeckel accounted for the origin of variations and the inheritance of acquired characteristics. But how exactly did external conditions cause variations to occur?

As shown in Figure 1, Haeckel represented the hereditary process in plastidules as a branching scheme, in which the larger spheres—for example, the one shown at the bottom center—give rise to the smaller ones (daughter plastidules) by division. The inherent motion of each plastidule, its “memory,” is designated by the darker designs within the spheres. The wavy lines indicate the vibrational motion the plastidule transmits during reproduction. The small black geometric shapes and arrows represent different environmental factors affecting the plastidules’ vibrational motion. Thus, proceeding from bottom to top of the diagram, ancestral plastidules produce descendants, each incorporating new variations (different wave motions) due to environmental inputs.

It is not surprising that this scheme resembles, in many ways, a phylogenetic tree, which is also customarily represented as developing through time from the bottom of a page to the top. Haeckel’s representation was purposefully drawn to suggest that it is exactly through the modification of plastidules’ motion over successive generations that we see the phylogenetically produced differences in the historical development of lineages diverging from a common ancestor. Haeckel’s theory of heredity fit logically with his biogenetic law and theory of descent. Like Darwin’s gemmules, Haeckel’s theory of perigenesis provided a mechanism—in his case a quasi-molecular one—for the origin of variations, and thus for creating the raw material on which selection could act. He also attempted to apply his theory to explain embryonic development, but I do not have space to discuss that mechanism here. Suffice it to say that the important point of Haeckel’s scheme is that the plastidules are particulate entities (large organic molecules) with the capacity to transmit traits and their variants from parent to offspring.

Haeckel’s scheme was a curious mixture of 19th-century mechanistic materialism and metaphysical speculation. It is difficult for modern readers to appreciate the value of such a speculative scheme, and it was criticized by many of Haeckel’s



**FIGURE 1**

Haeckel's diagram representing the units of heredity, the plastidules (larger spheres), which produce the smaller spheres by division. The wavy lines indicate the different transmitted vibrations imparted to the daughter spheres by various environmental inputs (geometric figures such as triangles, squares, octagons, etc). In this way, variations are introduced into the germ line in accordance with Haeckel's neo-Lamarckian theory.

SOURCE: HAECKEL 1876, 81.

contemporaries on just those grounds (Richards 2008; Robinson 1979). Among other things, by what physical process does a plastidule's vibrational motion get transmitted to its descendants? Haeckel noted that it was not the actual plastidules themselves that were passed on to the germ cells, but their vibrational motions, and for him this was no more abstract or metaphysical than physicists' description of the transfer of heat from one body to another as the transfer of increased molecular motion. However, an even greater problem for many of Haeckel's contemporaries was his claim that plastidules, like all atoms, were endowed with a kind of universal quality he called "soul." This idea of a grand universal unity in nature reflected Haeckel's background in German transcendental philosophy (known also as *Naturphilosophie*, or "nature philosophy"), the same tradition that gave rise to the idealistic notion of the archetype. Because of these rather metaphysical associations, a number of biologists found Haeckel's scheme, while admittedly mechanistic in style, simply too speculative in substance to provide any testable hypotheses.

The significance of Haeckel's theory for the examination of pre-1900 theories of heredity, however, is that it reflects Haeckel's strong propensity to unite the process of heredity and organic evolution (along with embryology) as a single coherent theory, expressed in some sort of materialistic, mechanical framework. Haeckel himself "believed that he was placing the subject of heredity and adaptation on a physical and chemical, or to use the term he considered most inclusive, a mechanical basis" (Robinson 1979, 48).

*Weismann and the Theory of the Continuity of the Germ Plasm*

Haeckel's ideas were rivaled for their sweeping generality by those of his countryman and contemporary, August Weismann (1834–1914). A cytologist of considerable merit at the University of Freiburg before eye trouble curtailed his laboratory work, Weismann turned his attention in the latter half of his career to the study of problems such as evolution, embryonic differentiation, and heredity (Churchill 1968). Early on he became a staunch Darwinian, and like Haeckel, sought to develop a comprehensive theory in which evolution, development, and heredity were united into a single, overarching theory (Churchill 1986). Weismann is best known today for his doctrine of the separation of germ plasm and somatoplasm: the idea that cells of the ovary and testes, which give rise to egg and sperm, represent distinct cell lines, or lineages, from the earliest stages of cleavage (cell-division) through the formation of the adult. Weismann put forward this theory to counteract the neo-Lamarckian view of the inheritance of acquired characters. After the first one or several cleavages, one of the two daughter cells (called blastomeres) was set aside to give rise, by further cell divisions, to the reproductive tissue of the adult. The other cells give rise to the remainder of the body's tissues and organ systems.

Because of this complete separation of the germ cell line from the somatic (body) cell lines, Weismann argued that changes in somatic cells during the organism's lifetime could not be transmitted from parent to offspring. To demonstrate this

point, he carried out a series of experiments on mice, in which he cut off the tails for a number of successive generations only to find that the offspring were still born with tails of the same average length as the original parents. In response, proponents of the theory of the inheritance of acquired characters argued, however, that Weismann's experiment involved mutilations, not truly acquired characteristics (as in the case of the continued use or disuse of a part), and thus had no bearing on their theory. Nonetheless, the theory of the separation of germ and somatoplasm gained a considerable following, and by the early 1900s it had been incorporated by many biologists into their understanding of Darwinian theory and Mendelian genetics. The issue of the inheritance of acquired characters through use and disuse and other forms of environmental effects, however, remained controversial through the first three decades of the 20th century.

Weismann went further in his hereditary thinking than merely demonstrating the implausibility of the inheritance of acquired characters. In an extremely ambitious conceptual scheme, he, like Haeckel, attempted to offer a single, unified explanation for evolution, heredity, and embryonic differentiation much more in line with details of cell structure and function (Weismann 1892a). Through his own and others' cytological studies detailing the highly regularized but perplexing movements of the chromosomes in mitosis and meiosis, Weismann had become convinced that the chromosomes were the primary agents of hereditary transmission. To explain the process of heredity and development, Weismann speculated that all the cells of the body, both germ and somatic, contained a hierarchical series of particulate elements, starting with what he called "idants," the visible chromosomes in the cell nucleus (Figure 2). Idants, in turn, were composed of units called "ids," arranged linearly along the idant. Each id contained all the elements necessary to form a complete individual. Ids were composed of "determinants," complex molecules representing the individual characters of the organism (Weismann 1892a, 1892b). Determinants were composed of the smallest particles in the hierarchy, which he termed "biophors"—organic molecules that were endowed with the properties of life and growth, and that chemically determined the development of that cell's specific characteristics. In developing this scheme, Weismann, in accordance with the observed facts of cytology, was trying to construct a theory of heredity that was ultimately mechanistic and particulate; it would also account for transmission of specific traits from one generation to another and the introduction of variation, all without recourse to neo-Lamarckian mechanisms. (Like Haeckel, Weismann also postulated a mechanism for how his system of units would account for embryonic development.)

Weismann's theory was more detailed, comprehensive, and rooted in then-known facts about cell structure than either Darwin's or Haeckel's. He used his observations carefully and, ambitious and premature as it may seem in retrospect, he made an honest attempt at unifying the disparate fields of heredity, development, and evolution. His ideas were far more carefully worked out than those of Haeckel

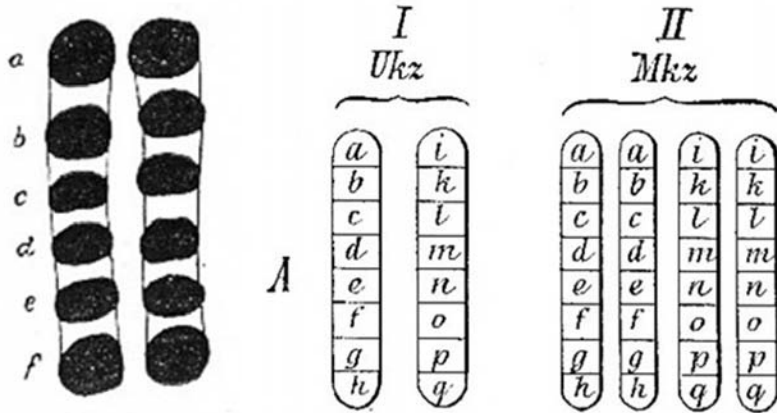


Fig. 2.  
Zwei Idanten  
mit ihren Iden,  
a—f.

FIGURE 2

Two examples of Weismann's representation of idants (chromosomes), with particulate ids (black ovals, left; lettered boxes, right) arranged along their length. Both show alignment of ids when the chromosomes have replicated. Ids contain all the hereditary material needed to produce an individual organism, though each id might differ from others in slight ways.

SOURCE: FIGURE 2A FROM WEISMANN 1892A, 91; 2B FROM WEISMANN 1892B, 137.

and, in some ways, commanded far more attention among serious biologists. Yet, like other morphological claims, Weismann's theory was highly speculative—the ids, determinants, and biophors were all hypothetical entities—and thus ultimately came to be regarded by younger investigators in the 20th century as futile because their existence, and thus their ascribed functions, was untestable (Allen 1978a).

### MENDELISM AND PARTICULATE HEREDITY

Under the pervasive influence of the atomic-molecular theory that was so prominent in the physical sciences in the latter half of the 19th century, students of heredity framed their theories in physico-chemical terms (as particles or atomistic units). Whether in terms of visible structures like chromosomes, sub-chromosomal components, or imaginary entities like gemmules, plastidules or biophors, the germ plasm was seen as a collection of units each in some way controlling a specific character or trait of the adult organism. Geneticist-turned-historian Leslie C. Dunn (1965) has referred to these germinal elements as “living units” (33) and, as we have seen in the case of both Weismann and Haeckel, this is not an inappropriate designation. In the late 19th century, with the spectacular advances in organic chemistry, much of it in Germany, the line between the organic and living and the

inorganic and nonliving was becoming increasingly blurred. But whether the term “living” was applied to germinal elements or not, the crucial feature was that these units were discrete and, at some level, thought to be composed of complex molecules. These various approaches were all a reflection of an underlying commitment to mechanistic materialism that, by 1900, characterized biology in general, and the study of heredity in particular.

It was in the tradition of these earlier, corpuscular notions of heredity that the rediscovery of Mendel’s work occurred, and thus conditioned the ways in which early-20th-century geneticists framed the new concept of the gene.

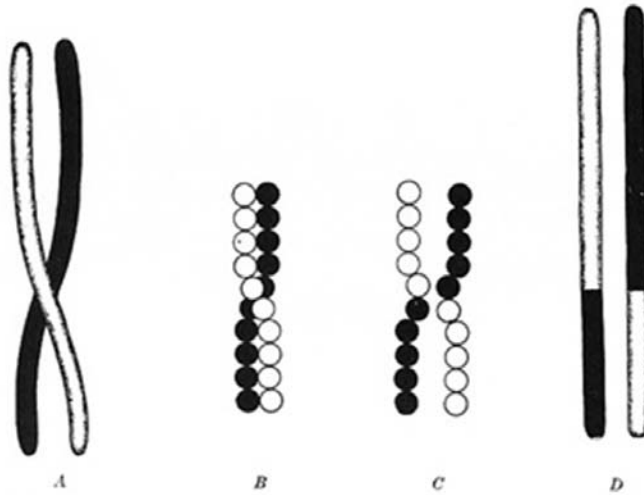
### *The Mechanistic Gene*

There has been much discussion among both historians and philosophers of biology about what was meant by the term *gene* in the early decades of the 20th century. How did it relate to Mendel’s “Factors,” “Anlagen,” or “Elemente”; to Bateson’s concept of “unit-characters” or “allelomorphs”; to the instrumentalist “gene” of Johannsen, E. M. East, and T. H. Morgan; and finally, to the functional/physiological focus of developmental geneticists such as Richard Goldschmidt or Boris Ephrussi (Burian 2005; Falk 2009; Gilbert 1978; Orel 2010). Nevertheless, despite these differences, as historian-philosopher Richard Burian (2005) has pointed out, there were core ideas on which various workers at the time could agree when they used the term *gene* that were independent of the investigators’ ontological positions about whether genes were real material entities or occupied distinct positions on the chromosomes.

That core position followed the basic mechanistic view that genes could be treated heuristically like the atoms of the chemist: they were discrete entities whose assortment and re-assortment followed certain statistical rules and could be used to make predictions, which could then be tested by making the appropriate experimental cross. The genotype, and in many ways the resulting phenotype, of the organism was thus a mosaic of particles (genes, making up the genotype) and characters (distinguishable traits making up the phenotype) of the adult. Such particles were, for the most part, independent of each other, and their history did not matter—that is, like atoms, whatever combinations any particular gene had participated in during previous generations did not matter to its functioning in the current generation. What *was* important was how genes combined and recombined in each new generation to produce particular combinations of characters. As Bateson put it as early as 1901:

Insofar as Mendel’s law applies, the conclusion is forced upon us that a living organism is a complex of characters of which some, at least, are dissociable and are capable of being replaced by others. We thus reach the conception of unit *characters*, which may be rearranged in the formation of reproductive cells. It is hardly too much to say that the experiments which led to this advance in knowledge are worthy to rank with those that laid the foundation of the Atomic laws of Chemistry. (qtd. in Punnett 1928, 2:1)



**FIGURE 3**

*Depiction of chromosomes as composed of subunits, discrete genes arranged in a linear order, like beads on a string. This figure shows a homologous pair of chromosomes undergoing chiasmata and crossing-over, exchanging genes. This figure shows clearly the discrete, atomistic way in which genes were conceived as parts of chromosomes, as well as the process of exchanging parts that formed the basis of their mapping procedure.*

**SOURCE:** MORGAN ET AL. 1915, 60.

Or, as he stated a year later in a speech to the New York Horticultural Congress: “The organism is a collection of traits. We can pull out yellowness and plug in greenness, pull out tallness and plug in dwarfness” (qtd. in Levins and Lewontin 1985, 180).

The early Mendelian notation made perfect sense in its correspondence to a generalized particulate, or atomistic, concept of heredity: *T* stood for the discrete entity that determined tallness, and *t* for a similar, alternative entity that determined dwarfness. For committed mechanistic materialists like T. H. Morgan, it did not make a difference whether *T* and *t* were totally operational units or were real material entities. From my reading of Morgan, however, it seems clear that he did believe genes were in some form physical, molecular entities in the real world, but knowing what they were or how they functioned was not crucial to explaining their behavior during recombination or during their interactions, as in epistasis. By contrast, Bateson’s much stronger commitment to a non-materialist epistemology, and thus his unwillingness to consider genes as associated with physical structures like chromosomes, led to his description of genes as abstractions, what he called “stable resonances,” and to his complex hypotheses of “attraction and repulsion,” and later “reduplication,” to explain the phenomena of linkage and recombination. Morgan, despite his agnostic position on what genes actually were, was nevertheless upfront about his philosophical preference for a materialist explanation when he

and his colleagues wrote in the first edition of *The Mechanism of Mendelian Heredity* in 1915: “Why, then, we are often asked, do you drag in the chromosomes? Our answer is that since the chromosomes furnish exactly the kind of mechanism that the Mendelian laws call for; and since there is an ever-increasing body of information that points clearly to the chromosomes as the bearers of the Mendelian factors, it would be folly to close one’s eyes to so patent a relationship” (viii). And clearly, the early depictions of the chromosome as a series of genes—the so-called “beads on a string” model—visually reinforced their particulate, atomistic nature (Figure 3). This rampant atomism was carried even further by R. A. Fisher who, in establishing the basis of population genetics, claimed that the mechanistic conception of the gene would do for evolution what the kinetic theory of gases had done for physics. The study of natural selection, he wrote in 1922: “may be compared to the analytic treatment of the Theory of Gases, in which it is possible to make the most varied assumptions as to the accidental circumstances and even the essential nature of the individual molecules, and yet to develop the general laws as to the behavior of gases, leaving but a few fundamental constants to be determined by experiment” (321–22; qtd. in Provine 1971, 149).

What I want to emphasize is that whatever the ultimate ontological view that biologists held about the nature of genes themselves, most tended to treat them heuristically as particulate elements, in most cases presumed to have some actual material existence, though of an unknown nature: perhaps as enzymes, hormones, or some other kind of complex organic molecule.

This original, simplistic conception of particulate inheritance quickly began to undergo various modifications, however, as new patterns emerged in breeding experiments. Gene interactions (epistasis), quantitative inheritance, position effects, the balance theory of sex determination all forced some reconceptualization of the mechanistic materialist concept of the gene. However, most if not all of the newer phenomena could be explained by some modifications of the original Mendelian paradigm, so the basic core of the corpuscular gene remained intact throughout the period of classical genetics. Thus, despite vocal opponents, including those with a special concern for embryonic development, such as Richard Goldschmidt, Edwin Grant Conklin and Albert Dalcq, the core notion of separate, discrete entities remained central to evolving understandings of the gene as both a structural and functional element. It was retained precisely because it was eminently successful in the early development of genetics as a new experimental science. It put biology in general and genetics in particular on the same footing as chemistry and physics.

I would now like to turn to one of the most important of the other factors that augmented—indeed, provided the basis for—the rapid development of Mendelian genetics: how the corpuscular gene resonated well with the developing economic imperative to move capital into the industrialization of agriculture in the early 20th century.



## THE MOVEMENT OF CAPITAL AND EXPANSION OF AGRICULTURE, 1890–1950

In recent decades, a number of authors have discussed the mounting desire in the early 20th century to industrialize agriculture and to develop more reliable methods of animal and plant breeding (Berlan and Lewontin 1986; Fitzgerald 2003; Harwood 1997; Kloppenburg 1988; Levins and Lewontin 1985; Palladino 1990, 1994). In this process, the application of the new science of Mendelian genetics increasingly seemed to provide direction. Several of these authors (Berlan and Lewontin, and Kloppenburg) have explicitly placed their analyses in the framework of Marx's theory of the movement of capital—that is, the need in a market, investment-driven economy to move capital from one sphere to another where profits can be higher, and to beat others to the draw in the process. (This analysis is admirably applied to the Human Genome Initiative by Rodney Loeppke [2005]). In this investment drive, science and technology have historically played crucial roles. Central to this notion is the commodification of agricultural products—that is, their production for sale, rather than for one's own use. Applied to agriculture, this has meant commodification of animals and plants with specific values, such as high productivity, low resistance to disease, and other marketable phenotypic traits.

It is clear that in the period of the later 19th century and throughout most of the 20th century, capital expansion into agriculture moved rapidly and aggressively. There are two major reasons for this. First, industrial growth in the latter half of the 19th century led to capital accumulation and thus the need for new arenas of expansion. Investors had always looked to agriculture as one possibility for expansion, since food was one commodity that was always going to be in demand. Second, industrialization had been accompanied by urbanization and the migration of workers to cities, creating more consumers and fewer farm hands as producers. The net result of this demographic shift was pressure for increased agricultural productivity outside of the traditional family farm, which often operated just slightly above subsistence level and depended largely on non-mechanized manual labor and its own inputs, such as animal power, natural fertilizers, and seeds saved from the previous year's harvest.

However, traditional agriculture had always posed difficulties for high-level investment: land was expensive and limited, climate was variable and unpredictable, and animal and plant husbandry was based on empirical rules-of-thumb that were neither very predictable nor easily brought into the large-scale market system. More important, traditional farms were small—cottage industries in a way—and were seen as inefficient units operating each on its own methods and individualistic principles. As Deborah Fitzgerald has shown in her book, *Every Farm a Factory* (2003), the industrialization of agriculture was a much-discussed goal of many agronomists and potential investors from the 1880s onward. The rationalization of agriculture—that is, placing it on a scientific base—had already entered its first phase with the agricultural chemistry of Justus von Liebig at Giessen during the

mid-19th-century, which had focused on issues such as soil chemistry, animal and plant nutrition, and the use of fertilizers. While this movement had achieved considerable success, it had also encountered skepticism and controversy—and at any rate had begun to reach the limits of its effectiveness. By the 1890s, however, the Progressive-era ideology of “scientific management” and “industrial efficiency” in both Europe and the United States created an environment for rationalizing agriculture anew—but this time, in addition to issues of improvements to the environment, particular attention was being paid to improvements to the hereditary makeup of animal and plant varieties. By applying scientific methods of animal and plant breeding, production yields could be taken to the next higher level. Many other related economic sectors also saw industrialization of agriculture as potentially profitable: the farm machine industry (John Deere, Ford, International Harvester), the chemical fertilizer industry (W. R. Grace, Occidental Petroleum), the railroads (Illinois Central, Great Northern, Southern Pacific), and a growing food-processing industry (Del Monte, Heinz), especially canning. In addition, the rise of grain exchanges as a source for profitable commodities trading and the potential for producing food for export provided yet another avenue through which increased agricultural output could be potentially profitable.

That all of these various economic potentials came together to ultimately transform agriculture from small-scale farming to what later came to be known as “agribusiness” is indicated in Table 1. Note that over the 100-year period, the contributions of capital and labor almost completely reversed. A major feature of the industrialization process was also to move many agricultural inputs to off-farm sources, where full-scale industrial relations of production already existed in full-swing: the production of farm machinery, fertilizer, and later pesticides—all of which under traditional practice were largely inputs from the farm itself—to the point where farming became what Jack Kloppenburg (1988) has referred to as “the most capital-intensive sector of the modern capitalist economy” (31).

**TABLE 1** CHANGING AGRICULTURAL PARAMETERS IN THE UNITED STATES, 1870–1970

<i>Year</i>	<i>Labor Input (% of Total)</i>	<i>Capital Input (% of Total)</i>	<i>Farms Over 1,000 Acres (in thousands)</i>	<i>Corn Harvested (Bushels/Acre)</i>	<i>% Corn as Hybrids</i>
1870	65	17	29	20	0
1900	57	24	47	25	0
1920	50	32	67	29	0
1940	41	41	101	30	15
1960	27	54	136	53	94
1970	19	58	216	70	95+

Source: U.S. Dept. of Commerce 1975, 1:467; Kloppenburg 1988, 89, 120.

Note: It should be pointed out that not all of the gain in yield is due to genetics. New fertilizers, pesticides, and other inputs also contributed to the increases shown in bushels/acre. Nevertheless, genetics did make a substantial contribution, especially after World War II.

So, how did the industrialization of agriculture impact genetics in any direct or measurable way, and in particular, how did it relate to the mechanistic view of the gene? There are several routes by which the capital expansion of agriculture had a major impact on the new field of genetics. Going back to the root of genetics itself, it is worth noting that Vitezslav Orel and Roger Wood, among others, have produced persuasive evidence that Mendel's own work was carried out with agricultural interests in mind, and that he was trying to develop a systematic, scientific approach to understanding regularities, or patterns, of hybridization (Orel 1996; Orel and Wood 2000; Wood and Orel, 2001). He was not, as has been traditionally portrayed, trying to develop large-scale theoretical concepts of heredity in the Darwin, Haeckel, or Weismann mode. Thus, when Mendelian genetics was rediscovered, it already carried a certain agricultural tradition, or at least a ready-made applicability to agriculture, embedded within it. It is not irrelevant to note that in 1902, when Bateson came to the United States, he wrote back to his wife that his most enthusiastic Mendelian supporters were farmers and agronomists. They greeted him at the railroad station in Ithaca, New York, for example, where he had been invited to speak by Liberty Hyde Bailey, the dean of the agricultural college at Cornell, who is reported as having waved copies of Bateson's recent book, *Mendel's Principles: A Defense*, shouting "Mendel, Mendel all the way!" (qtd. in Paul and Kimmelman 1988, 283).

But more directly, Mendel's work appeared to provide the first set of breeding results that followed a regular pattern across a wide variety of species—both animal and plant—and that could be predicted with any reliability. While numerous anomalies and later alterations added to the complexity of the original Mendelian scheme, predictable results continued to emerge out of the basic methods of genetic analysis. An increasingly important component of Mendel's work was his method: (1) the meticulous categorizing and measuring of discrete phenotypic characters; (2) the detailed record-keeping associated with making testable parental crosses and counting numerical ratios of offspring categories; (3) the repeatability of crosses made with statistically significant numbers of offspring; and (4) the importance of controlled conditions. These practices all made Mendelian genetics appear to be the rational, scientific approach to animal and plant breeding that had heretofore been lacking. It was what Philip Thurtle (2007) has termed "the emergence of genetic rationality"—that is, the systematic approaches to collecting, recording, and organizing data/information applied specifically to genetics. Thurtle emphasizes that these methods had been developed to a high degree of efficiency by modern industry (since the 1860s) and included input and output tables, methods of tracking items over complex transportation systems, and the use of statistical analysis of consumer habits. That these practices were absolutely essential to the development of early genetic thinking is quite clear, but of course they were also standard methods in the physical sciences at the time, so it is not clear that emerging industrial practices were necessarily the only, or major, source of such thinking in the life sciences. However,

Thurle argues persuasively that the emphasis on being systematic and rational was very much a component of Progressive-era thinking in general, and so was part and parcel of the development of industrial methods in particular. At any rate, Mendel's methodology, his focus on discrete hereditary elements (whether material or symbolic is not crucial), and his highly rational, systematic approach made a perfect fit with the industrial ideal in general, and with industrial agriculture in particular.

Another feature of Progressive-era industrialization was the emphasis on standardization and uniformity. As Fitzgerald has shown in *The Business of Breeding* (1990), most varieties of corn in the Midwest were highly variable, as they were adapted to local conditions and could not be grown as well when planted elsewhere—even a few counties away. If we consider just seed production as part of the industrialization of agriculture, this would be equivalent to manufacturing different automobiles for every city or town—hardly an attractive approach for efficiency and large-scale profit. Mendel's methods, especially the theory of inbreeding and outbreeding as developed by E. M. East, George Harrison Shull, and others, offered the prospect of achieving a kind of uniformity in seed production and growth that appealed to industrial modes of production.

But what about the mechanistic gene itself: why did it have a greater appeal than, say, a non-particulate theory of heredity? In the latter case, “blood” or “blending” theories of inheritance had been prominent for centuries and made it difficult to conceive of ways to keep a breed or variety stable and pure. Full mixing of hereditary contributions from bi-parental reproduction tended toward homogenization of the germinal material and thus would “swamp” any new variations that arose. (This had been one of Darwin's major difficulties, since he did believe in a form of blending inheritance.) Particulate theories, however, could avoid this problem, since if particles of heredity, like atoms of chemistry, retained their integrity and basic properties from one combination to another, they would not be lost in subsequent generations, even if they were recessive or became latent.

However, particulate theories also had two additional appeals. First, mechanistic materialist views grew up with the machine analogy, as the foundation of these views derived directly from the rapid introduction of various forms of machine-based labor (in mining, transport, textiles, and the like) in the 17th and 18th centuries. Since mechanistic thinking clearly dominated the metaphorical landscape of the industrial revolution and beyond, the idea of a genome composed of separable parts that could be “plugged in” and “taken out” at will, without altering the whole organization of the machine/organism, was likely to have resonated well with those frustrated by traditional methods of breeding, in which new traits were constantly being lost or modified in unpredictable ways. To make the analogy explicit, in a bill introduced into the U.S. Congress in 1906 to patent seeds, one proponent stated that “every seed is a mechanism as is a trolley car.”

A second way the mechanistic gene would have fit in well with the ideology of industrial agriculture is that genes provided the basis for differentiating between varieties as commodities: they are the real, substantive differences between one strain

of wheat, corn, or poultry and another. While it was not possible to patent genes at the time (legal battles over that issue would come only much later), it was possible to construct hybrids or particular genetic combinations from strains only the seed producer maintained—and of course, since hybrids do not breed true, they become a true commodity in that they must be bought anew every season.<sup>2</sup> The fact that many hybrids were more vigorous and gave higher yields than most inbred strains (known as heterosis or “hybrid vigor”) was the special selling point, compensating for the added expenses they incurred, such as increased fertilizer and pesticide inputs, large farm machinery for plowing and harvesting, and having to purchase new seeds every year. In this way, hybrid seeds favored the larger, industrialized farmer, who could make the system work profitably only by growing on a large scale (Berlan and Lewontin 1986; Levins and Lewontin 1985).

Mendelian genetics certainly was not the only system of heredity that could have been, or was, the focus of attempts to increase agricultural yield during the period of the industrialization of agriculture. Nor did profit-driven investors simply “invent” out of whole cloth a genetics that fit their specific needs. In the United States and Europe, numerous agronomists were initially attracted to alternative theories of heredity in addition to Mendel: for example, de Vries’s mutation theory (United States, Germany) and neo-Lamarckism (France, Germany, Soviet Union). What is important to emphasize here—and I think it applies to the interaction of science, technology, and capitalist development overall—is that in any historical epoch, a variety of approaches exist in the scientific/technological sphere from which those with the funds to control research choose, in order to solve the particular economic problems at hand. Thus science, technology, and the development of capital have both independent and interdependent lines of development that can converge on occasion to push science/technology along one line rather than another. But it is ultimately the sources of funds coupled with the science/technology that is available, in either partially developed or undeveloped forms, that determines which research gets pursued and which does not.

Although all this sounds logical enough, how do we know such realizations were consciously recognized and promoted in a Mendelian context? From a historiographical point of view, there has been much controversy about whether genetics did in fact have, or was ever expected to have, much real impact on the development of 20th-century agriculture. Individuals from a variety of sectors of American society in the early 20th century—scientists, industrialists, potential investors, and government officials—all had high hopes for a scientific agriculture that would provide increased yields, more efficient means of production, and considerable profit.

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<sup>2</sup>Shull’s and Jones’s double-cross method of seed production involved creating two hybrid strains and then crossing the offspring with each other, so that the segregation of traits in future generations was insured. Thus there was virtually no likelihood that any of the original parental combinations would be retained in future offspring.

It is probably no exaggeration to state that one of the most potent investors and capitalists in the early 20th century was Andrew Carnegie. In his philanthropic efforts to fund biological science, in 1903 he established the Carnegie Institution of Washington (CIW), one of whose main aims was to promote a scientific approach to agriculture. At a meeting of the Scientific Advisor Board of the CIW in December 1908, part of the discussion revolved around whether to continue funding the work of plant breeder and “Wizard of Santa Rosa” (California), Luther Burbank (1849–1926). Burbank was becoming famous for creating all sorts of new varieties of fruits, vegetables, and ornamental plants. He worked by a combination of practical experience, trial-and-error, and some self-taught biological principles, including grafting and hybridization. The Directors had raised questions about the relative contribution of scientific theory to commercial products coming out of Burbank’s work (Rheingold 1979). After listening to the discussion for a while, Carnegie chipped in: “My friend here said the only thing we expect is a scientific report, and my other friend here said the only thing we would get would be an economic result. . . . I would like to know what our scientific reports avail us if the end be not economic gain, that we shall get plants which will yield revenue . . .?” (CIW 1908)

Clearly, supporting agricultural research that would lead to “economic gain” was an important criterion for the CIW’s decision about which research to support. Although controversial from the scientific point of view, so highly was Burbank regarded by some scientists—Liberty Hyde Bailey, Hugo de Vries, and David Starr Jordan (then President of Stanford University), among others—that the entire CIW Committee of the Division of Biology visited Santa Rosa in 1906 to inspect his work; they also decided that George Harrison Shull, a pioneer in hybrid corn breeding, should spend a part of the next several summers working with Burbank, recording and evaluating his methods (Glass 1980). While the CIW ultimately withdrew their support after Shull found the work had no underlying scientific foundation, it did fund, in 1904, the Station for Experimental Evolution at Cold Spring Harbor, New York, whose Director, Charles B. Davenport, set up the institution specifically to pursue studies on heredity and selection in agriculturally important animals and plants (Allen 1986, 2004). This included not only Davenport’s own work on breeding chickens, but also Shull’s early work on hybrid corn, which was carried out at the station from 1904 until 1915. Later, as the CIW’s Department of Genetics, the Station served as the research home of Barbara McClintock, who also worked on maize, from 1941 until 1992. Through external grants, the CIW also funded a variety of genetics research programs, most notably that of T. H. Morgan and his group at Columbia University (1915–1928) and thereafter at the California Institute of Technology. The CIW was thus a major financial backer for work in heredity with a distinct leaning toward agricultural development.

Scientists at the U.S. Department of Agriculture (USDA) were equally excited about new prospects for introducing scientific breeding into agricultural practice

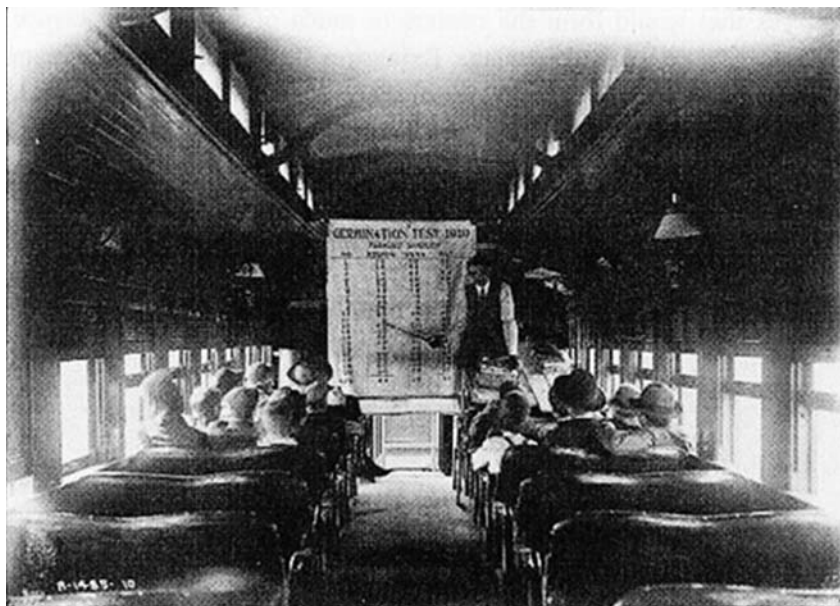
at the turn of the century (Paul and Kimmelman 1988). Several, such as Willett M. Hays of the USDA Experiment Station in Minnesota, W. J. Spillman at the USDA in Washington, and H. J. Webber at the USDA Experiment Station in Florida, were all involved in founding the American Breeders' Association in 1903, an organization designed to bring together academic biologists and practical breeders to exchange ideas in many areas of mutual interest (Kimmelman 1983, 1997; Paul and Kimmelman 1988). The organization's journal (at first the *ABA Annual Report*, and from 1910–1913, *The American Breeders' Magazine*) published articles side-by-side on theoretical issues of Mendelian genetics or Hugo de Vries's controversial "mutation theory" and on breeding pears, carnations, or horses. Many supporters of this new movement, such as Hays, saw the immense economic potential in harnessing the "power of heredity" to improve animal and plant production. Hays once calculated that investing \$100,000 in creative breeding would lead annually to \$100 million in gross returns (Hays 1905a). He also noted that a great advantage of breeding was that, once developed, the new strains would reproduce themselves in perpetuity (Hays 1905b).

Similar views were expressed a few years later at the highest level of the USDA. In 1910, Secretary of Agriculture James Wilson was invited to write an introduction to the newly transformed *American Breeders Magazine*. In his short three-page introduction, Wilson noted the important potential that lay in the new approach to animal and plant breeding:

Recent work in heredity and improved breeding has inaugurated a new era in research, in improved methods, and in the demand by growers for improved plants and animals. . . . Judging from achievements already accomplished, 10 per cent is a conservative estimate of the increase which can thus be made. . . . Improvements by breeding are unlike those secured by adding new acres to the cultivated areas of the country, by deeper plowing, by more frequently cultivating the crop, by adding to the soil larger supplies of fertilizers, or by giving a more expensive ration to farm animals. These improvements, though they greatly increase the farmers' profits, are secured at a cost which sometimes equals the value of the added product. But the cost of improvements through breeding usually represents only a small fraction of the added values. The increase of products secured by breeding pays the cost in a short time, and, since there is no further expense, the annual increase afterward is pure profit. (4–5)

Wilson went on to note that a new scientific approach to breeding would have economic spin-offs well beyond the breeding industry itself: "The farmer will be able to retain a part of the larger production in the form of added profit, and part will help reduce the cost of living to those in our cities. Larger production on the farm will also give increased business for the transportation company, the manufacturer, and the merchant, and will provide the nation was a larger product with which to hold our balance of trade" (5).



**FIGURE 4**

*Demonstration train showing a lecture by Iowa State University extension service representative giving a talk on “Seed Germination.”*

**SOURCE:** AMIDON 2008, 325.

Wilson was right, as many other industrial developments would benefit from increased agricultural output. One was the railroads. In an attempt to increase their business from farmers, railroads even initiated various extension programs, bringing farmers and genetics experts together in railroad car classrooms (Figure 4), where the latest findings in various areas of agronomy would be presented (Amidon 2008). At the time, Wilson failed to see that seed companies would not find much incentive in producing new strains that the farmer only bought once, but the general principle that breeding results can provide higher profits because the organism reproduces its improved traits was clear enough to act as a significant incentive.

Biologists working on the improvement of the hereditary makeup of agriculturally important plants and animals also saw the economic potential to be gained from scientific breeding. Edward Murray East at Harvard and his student Donald F. Jones, later at the Connecticut Agricultural Station at Storrs, were major contributors to understanding the effects of hybridization in corn. In their highly influential publication of 1919, *Inbreeding and Outbreeding*, they noted that hybrids would provide the way for seed companies to develop a product that would at last be profitable. Mendelism, they wrote: “is not a method that will interest most farmers, but it is something that may easily be taken up by seedsmen; in fact, it is the first time in agricultural history that a seedsman is enabled to gain the full benefit from a desirable origination of his own” (224). East and Jones did go on to



point out that in contrast to other types of inventions, which can be patented, the legal obstacles to patenting seeds and organisms reduced the incentive for private investment. However, as they pointed out: “The utilization of the first generation hybrids enables the originator to keep the parental types and give out only the crossed seeds, which are less valuable for continued propagation” (224).

One further example will indicate the degree to which academic biology, in the form of Mendelian genetics, was seen as a viable handmaiden to agricultural improvement in the Progressive era. In perusing the correspondence files between T. H. Morgan and Raymond Pearl at the American Philosophical Society several years ago, a proposal turned up to establish a Department of Genetics at Columbia University, written somewhere around 1920. Typewritten but unsigned, it seemingly was intended to be submitted (or perhaps was submitted) to the Columbia administration. Although no such department was created, the rationale for doing so placed agricultural interests at the forefront:

The science of genetics is fundamental for all agriculture. By purely empirical methods breeders have brought certain of the domestic animals to a high state of development. But an exact and comprehensive knowledge of how these results have been attained, and may be attained again, is, in general, lacking. In the last decade definite knowledge of the laws of inheritance has made greater advance than in the entire previous history of mankind. (Morgan Correspondence, Raymond Pearl Papers, American Philosophical Society, pp. 1–2)

Even granting that applications for new resources (funds, departments, facilities) may have overemphasized the importance of practical outcomes, it is noteworthy that such a department was proposed in the first place for a high-level research institution such as Columbia University. Similarly, the fact that the application of Mendelian principles to agricultural improvement did not pay off immediately and the industrialization of agriculture did not begin to become profitable until the 1940s does not negate the immediate importance that was attached to supporting genetic work in the first three decades of the 20th century. Without that support, I argue, genetics certainly would not have developed as rapidly as it did, nor perhaps have engendered as much enthusiasm and excitement among biologists and agronomists alike. As just one indication of how agricultural interests contributed to the development of genetics, the Appendix provides a partial list of major geneticists in the United States and Europe who worked in agriculturally related institutions or were directly funded by agricultural interests. While many of these geneticists were not always motivated by specific agricultural applications, agriculturally based institutional or financial resources allowed them to pursue the work in a way, and at a pace, that otherwise would have been difficult or impossible.

Finally, the growth of genetics rode high on the wave of professionalization that was sweeping through the life sciences in the early 20th century, as it had through the physical sciences in the latter half of the 19th century (Appel 1988; Palladino

1994). Indeed, genetics became the crown jewel for biologists wishing to become as professionally recognized as physicists and chemists, and to be comparable in the analytical quality and rigor of their science. Genetics had all the earmarks associated with the high-status physical sciences: it was experimental, quantitative, mathematical, and predictive. It was based on a corpuscular view like the atomic-molecular theory. Philosophically, it provided a method for rigorously testing and confirming or rejecting hypotheses. It was mechanistic and atomistic without the large-scale speculations associated with Weismann, Haeckel, or others of the previous generation. I would argue that one of the reasons young biologists so promoted experimentalism as an ideal was that it signified the new, professionalized side of the life sciences that was emerging—especially in the form of genetics—at the time. Thus genetics suited the needs not only of agricultural breeders, government, and investors, but also of a burgeoning group of young and some not-so-young biologists seeking increased status, positions, and funding for their work.

All of these strands came together to help propel genetics to the forefront of the life sciences, and to give biology as a whole increasing stature among the sciences—a stature that has only continued to increase through the era of molecular genetics down to the present day. The whole second half of the 20th century saw another massive wave of capital movement into genetics, not only in the agricultural realm with GMOs, but now greatly augmented by the medical and pharmaceutical industries. Clearly by now, genetics has become one of the biggest players in the global economy.

### CONCLUSION

The idea of the corpuscular—discrete and atomistic—gene that became the dominant paradigm for genetics in the first half of the 20th century rose to prominence from the confluences of several economic, social, and intellectual factors, without which the field could not have developed so rapidly and expanded so widely as it did. These factors include: the rediscovery of Mendel's work on hybridization; the economic forces promoting the rapid expansion of agriculture to keep up with the needs of a growing urban, non-agricultural work force; and the need for new arenas of investment that reconfigured agriculture along industrial lines; and the needs of a growing community of biologists aiming to professionalize their field and raise its status among the sciences as a whole. Behind all this was the new ideology of progressivism in the United States and its counterparts (such as the industrial and national efficiency movements in Britain and Germany), which encompassed managed (regulated) capitalism, rational planning, efficiency, and the call for stronger, centralized government regulation of the economy and its institutions.

The corpuscular or atomized view of the gene fit well into this complex of economic, social, and intellectual developments: it was measurable, it could be manipulated and its effects predicted, and because it was a material entity, it could

ultimately be commodified. It was also a simplified view that could be communicated and presented in textbooks and even applied to the solution of social problems in the form of eugenics, whose motto was “the self-direction of human evolution.” But these added values to the genetic capital came with a price. They led many biologists to promote a simpler picture of what genes were and what they do than ultimately turned out to be the case. This oversimplified view in turn led to serious social claims in the name of eugenics that extended beyond the eugenic era to today—to the ideology of genetic determinism, the claim that genes are the basis for much of human social behavior and personality traits. “Genes for” alcoholism, criminality, IQ, religiosity, or laziness remain one of the most troublesome legacies of the atomistic gene concept.

The relationship between economic and social factors and the rise of the corpuscular gene is not, however, a matter of simple cause-and-effect, in which capital investment requires a marketable produce and science/technology provides it. Rather, the economic and social conditions provide an environment in which certain investment opportunities are available, or seem to have potential; these are encouraged in various ways through private funding (the CIW) or government support (the USDA and its network of Experiment Stations). Various scientific technologies may be available in well- or less well-developed forms, and one or more of these may be promoted at the same time or in tandem. Other scenarios exist in which an economic need stimulates research to find a particular solution, as in selection for resistance of wheat to infection by rust (*Puccinia graminis*). The point is that while there is no one-to-one or linear relationship between economic imperatives and scientific/technological outcomes, the former do provide the conditions in which the latter develop. All of the developments discussed above existed in an environment in which agriculture was being expanded along an industrial model that promoted large-scale production, commodification (and standardization) of products, post-harvest longevity, disease and drought resistance, predictability of yield and quality, and transportability. Particularly important, industrially developed agricultural commodities needed to be protected as private property, whether by patents or other means, in order to insure their investment return. In all of these respects, Mendelian theory in general, and its incarnation as the atomistic gene, fit the bill perfectly.

The entire Mendelian research program or paradigm promoted a quantitative, experimental approach to heredity that was, at one and the same time, based on a mechanistic materialist approach in tune with the prevailing ethos of the hard sciences. The atomistic gene concept could lead to predictable results, could be manipulated to provide novel combinations (analogous to the invention of machines with removable/exchangeable parts), and could be privatized by patenting the process for producing the strains (as in the double-cross method) or by maintaining exclusive combinations of traits in parental forms owned only by the breeders. Ultimately, even as early as the first decade of the 20th century, it was hoped that

individual genes or combinations of genes could someday be subject to individual patents (which has now happened ). While the products of other hereditarian approaches—blending inheritance, neo-Lamarckism, or de Vriesian mutations—might have seemed able to meet some of these needs at the outset, the fact that they did not produce predictable results eventually led to their rejection. Mendelian genetics survived not only because it was the most successful theoretical approach to understanding heredity to have been developed to date, but it also appeared early on to offer the most viable approach to a new, mechanized and industrialized agriculture that would provide a new arena for investment in the Progressive Era.

**APPENDIX** GENETICISTS ASSOCIATED WITH AGRICULTURAL OR COMMERCIAL ORGANIZATIONS AND INSTITUTIONS OR FUNDED BY THEM

<i>Name/ Dates</i>	<i>Education/ Institutional Affiliations</i>	<i>Areas of Work</i>
ANDERSON, Ernest Gustav (1891–1973)	BA, U of Michigan; PhD, Cornell under R. A. Emerson (1920)	maize genetics
ANDERSON, Edgar S. (1897–1969)	BA, Michigan State; DSc under East at Bussey Institution, Harvard (1922); Missouri Botanical Garden (1922–29, 1937–67); John Innes Horticultural Institution (1929–31)	genetics of <i>Nicotiana</i> and <i>Zea mays</i> ; population genetics of hybridization ( <i>Introgressive Hybridization</i> , 1949); consultant for Pioneer Hybrid
BABCOCK, E. B. (1877–1954)	BA, Lawrence College; PhD, U of California, Berkeley College of Agriculture; Prof, UC–Berkeley (1908–47)	genetics of <i>Crepis</i> ; reorganized curriculum at UC College of Agriculture, founded Dept of Genetics (1913)
BATESON, William (1861–1926)	AB, Cambridge; Prof of Genetics, Cambridge (1908); John Innes Horticultural Institute (1910)	introduced Mendelism to the English-speaking world; coined term <i>genetics</i> ; genetics of poultry
BEADLE, George W. (1903–1989)	BA, MA, Nebraska College of Agriculture; PhD, Cornell under Emerson (1930); post-doc, Caltech (1930–35); Professor, Harvard (1936–37), Stanford (1937–46); Caltech (1946–61); President, U of Chicago (1961–68)	crossing-over in maize; compendium of maize chromosome loci; genetic function in <i>Drosophila</i> and with E. L. Tatum in <i>Neurospora</i> ; maize origins
BLAKESLEE, Albert F. (1874–1954)	BA, Wesleyan; PhD, Harvard (1904); Connecticut Agricultural College (1904–15); Station for Experimental Evolution, Cold Spring Harbor (1915–41)	genetics of <i>Datura</i> , a noxious agricultural weed; use of colchicine to induce poly-ploidy, promoted de Vries's mutation theory
BURBANK, Luther (1849–1926)	no formal education; CIW grants (1904–9)	inspired by Darwin's <i>Variations</i> to become a plant breeder, Santa Rosa, CA (1875–1926); breeding, grafting plant varieties; new fruits and vegetables; Burbank Seeds; admired by de Vries, E. B. Babcock, and D.S. Jordan
CASTLE, William E. (1867–1962)	BA, Denison U, Harvard; PhD, Harvard (1895); Bussey Institution, Harvard (1897–1936)	early Mendelian; mammalian genetics; genetics of coat color; effects of selection on genes; genetics of horses
CREIGHTON, Harriet B. (1909–2004)	BA, Wellesley; PhD, College of Agriculture, Cornell (1933); Instructor, Cornell (1932–34), Connecticut College, Wellesley (1934–74)	student of Emerson and McClintock; cytological proof of crossing-over in maize
DARLINGTON, Cyril D. (1903–1981)	BA, Southeastern Agricultural College, Wye; Cytologist, John Innes Horticultural Institution (1924–37), Director (1937–53); Sheradian Prof of Botany, Oxford (1953–61)	chromosomal variation and evolution

<p>DAVENPORT, Charles B. (1866–1944)</p>	<p>BA, Harvard; PhD, under E. L. Mark (1892); Professor, U of Chicago (1899–1904); Director, Station for Experimental Evolution, Cold Spring Harbor (1904–34), funded by the Carnegie Institution of Washington (CIW)</p>	<p>early Mendelian; genetics of chickens, other agriculturally important animals and plants; eugenics</p>
<p>DUNN, Leslie C. (1893–1974)</p>	<p>BA, Dartmouth College; PhD, Bussey Institution under Castle (1920); Connecticut Agricultural Station (1920–28); Prof of Zoology, Columbia U (1928–62)</p>	<p>genetics of rabbits, mice; at Storrs, chickens; developmental genetics of T-locus (tailless) in mice</p>
<p>EAST, Edward M. (1879–1938)</p>	<p>BA, U of Illinois; PhD, U of Illinois (1907); Connecticut Agricultural Station (1905–9); Bussey Institution, Harvard, (1909–38)</p>	<p>chemistry of oil production and later genetics of hybrid corn, especially inbreeding and out-breeding</p>
<p>EMERSON, Rollins A. (1873–1947)</p>	<p>BS, Nebraska College of Agriculture; Editor, USDA; Lecturer/Asst Prof, U of Nebraska until 1914; Prof, Cornell (1914–47)</p>	<p>variegation in pericarp coloration in calico maize, demonstrating Mendel's laws in maize (color patterns)</p>
<p>FISHER, Ronald A. (1890–1962)</p>	<p>BA, Cambridge; Statistician, City of London (1914–18); Statistician, Rothamstead Experimental Station (1919–33); Galton Prof of Eugenics, U College, London (1933–43); Balfour Prof of Genetics, Cambridge (1943–retirement); Visiting Prof of Statistics, Iowa State (1935–36)</p>	<p>statistical analysis of variance and foundations of population genetics (1930); eugenics; decline of western civilization</p>
<p>JOHANNSEN, Wilhelm (1857–1927)</p>	<p>Asst in Chemistry, Carlsberg Laboratory (1881), Copenhagen Ag College (1892–1905), U of Copenhagen (1905–27)</p>	<p>genotype-phenotype distinction, pure line theory; limits of selection in pure-line populations</p>
<p>JONES, Donald F. (1890–1963)</p>	<p>BA, Kansas State Agricultural College; PhD, Bussey Institution, Harvard (1916); Arizona Experiment Station (1911–14); Connecticut Agricultural Station (1915–60)</p>	<p>hybrid corn, double-cross method; cytoplasmic male sterility (CMS)</p>
<p>LANDAUER, Walter (1896–1978)</p>	<p>PhD, Heidelberg (1922); Prof of Animal Genetics, U of Connecticut, Connecticut Agricultural Station, Storrs (1924–64)</p>	<p>genetics of development (chickens), specifically the relation of specific gene mutations to abnormalities of development</p>
<p>McCLINTOCK, Barbara (1902–1992)</p>	<p>BS, Cornell; PhD, Cornell (1927); Prof, U of Missouri and USDA, Columbia, MO (1936–41); Dept of Genetics, Carnegie Institution of Washington (CIW), Cold Spring Harbor Laboratory (1941–92)</p>	<p>cytogenetics of maize and proof of crossing-over; transposable elements in maize; genetic control of development via cytoplasmic signaling</p>
<p>NILSSON-EHLE, Hermann (1873–1949)</p>	<p>Candidate and Licentiate degrees, U of Lund; PhD, Lund (1909); Chair of Plant Physiology, U of Lund (1915), Genetics (1917); Swedish Seed Association, Svalöf, Assistant (1900), Director (1925–39),</p>	<p>one of first to demonstrate that economically important plants followed Mendelian laws; Mendelian basis of quantitative inheritance (1908–11)</p>
<p>PEARL, Raymond (1879–1940)</p>	<p>BA, Dartmouth; PhD, U of Michigan (1902); Head, Dept of Biology, Maine Agricultural Station (1907–18); Head, US Food Administration (1917–19); Prof of Biometry, Johns Hopkins (1918–40)</p>	<p>genetics of poultry and cattle; effects of alcohol on germ cells; application of statistics to animal and human breeding, life cycles and population growth</p>

<p>RHODES, Marcus M. (1903–1991)</p>	<p>BA, MS, U of Michigan; PhD, Cornell, under R. A. Emerson (1932); Research Fellow, Cornell (1932–35); Research Geneticist USDA, Ames, IA (1935–37); Arlington Experimental Farm, VA (1937–40); Prof, Columbia U (1940–48); Prof, U of Illinois (1948–58); Prof, Indiana U (1958–74)</p>	<p>cytoetics of maize; cyto-plasmic male sterility and <i>iojap</i> gene-chloroplast interaction; preferential segregation in abnormal chromosome 10; numerous theoretical and practical problems in genetics of maize</p>
<p>SHULL, George Harrison (1874–1954)</p>	<p>BA, Antioch; PhD, U of Chicago (1904); US Bureau of Plant Industry; Station for Experimental Evolution, CSH (1904–15); Prof of Biology, Princeton (1915–42)</p>	<p>worked on cytology of <i>Oenothera</i>, hybridization in maize and peas; studied heterosis; methods of out-crossing in breeding to improve crop yields</p>
<p>STADLER, Lewis J. (1896–1954)</p>	<p>BS, U of Florida; graduate study, Cornell, with Emerson (1919); PhD, U of Missouri (1922); Prof, Dept of Field Crops, U of Missouri/USDA (1922–54)</p>	<p>X-ray and UV induction of mutations in field crops, especially corn</p>
<p>TSCHERMAK, Erich von Seysenegg (1871–1962)</p>	<p>Agricultural Diploma, U of Halle; PhD, U of Halle (1896); Prof, U of Agricultural Sciences, Vienna (1901–?)</p>	<p>breeding disease-resistant hybrids of rye, wheat, and oats</p>
<p>WRIGHT, Sewall (1889–1988)</p>	<p>BSc, Lombard College; PhD, Bussey Institution, Harvard under Castle (1916); USDA in Washington, DC (1916–25); Prof, Chicago (1925–55), Wisconsin (1955–88)</p>	<p>mammalian genetics; physiology of pigmentation; cattle breeding; population genetics and genetic drift</p>
<p>ZELENY, Frank (1878–1939)</p>	<p>BA, MA, U of Minnesota; PhD, U of Chicago (1901); Indiana U (1904–9); Prof, U of Illinois, USDA Experiment Station, Champaign-Urbana (1909–39)</p>	<p><i>Drosophila</i> genetics; linkage, position effect, rates of back-mutation</p>

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